

ABSTRACT

SOME ASPECTS OF THE ECOLOGICAL LIFE HISTORY
OF
SARRACENIA PURPUREA

by Adrienne J. Mandossian

This is an investigation of several aspects of the ecological life history of Sarracenia purpurea. The main areas concern the constance of plant associates of this species, the nature and role of certain factors of its environment, variation in form, size and number of leaves, mode of pollination of the flower, and germination of seeds.

The constance of the associated plant species was determined from a species composition list made for five bogs in central lower Michigan which supported S. purpurea. This list was compared with a species list for northern lower Michigan bogs compiled by F. C. Gates and a list from J. T. Curtis for Wisconsin bogs. It was found that while most of the bogs had certain species in common, no single plant species consistently appeared with S. purpurea in all bogs.

A comparison was made of the available amounts of essential nutrients in an acid area of a bog with those of an alkaline area of the same bog, both supporting S. purpurea. It was found that in both areas, nitrogen was present in such low quantities as to be

regarded as limiting in agricultural ecosystems. Calcium was abundant, potash was adequate, while phosphorus was in very short supply but probably adequate during the growth period of this plant.

Leaves of Sarracenia were counted and length and width measurements taken in two acid and two alkaline bogs. The results indicated that the plants in the acid bogs had fewer but larger leaves than those of the alkaline bogs.

Mutual transplants of Sarracenia between two acid and two alkaline bogs were made. A study of leaf size of the transplants over a two year period indicated that there was a gradual adjustment to their new habitat. Since the roots were not washed free of soil before transplanting, the lag in coming to adjustment with the new site could be due to the attenuation of this soil block or it could be an attenuation of internal pools.

To check on reports of variation in leaf shape from pitchers to flat leaves, freshly dug out Sarracenia were placed in low light intensity on a window sill. All leaves produced in this location during the one-month period were flat and the light intensity measured at noon was about one-half that of the bog. It was concluded, therefore, that leaf size, number and form are highly variable in S. purpurea, and that these variations are determined by environmental factors.

In order to determine the mode of pollination in this plant, flower buds in a natural field population were deanthered, bagged and cross pollinated by hand. Other buds were bagged and left undisturbed and still another group was self pollinated by hand and bagged. Results indicated that cross pollination, promoted by the structure of the flower, is the most effective means of pollination in this plant, producing the largest number of seeds. However, the flower was found to be physiologically and genetically capable of producing seed by self pollination. The flower was visited by Sarcophaga sarraceniae Riley, Bombus impatiens Cresson, B. griseocollis (Degeer), B. terricola Kirby, B. vagans Smith and Apis mellifera Linn.

Seed germination experiments were made with various moistening agents, with different pre-chilling periods, under varying temperature and light conditions. Type of moistening agent made no difference in the rate of germination except in total darkness where .2% KNO_3 promoted germination. In alternating light and temperature (in light at 22°C. for 8 hrs. and in darkness at 5°C. for 16 hrs.) seeds pre-chilled for various periods gave uniformly high germination results. These experimental conditions favorable to germination of seeds of this species roughly approximate natural conditions in a northern bog in the spring.

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OF
SARRACENIA PURPUREA

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INTRODUCTION

The study reported here was undertaken in an attempt to fill in some of the existing gaps in our knowledge of the ecological life history of Sarracenia purpurea L. An examination of the literature disclosed that despite the voluminous bibliography about this plant, many facets of its life history and ecology had not yet been explored, or were partially investigated. For example, Kurz (1928) and Wherry (1929) reported that Sarracenia purpurea, universally considered an acid bog plant, was also found in neutral or alkaline situations. This needed further confirmation. Variations in leaf size and form, while noted by several observers, remained largely unexplained. Germination of seeds had not been studied to any extent. The generally accepted hypothesis that the flower of this plant was insect pollinated had not been substantiated by experimental work.

It was therefore decided to investigate these problems in the following specific areas: I. Plant associates of Sarracenia purpurea in acid and alkaline habitats. II. Sarracenia purpurea and factors of its environment. III. Variations in the leaf of Sarracenia purpurea. IV. Pollination in Sarracenia purpurea. V. Germination of seeds of Sarracenia purpurea. It was hoped that such investigations would make our understanding of the ecological life history of this plant more complete.

To achieve this goal the research methods of field observation were used, as well as controlled experiments both in the field and in the laboratory. Specific methods employed for each investigation have been placed in each section.

Throughout this study the word "bog" has been used in a general sense, i. e., to mean a wet area in which Sarracenia purpurea is found growing. It does not necessarily bear any of the connotations ascribed to it by Rigg (1925), Waterman (1926), Gates (1942) and others.

LITERATURE SURVEY

The Sarraceniaceae are perennial herbs with a basal rosette of pitcher-leaves. They are native to the western hemisphere, yet the three genera are completely segregated from each other in geographic distribution. According to Wood (1960), Heliampora Benth., represented by six species, is found growing in table-top mountains of northern South America. Darlingtonia Torr., with one species, is confined to northern California and southwestern Oregon. The third genus, Sarracenia, consists of eight species, all of which have essentially similar flowers, differing only in color and size. Thus, the flower is not used to any great extent in the delimitation of the species. On the other hand, the morphology of the leaves of the different species is quite constant and is generally used as the main criterion to separate them. Following is a list of the species of Sarracenia, given by Macfarlane (1908), modified by Wherry (1929, 1933a, 1935), Bell (1949, 1954) and Wood (1960).

Species with erect pitchers

With maroon petals

Sarracenia leucophylla Raf.

Sarracenia rubra Walt.

Sarracenia rubra f. Jonesii (Wherry) Bell

With yellow petals

Sarracenia minor Walt.

Sarracenia flava L.

Sarracenia oreophila Wherry

Sarracenia alata (Wood)

Species with decumbent pitchers and maroon petals
Sarracenia psittacina Michx.
Sarracenia purpurea L.
Sarracenia purpurea L. f. heterophylla

As to any cytotaxonomic study of this genus, a survey of the literature shows that serious work on chromosome count was not started until about fifteen years ago when technical advances permitted such study. Before that time any mention of chromosome count by botanists was purely incidental and inaccurate. For example, Shreve (1906) counted 12 chromosomes in the pollen mother cells of S. purpurea. Nichols (1908) reported this same count in S. rubra and S. variolaris (now called S. minor, Walt.). Darlington and Janaki-Ammal (1945) listed two species of Sarracenia but avoided any mention of chromosome numbers. It was not until 1948 that Tjio, using root tip material, reported 26 chromosomes for the somatic cells of two Sarracenia hybrids. Hecht (1949), also working with root tips, found the diploid number of chromosomes to be 26 for six species of Sarracenia, including S. purpurea. By far the most exhaustive study of chromosomes was made by Bell (1949) who, using mainly antheridial material, counted $2n=26$ chromosomes in all species of Sarracenia.

In the present study, primary root tips from germinating seeds were used and a count of 26 chromosomes was obtained for S. purpurea, thus confirming the above findings. The fixation and staining methods are given in Appendix I, p. 159.

Sarracenia purpurea has appeared under many names in the past. Soon after its discovery in North America, isolated leaves reached Europe as items of curiosity and botanists hurried to describe the plant, mainly from hearsay evidence, as early as 1570 (Masters 1893). The first accurate description of the plant was given in 1601 by Clusius (Masters 1893), who sketched a tuft of pitcher-leaves surrounding the remains of a flower stalk in his Historia Plantarum Rariorum from a drawing sent to him some years earlier from Lisbon. Not having seen the flower, he called it Limonio congener, supposing it to be a close relative of the sea lavender. Parkinson (Russell 1919) in his Theater of Plants, 1640, reproduced Clusius's figure and referred to it as "the hollow-leaved strange plant of Clusius." The flower remained unknown to botanists until 1683 when Morison (Anon. Flore des Serres, 1854-55) gave a full description of the plant in his New England Rarities and named it Coilophyllum virginianum, folio brevior, flore purpurascens. Before the end of the century the plant was to receive still another name: Bucanephyllum americanum by Plukenet in Amaltheum (1691).

Tournefort (Masters 1893), ignoring all these former appellations, named the plant Sarracenia canadensis foliis cavis et auritis in honor of his friend, Dr. Michel Sarrazin, physician at the court of Quebec, who had sent

the plant to him (Institutiones Rei Herbariae, 1700). In 1737, Linnaeus (Lloyd 1942), in Hortus Cliffortianus modified Tournefort's descriptive name into the binomial Sarracena purpurea. In Species Plantarum (1753), he changed the spelling to Sarracenia.

In 1840 Rafinesque separated the plant into two species, basing his decision on marked differences in pitcher form. The plants of the northeastern United States and Canada were named Sarazina gibbosa and those of the southeastern United States, Sarazina venosa.

In 1933 Wherry considered these differences not great enough to warrant the classification of the northern and southern forms as distinct species. Instead, he separated them as sub-species. The northern leaf type was named then, Sarracenia purpurea gibbosa. This is the plant with long pitchers and a small hood, the hollow part averaging over three times as long as wide, and rarely pubescent outside. The form prevalent in the southeastern United States, with the broader pitcher and a larger hood, often pubescent outside, was called Sarracenia purpurea venosa. Lloyd (1942) in his Carnivorous Plants followed Wherry's classification.

In 1949, Bell argued that the minor differences of pitcher form were environmental rather than hereditary, and that many plants of intermediate leaf forms or with both forms were found throughout the range of this plant.

He therefore consolidated Rafinesque's two species and Wherry's two sub-species back into the Sarracenia purpurea of Linnaeus.

The following year, Fernald, in the Eighth Edition of Gray's Manual, emphasized the fact that this plant is very variable. He called the northern variant Sarracenia purpurea (typical), while the southern one was named Sarracenia purpurea var. venosa. No further changes in the taxonomy of this plant have been reported to date.

Some of the common names ascribed to Sarracenia purpurea are: Indian Dipper, Indian Cup, Indian Jug, Adam's Cup, Owl's Moccasin, Forefather's Cup, Indian Teakettles, Whippoorwill's Shoes, Watches, Huntsman's Cup, Ko-ko-Moccasin and Side-Saddle Flower.

All the species of Sarracenia, with the exception of Sarracenia purpurea, are native only to the southeastern United States, from Virginia southward, most of them being concentrated in the southern half of Georgia, Alabama and northern Florida. A detailed geographical distribution of all the species may be found in Wherry (1935).

Sarracenia purpurea does not occur in large numbers in a particular location. However, it is the hardiest of all the pitcher plants and is found more or less widely distributed over the entire eastern part of North America from longitude 60° west to longitude 95° west. In the south, its range extends eastward from the Mississippi

River north of New Orleans to S. Alabama, N. E. Florida and S. E. Georgia. Isolated colonies occur in N. Carolina, Maryland, Delaware and New Jersey. It may be found westward and northward far into central Canada, through N. Pennsylvania, N. Ohio, N. Indiana, Michigan, N. Illinois, Wisconsin and Minnesota (Wherry 1935).

THE PLANT

Sarracenia purpurea is an herbaceous perennial with a reduced fibrous root system which grows adventitiously from a thick rhizome. Its flower is solitary, borne at the end of a long scape, and is composed of 3 bracts, 5 sepals, 5 petals, 70-80 stamens and a 5-celled ovary with an umbrelloid style bearing 5 minute stigmas. (A more detailed description of the flower will be given in the section on pollination, p. 93.

The individual leaves are pitcher-shaped and arranged in a tight spiral forming a rosette. They are produced from the shoot apex on the tip of the rhizome. Newly formed leaves are erect at first but as they become larger and are pushed outward by younger leaves, they become repent with the opening remaining upward. Large leaves may attain a length of up to three decimeters. The leaf has a solid petiole rising from a sheathing base. The blade is a hollow cylinder, usually containing a variable amount of liquid of an aqueous nature. Along its upper, ventral, side is an undulating wing which is widest near the middle and extends up to the opening. At the tip of the cylinder is found a rounded, wavy hood with two lateral lobes which are bent forward in such a way that rain falling on them tends to run into the pitcher. The leaf is evergreen and can survive months of freezing. However, freezing temperatures in late spring were observed to extensively damage both new and old leaves.

The entire external surface of the leaf has a network of red-purple veins, giving it a flower-like appearance. This coloring, together with nectar glands, are thought to attract insects into the interior of the pitcher-leaf where downwardly pointed hairs and slippery epidermal cells make escape difficult for many.

Because of the insectivorous nature of the leaf, research in this as well as the other species of Sarracenia has been concentrated mainly on this structure. Hooker (1874) gave a detailed description of the interior surface of the pitcher-leaf, advancing the idea that perhaps some digestion of insect matter occurs here. Mellichamp (1875), Higley (1885) and Robinson (1908) made notable contributions in verifying Hooker's supposition.

The most exhaustive work was undertaken by Hepburn et al. (1920). They discovered that the secretion in Sarracenia purpurea is very small in amount, being found in the form of beads of fluid on the walls. It was shown conclusively by this team of workers that special glands in the walls of the pitchers secreted liquid containing an active enzyme, protease, by which the proteins in the bodies of the drowned insects were digested. It was also shown that the secretion retained its proteolytic properties even after dilution with large amounts of water. Obviously this would be of advantage to Sarracenia purpurea since rain water has relatively free access to its pitchers and secretion is small.

The fluid in closed pitchers was always found to be sterile while that of open pitchers which had captured insects always contained bacteria. At first the bacteria observed by many other scientists were thought to play an important role in the digestion of the trapped insects. However, Hepburn and his associates demonstrated that the major role in protein digestion is performed by the protease secreted by the pitcher itself while digestion by bacteria was very slow and of minor importance.

In one experiment, lithium citrate solution was introduced to the pitchers. In due time lithium appeared in the pitcher tissue even though it is not normally found there. Thus, Hepburn and his co-workers were able to prove conclusively that absorption of substances in solution does take place from the pitchers.

SECTION I. PLANT ASSOCIATES OF

SARRACENIA PURPUREA

IN ACID AND ALKALINE HABITATS

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A. INTRODUCTION

The floristic structure of a bog is characteristically different from that found elsewhere. This is due to two factors. One is the physical condition of the habitat that plays a selective role on the flora. This will be considered in the section on environment, p. 35. The second factor is the reaction of the bog flora to the habitat and their interaction with each other. This second factor will be studied here, particularly in relation to Sarracenia purpurea. An attempt will be made to answer the question: "Does Sarracenia purpurea form a definite association with another plant or group of plants?"

The five Sarracenia habitats selected for this study are located within twenty-five miles of the Kellogg Gull Lake Biological Station of Michigan State University. The first one, at Purdy Lake, and the second one, at Otis Lake, are Sphagnum bogs. The third one, at McKay Lake, and the fourth one, on the northeastern shore of Deep Lake, are alkaline bogs. The fifth bog, on the southeastern shore of Deep Lake, has both acid and alkaline zones within a few feet of each other. Map coordinates and descriptions of these Sarracenia habitats will be given in the immediately following pages.

B. MATERIALS AND METHODS

The method used for this study was an examination of the reproductive vigor of Sarracenia purpurea in several different types of bog and a study of the species composition in sites supporting this plant. No attempt was made to make a statistical study of the floristic structure of each bog. Instead, an alphabetical list was made of all the species of plants present in each bog in order to sort out any plants that were found in all five bogs along with Sarracenia purpurea. Lack or relative abundance of seedlings, size and number of pitchers of Sarracenia were noted as an indication of how well this plant was established in a particular bog. Nomenclature for species follows that in Gleason (1952). The Bryophytes were identified by Dr. Howard Crum of the National Museum of Canada.

The field work was done during the month of August, 1960. Determinations of pH in four of the five habitats were made on August 26 and 27, 1961, by inserting the electrodes of a portable Beckman pH meter into the substrate, and the average of five readings was used. The fifth bog, located at the northeast shore of Deep Lake, was not discovered until the following year and pH determinations were made by the Soil Testing Laboratory of Michigan State University from oven-dried soil samples removed during the first and second weeks of August, 1962.

C. RESULTS

1. Purdy Lake Bog. Purdy Lake (Barry Co., Michigan, T1N, R9W, Sect. 36) is located about five miles east of the Kellogg Gull Lake Biological Station of Michigan State University. It is a typical acid bog lake (pH of surface water, 6.5 in August, 1961) which is becoming gradually shallower. Long-time residents of the area as well as Dr. W. E. Wade, professor of Aquatic Plants at the Biological Station, attest to this fact. The surrounding organic soil was characterized as Greenwood Peat in the Soil Survey of Barry Co. of 1928.

One well established colony of Sarracenia purpurea was found over a partially grounded Sphagnum mat within a few meters of the lake. The entire circumference was not examined, and the statements apply to an area of about 50 x 150 meters on the southern shore of the lake.

The large leaves (See Table X, p. 79) of the pitcher plants were partially buried in a more-or-less continuous cover of Sphagnum, and the primary associated plant species at this point, listed in approximate order of cover were: Sphagnum capillaceum var. tenellum, Drosera rotundifolia, Vaccinium macrocarpon, Andromeda glaucophylla, Rhynchospora alba and Utricularia cornuta. A thorough search of this area revealed only about a dozen Sarracenia seedlings. Sarracenia was not found on the older and outer parts of the bog mat where Chamaedaphne

calyculata is the dominant species. A list of all the plant species in the pitcher-plant area and on the immediately surrounding organic soil is found in Table I, p.29. The pH readings taken in August, 1961, are listed in Table II, p. 34, all showing varying degrees of acidity.

2. Otis Lake Bog. Otis Lake (Barry Co., Michigan, T3N, R9W, Sect. 30 and 31) is located approximately twenty miles northeast of the Biological Station. Surface lake water is quite alkaline (pH of 7.9 in August, 1961). The tamaracks on the surrounding peat are young and during the six years that the bog has been under observation by the writer, conspicuous development of the floating mat into the open water has taken place. Blueberry pickers questioned at the scene have substantiated this observation. The surrounding organic soil was classified as Rifle Peat in the Soil Survey of Barry County of 1928.

About one-half of the circumference of the lake was examined but no Sarracenia colonies were found except on the south shore of the lake in a narrow band of about 10 x 200 meters. They were young, vigorous plants, with large red leaves (See Table X, p. 79), growing in the open, close to the water's edge with Sphagnum recurvum and Decodon verticillatus. There were many seedlings in various stages of development. Farther away from the water's edge, Chamaedaphne calyculata was the dominant

plant species instead of Decodon and pitcher plants did not occur here. A checklist of the vegetation of the pitcher-plant area and the immediately surrounding organic soil is found in Table I, p. 29.

The pH readings of this bog, made on August 27, 1961, are listed in Table II, p. 34. As has already been noted above, the lake water was distinctly alkaline (pH 7.9). The surface Sphagnum was distinctly acid (pH 6.0 and 6.6), while about 10 cm. below, where the roots of Sarracenia penetrate, the substratum had a pH of 7.0 and 7.1.

3. McKay Lake Bog. McKay Lake (Kalamazoo Co., Michigan, T1S, R8W, Sect. 24) is located about eight miles southeast of the Biological Station. It is a small alkaline lake (pH of 9.1 in August, 1961) east of Stony Lake, adjacent to property belonging to Mr. H. H. McKay. I have named it "McKay Lake" for this study. Fifteen small pitcher plants were found here on the north shore of the lake, on marly substrate in a clearing of about 20 square meters bounded on three sides by tamarack. The Sarracenia was concentrated in a rectangular area of about 5 x 10 meters in the center of this clearing, about 20 meters from the water's edge. The entire circumference was not examined as it was privately owned and the owners could not be located.

The pitcher plants appeared healthy, with a large number of small leaves (See Table X, p. 79), ranging

from 1 cm. up to 12 cm. in length. No Sphagnum was found here. There were no Sarracenia seedlings and the pitcher plants were associated with the moss Thuidium delicatulum. Besides this moss, the dominant plant species associated with Sarracenia were Potentilla fruticosa, Scirpus acutus, and Solidago spathulata. Other common species nearby were: Cornus Amomum, Aster junciformis, Thelypteris palustris, Eupatorium maculatum, E. perfoliatum, Triadenum virginicum, Lobelia Kalmii, Parnassia glauca and Pycnanthemum virginianum. A checklist of all plant species in the clearing and on the immediately surrounding organic soil is given in Table I, p. 29.

The pH readings taken on August 26, 1961, are listed in Table II, p. 34. It will be noted that not only the lake water but also the marly material in which the small Sarracenia plants were growing, was decidedly alkaline, with a pH of 9.1 and 8.9, respectively.

4. Deep Lake (Northeast Bog). Deep Lake (Barry Co., Michigan, T3N, R10W, Sect. 26) is located in the Yankee Springs Recreation Area, about twenty miles northeast of the Biological Station. No pitcher plants were found on its northeastern shore until the summer of 1962, even though a thorough search had been made the previous summer of the entire shoreline of the lake from

a boat. The bog is completely hidden from the lake side behind Cornus stolonifera shrubs. The substrate in the study site is a marly material of about 25 square meters, with a large colony of small-pitched Sarracenia (See Table X, p.79). The soil type is classified as Rifle Peat in the Soil Survey of Barry County of 1928.

There was no Sphagnum or any other moss associated with the pitcher plants, over this white marly substratum. Instead, Rhynchospora capillacea, Scleria verticillata, Parnassia glauca and Tofieldia glutinosa grew at the base of Sarracenia and all over the bog. There were many seedlings and young plants of Sarracenia interspersed with the older plants. A list of the species of plants found in this small bog area is given in Table I, p. 29.

Surface lake water was alkaline (pH of 8.9 in August, 1961), with clear water and a large amount of marl-encrusted Chara on the bottom. A pH value of 7.8 at both surface and root-level of Sarracenia purpurea was reported by the Soil Testing Laboratory of Michigan State University from oven-dried soil samples taken in August, 1962 (Table II, p. 34).

5. Deep Lake (Southeast Bog). The southeastern bog of Deep Lake is an extremely interesting one as it includes both acid and alkaline situations in an area of about 200 square meters.

On the east, about 50 meters from the water's edge is the tamarack zone with Sphagnum and several species of ferns. Here Sarracenia grew in the shade and protection of tamaracks, partially embedded in Sphagnum. pH readings on August 27, 1961, were 6.5 and 7.5 at the surface and depth of 10 cm., respectively. (See Table II, p. 34). The plants had large, green pitcher leaves but no fruits were seen during the summers of any year between 1960 and 1964. No seedlings of pitcher plants were discovered here.

Associated plants in the tamarack zone were: Sphagnum magellanicum, Osmunda regalis, Rhus Vernix, Andropogon scoparius, Cirsium horridulum, Amelanchier spp., Thelypteris palustris, Epilobium coloratum, Equisetum pratense, Steironema quadriflorum, Eupatorium maculatum and E. perfoliatum.

In the center of the bog, about half way between the lake and the tamarack zone, some pitcher plants grew on small hummocks not necessarily associated with Sphagnum but with other mosses such as Thuidium delicatulum or Campylium stellatum. All looked rather small in size, with many leaves (See Table X, p.79) and all were fruiting in August, 1960. No seedlings or young plants were found here. The pH readings on August 27, 1961, are given in Table II, p. 34, and show these sites to be more alkaline than the former (3.4 at base of Sarracenia and 3.0 at depth of 10 cm.).

The associated vegetation growing on the hummocks with Sarracenia were: Cladium mariscoides, Eleocharis Robbinsii, Gerardia purpurea, Lobelia Kalmii, Campanula aparinoides, Potentilla fruticosa, Scleria verticillata and Solidago spp.

South of this area is a slough formed from bubbling springs. The pH of the spring water on August 27, 1961, was 8.1 and that of the slough, 8.8. Sarracenia with fruits grew around the slough associated with Nymphaea odorata, Nuphar advena, Triadenum virginicum, Scirpus acutus, Eleocharis rostellata and Utricularia cornuta. Of 45 plants counted in this area, all but seven had capsules in August, 1960. However, no seedlings or young plants were discovered in the entire bog.

D. DISCUSSION

Among the five lake shores studied, Sarracenia purpurea seems to form no consistent close association with any other plant species. Along a slough or spring, it grows alongside such aquatic plants as Nymphaea odorata and Nuphar advena. In marly substrate, it thrives in the company of such basicolous plants as Scleria verticillata and Eleocharis rostellata. In the shade of tamaracks, it associates with ferns such as Woodwardia virginica and Osmunda regalis. However, in most situations, there seem to be some species of moss with which it is closely associated. If the moss is Sphagnum, as in Purdy Lake, Otis Lake, and under the tamaracks of Deep Lake, the substrate is acid, and the pitchers of Sarracenia are large in size but few in number (Table X, p. 79). In alkaline areas, as in McKay Lake, and the marly zone of the southeastern bog of Deep Lake, although Sphagnum is present, Sarracenia does not necessarily grow in close association with it. Some other moss, such as Campylium or Thuidium is more often found at the base of Sarracenia than is Sphagnum. In the small alkaline bog at the northeastern shore of Deep Lake, neither Sphagnum nor any other species of moss is found growing with Sarracenia purpurea. The pitcher leaves in the alkaline areas are smaller in size but greater in number (See Table X, p. 79).

In "The Bogs of Northern Lower Michigan", Gates (1942) regards Sarracenia purpurea as one of the most striking plants of the Chamaedaphne association. Other plants characteristic to this association are given as: Drosera rotundifolia, a few species of orchids, Scheuchzeria palustris, several species of Carex, Andromeda glaucophylla, Kalmia polifolia, Ledum groenlandicum and Vaccinium Oxycoccus. A complete list of plant species in this association, as reported by Gates, is placed in Column 6 of Table I, p. 29.

A comparison of the plant species of the five bogs of this study with those of northern lower Michigan (Gates 1942) and those of Wisconsin (Curtis 1959; Column 7 of Table I, p.29) will show that Cladium mariscoides and Thelypteris palustris are the only plants common to all areas supporting Sarracenia. However, as noted in the description of the lake shores, pages 14-20, these plants are not always found in close association with Sarracenia in the present study sites. Curtis (1959) considers only one of them, Cladium, as modal for an open bog. Thelypteris is merely rated as prevalent. Gates (1942) does not consider either one of these species of plants as characteristic to a Chamaedaphne association, but only relicts of a former association. Waterman (1926) too, does not include them among his typical bog species.

Four of the five lake shores of this study (all except the very small alkaline area on the northeastern shore of Deep Lake), and the bogs studied by Gates, have Larix laricina in common. This one exception, however, would seem to eliminate this species from the role of indicator plant for Sarracenia purpurea.

Again, the above mentioned four lake shores and the bogs of Wisconsin (Curtis 1959) have Rhus Vernix in common which Gates does not list because this plant does not grow that far north. This species cannot be considered as an indicator plant because it, too, is missing from the very small alkaline bog located on the northeastern shore of Deep Lake.

The two acid bogs of this study, the bogs of northern lower Michigan (Gates 1942) and the bogs of Wisconsin (Curtis 1959) have, in addition, the following plants in common: Andromeda glaucophylla, Chamaedaphne calyculata, Potentilla palustris and Vaccinium macrocarpon. These species are missing from the alkaline areas of this study. Therefore, they cannot be considered as essential for the presence of Sarracenia purpurea.

Bird (1923) reports that in an artificially constructed bog he was able to grow a number of bog plants from widely separated localities, which do not usually occur together in nature. In the experiment cited he had brought together a group of mature plants.

Whether or not seeds of these plants would germinate in this artificial environment was not investigated. As is well known, a bog has a plant population quite distinct from the surrounding area. Therefore, significant invasion of species adapted to non-bog conditions is quite unlikely. Germination obviously must occur before any plant species may become established in a bog. Then, the species must be adapted to an environment characterized by low levels of dissolved nutrients, periodic flooding, lack of aeration in the substrate, etc., perhaps generally unfavorable to most species, but favorable to others. The section on germination, p. 120, will show that Sarracenia purpurea seeds will germinate under conditions normally prevailing in a bog. Once past the hurdle of germination, this species, like other bog species, has many adaptations for life in a bog. Like many of them, it can reproduce vegetatively and can hold its own against the competition of other species for space and nutrients. In addition, it has evolved the insectivorous habit by means of which it is generally assumed that it has become partially independent of the substrate for minerals and can supply itself with nutrients throughout the growing season.

It would appear, therefore, that the presence of Sarracenia purpurea in an area is not dependent on the presence of any other particular species of plant. Rather,

it is due to the special adaptations that this species has evolved for competing successfully with other species growing in a bog.

E. SUMMARY AND CONCLUSIONS

1. In the two acid bogs of this study (Purdy L. and Otis L.), Sarracenia purpurea was found associated with Larix laricina, Cladium mariscoides, Rhus Vernix, Andromeda glaucophylla, Chamaedaphne calyculata, Eriophorum virginicum, Vaccinium macrocarpon and Sphagnum spp.
2. This list of plant species corresponds with that compiled by Gates for the Chamaedaphne association of northern lower Michigan bogs, with the exception of Rhus Vernix which does not grow in the north, and several plants in the north which do not grow in the south.
3. The list of plant species given in No. 1 above also corresponds with that compiled by Curtis for the bogs of Wisconsin with only two exceptions. Larix laricina is not listed among the Sarracenia associates even though it is treated as a bog tree, and Eriophorum virginicum is not listed at all.
4. In the two acid bogs (Purdy L. and Otis L.), in one alkaline bog (McKay L.) and both the acid and alkaline zones of the southeastern bog of Deep Lake, Sarracenia purpurea was found growing with Larix laricina and Rhus Vernix. In the very small alkaline bog (northeastern bog of Deep Lake), neither of these plant species was present.

5. Sarracenia purpurea was usually closely associated with a moss. If the substrate was acid, the moss was Sphagnum, and the pitchers were large in size but few in number, as in Purdy Lake, Otis Lake and the southeastern shore of Deep Lake (under the tamaracks.)
6. If substrates were alkaline, as in McKay Lake and the marly zone of the southeastern shore of Deep Lake, the moss with which Sarracenia was associated was not necessarily Sphagnum, even though some Sphagnum was present. Rather, the moss was Thuidium or Campylium. Here the pitchers were small in size but great in number.
7. In the northeast bog of Deep Lake, again an alkaline bog, Sarracenia was not found associated with any moss at all. Rather, it grew in close association with basicolous plants such as Scleria verticillata, Rhynchospora capillacea, Parnassia glauca and Tofieldia glutinosa. The pitcher leaves were small in size but great in number as in the two alkaline bogs mentioned in No. 6 above.
8. Of the two acid bogs, Purdy Lake contained about a dozen seedlings; Otis Lake bog a large number of seedlings. The acid zone under the tamaracks of Deep Lake had no seedlings.

9. Of the three alkaline bogs, only the north-eastern bog of Deep Lake had Sarracenia seedlings.
10. It would appear from the study of these five bogs of central lower Michigan that Sarracenia purpurea grows over a variety of substrates (semi-aquatic, soft organic soil and hard marl), over a pH range of 5.2 to 8.9, that it forms no consistent association with any single plant species and that within the range examined its reproductive vigor is not determined by the reaction of the substrate.

Table I. Species list of 5 lower central Michigan bogs of this study compared with those of northern lower Michigan (Gates) and of Wisconsin bogs (Curtis)*.

	1	2	3	4	5	6	7
<i>Acer rubrum</i> L.	.	x	x	.	.	x	.
<i>Acer rubrum</i> L. (seedling)	x	x	.	x	x	.	.
<i>Alisma subcordatum</i> Raf.	x	.	.	.	.	.	.
<i>Alnus incana</i> (L.) Moench.	.	.	.	.	.	x	.
<i>Amelanchier</i> spp.	x	.	.	.	x	.	.
<i>Andromeda glaucophylla</i> Link.	x	x	.	.	.	x	x
<i>Andropogon scoparius</i> Michx.	.	.	.	.	x	.	.
<i>Apios americana</i> Medic.	.	.	.	x	x	.	.
<i>Arethusa bulbosa</i> L.	.	.	.	.	.	x	x
<i>Aronia arbutifolia</i> (L.) Ell.	.	.	.	.	.	x	.
<i>Aronia prunifolia</i> (Marsh.) Rehder.	x	.	.	.	.	x	.
<i>Asclepias incarnata</i> L.	.	x	.	x	x	.	.
<i>Asclepias syriaca</i> L.	.	.	.	.	x	.	.
<i>Aster</i> spp.	.	.	.	x	.	.	.
<i>Aster junciformis</i> Rydb.	.	.	x	.	x	x	.
<i>Aster parviceps</i> (Burgess) Mackenzie & Bush.	.	.	.	.	x	.	.
<i>Aster pilosus</i> Willd.	.	.	.	.	x	.	.
<i>Aulacomnium palustre</i> (Hedw.) Schwaegr.	.	.	.	.	x	.	.
<i>Betula</i> spp.	.	.	.	x	.	.	.
<i>Betula glandulosa</i> Michx. var. <i>Glandulifera</i> (Regel) Gl.	.	.	.	.	.	x	x
<i>Betula papyrifera</i> Marsh.	.	.	.	.	.	x	.
<i>Bidens coronata</i> (L.) Britt.)	.	x	.	.	.	.	.
<i>Bidens tripartita</i> L.	.	.	.	.	.	.	x
<i>Boehmeria cylindrica</i> (L.) Sw.	.	.	.	x	x	.	.
<i>Brasenia Schreberi</i> Gmel.	.	x	x	.	.	.	x
<i>Calla palustris</i> L.	.	x	.	.	.	.	x
<i>Calopogon pulchellus</i> (Sw.) R. Br.	.	x	.	.	.	x	x
<i>Campanula aparinoides</i> L.	.	.	x	.	x	.	.
<i>Campylium stellatum</i> (Hedw.) C. Jens	.	.	.	.	x	.	.
<i>Carex</i> spp.	.	.	x	.	.	.	.
<i>Carex aquatilis</i> Wahl.	.	.	.	x	x	.	.
<i>Carex comosa</i> Boott.	.	x	.	.	.	.	.
<i>Carex lasiocarpa</i> Ehrh.	.	.	.	.	x	x	x
<i>Carex limosa</i> L.	.	.	.	.	.	x	.
<i>Carex oligosperma</i> Michx.	x	.	.	.	.	.	.
<i>Carex pauciflora</i> Lightf.	.	.	.	.	.	x	.
<i>Carex paupercula</i> Michx.	.	.	.	.	.	x	.
<i>Carex rostrata</i> Stokes	x	.	.	.	.	.	.
<i>Carex trisperma</i> Dewey	.	.	.	.	.	.	x
<i>Cephalanthus occidentalis</i> L.	x	x	.	.	.	.	.
<i>Chamaedaphne calyculata</i> (L.) Moench.	x	x	.	.	.	x	x

* Column 1 = Purdy Lake bog (acid)

" 2 = Otis Lake bog (acid)

" 3 = McKay Lake bog (alkaline)

" 4 = Deep Lake bog, northeast (alkaline)

" 5 = Deep Lake bog, southeast (acid and alkaline)

" 6 = Bogs of northern lower Michigan (Gates, 1942)

" 7 = Bogs of Wisconsin (Curtis, 1959)

[illegible][illegible]

	1	2	3	4	5	6	7
<i>Chara</i> spp.	.	x	.	.	x	.	.
<i>Cirsium horridulum</i> Michx.	.	.	x	.	x	.	.
<i>Cladium mariscoides</i> (Muhl.) Torr.	x	x	x	x	x	x	x
<i>Cornus Amomum</i> Mill.	.	.	x	.	x	.	.
<i>Cornus canadensis</i> L.	.	.	.	.	.	.	x
<i>Cornus racemosa</i> Lam.	.	.	.	.	x	.	.
<i>Cornus stolonifera</i> Michx.	.	x	.	x	x	x	.
<i>Cypripedium</i> spp.	.	x	.	.	.	.	.
<i>Cypripedium acaule</i> Ait.	.	.	.	.	.	.	x
<i>Decodon verticillatus</i> (L.) Ell.	x	x	x	.	.	.	.
<i>Drosera intermedia</i> Hayne	x	.	.	.	.	x	x
<i>Drosera rotundifolia</i> L.	x	x	.	x	x	x	x
<i>Dryopteris Boottii</i> (Tuckerm.) Underw.	.	.	.	.	.	.	x
<i>Dryopteris cristata</i> (L.) Gray.	.	.	.	.	.	.	x
<i>Dulichium arundinaceum</i> (L.) Britt.	.	x	.	.	.	.	.
<i>Eleocharis compressa</i> Sulliv.	.	.	.	.	.	x	.
<i>Eleocharis equisetoides</i> (Ell.) Torr.	.	x	.	.	.	.	.
<i>Eleocharis flavescens</i> (Poir.) Urban.	.	x	.	.	.	.	.
<i>Eleocharis obtusa</i> (Willd.) Schult.	x	.	.	.	.	.	.
<i>Eleocharis palustris</i> (L.) R. & S.	.	x	.	.	.	.	.
<i>Eleocharis Robbinsii</i> Oakes	.	x	.	.	x	.	.
<i>Eleocharis rostellata</i> Torr.	.	.	.	x	x	.	.
<i>Epilobium adenocaulon</i> Haussk.	.	.	.	.	.	x	.
<i>Epilobium coloratum</i> Biehler.	x	.	.	.	x	.	.
<i>Epilobium strictum</i> Muhl.	.	.	.	.	x	.	.
<i>Equisetum pratense</i> Ehrh.	.	.	.	.	x	.	.
<i>Eriocaulon septangulare</i> With.	x	.	.	.	.	.	.
<i>Eriophorum angustifolium</i> Honckeney	.	.	.	.	.	.	x
<i>Eriophorum spissum</i> Fern.	.	.	.	.	.	x	x
<i>Eriophorum virginicum</i> L.	x	x	.	.	.	x	.
<i>Eriophorum viridi-carinatum</i> (Engelm.) Fern.	.	.	.	.	.	x	.
<i>Eupatorium maculatum</i> L.	x	.	x	.	x	.	.
<i>Eupatorium perfoliatum</i> L.	.	x	x	x	x	.	.
<i>Fissidens adianthoides</i> Hedw.	.	.	.	.	x	.	.
<i>Galium</i> spp.	.	.	x	.	x	.	.
<i>Galium lanceolatum</i> Torr.	x	.	.	.	.	.	.
<i>Gaultheria hispidula</i> (L.) Muhl.	.	.	.	.	.	.	x
<i>Gaultheria procumbens</i> L.	.	.	.	.	.	.	x
<i>Gerardia purpurea</i> L.	.	x	.	x	x	.	.
<i>Glyceria canadensis</i> (Michx.) Trin.	x	.	.	.	.	.	.
<i>Glyceria striata</i> (Lam.) Hitchc.	.	.	.	.	x	.	.
<i>Habenaria blephariglottis</i> (Willd.) Hook.	.	x	.	.	.	x	.
<i>Habenaria dilatata</i> (Pursh) Hook.	.	.	.	.	.	.	x
<i>Hypericum boreale</i> (Britt.) Bickn.	.	x	.	.	.	.	.
<i>Hypnum Lindbergii</i> Mitt.	.	.	.	.	x	.	.
<i>Ilex verticillata</i> (L.) Gray	.	.	.	.	.	x	.
<i>Impatiens biflora</i> Willd.	x	.	.	x	x	.	.
<i>Iris</i> spp.	.	.	.	.	x	x	.
<i>Iris versicolor</i> L.	.	.	.	.	.	x	x

	1	2	3	4	5	6	7
<i>Iris virginica</i> L.	.	.	.	.	.	x	.
<i>Isopyrum bitermum</i> (Raf.) T. & G.	.	.	.	.	x	.	.
<i>Juncus acuminatus</i> Michx.	.	.	.	.	x	.	.
<i>Juncus brevicaudatus</i> (Engelm.) Fern.	.	.	.	.	x	.	.
<i>Juncus canadensis</i> J. Gay	.	x	.	.	x	.	.
<i>Juncus effusus</i> L.	x	.	.	.	.	.	.
<i>Kalmia polifolia</i> Wang.	.	.	.	.	.	x	x
<i>Larix laricina</i> (Du Roi) K. Koch	x	x	x	.	x	x	.
<i>Lathyrus palustris</i> L.	.	.	.	.	x	.	.
<i>Ledum groenlandicum</i> Ceder.	.	.	.	.	.	x	x
<i>Liatris spicata</i> (L.) Willd.	.	.	.	.	x	.	.
<i>Liparis Loeselii</i> (L.) Rich.	.	.	.	.	x	.	.
<i>Liverwort</i> spp.	.	x	.	.	.	.	.
<i>Lobelia Kalmii</i> L.	.	.	x	x	x	.	.
<i>Lobelia siphilitica</i> L.	.	.	.	.	x	.	.
<i>Lycopus</i> spp.	.	.	.	x	.	.	.
<i>Lycopus americanus</i> Muhl.	.	.	.	.	.	x	.
<i>Lycopus asper</i> Greene	.	.	.	.	x	.	.
<i>Lycopus rubellus</i> Moench.	.	.	.	.	x	.	.
<i>Lycopus uniflorus</i> Michx.	.	x	.	.	x	.	.
<i>Lycopus virginicus</i> L.	.	x	.	.	.	.	.
<i>Lysimachia quadrifolia</i> L.	.	.	x	.	.	.	.
<i>Lysimachia terrestris</i> (L.) BSP	.	x	.	.	x	x	.
<i>Maianthemum canadense</i> Desf.	.	.	.	.	x	.	.
<i>Mentha arvensis</i> L.	.	.	.	.	x	.	.
<i>Menyanthes trifoliata</i> L.	.	x	.	.	.	x	x
<i>Monarda fistulosa</i> L.	.	.	x	.	.	.	.
<i>Muhlenbergia racemosa</i> (Michx.) BSP	.	.	.	.	x	.	.
<i>Myrica Gale</i> L.	.	.	.	.	.	x	x
<i>Najas flexilis</i> (Willd.) Rostk. & Schmidt.	.	.	.	.	x	.	.
<i>Nemopanthus mucronatus</i> (L.) Trel.	.	.	.	.	.	x	x
<i>Nuphar advena</i> Ait.	x	x	.	.	x	x	.
<i>Nymphaea odorata</i> Ait.	.	x	.	.	x	.	.
<i>Onoclea sensibilis</i> L.	.	x	.	.	.	.	.
<i>Osmunda cinnamomea</i> L.	.	.	.	.	x	x	.
<i>Osmunda regalis</i> L.	.	x	.	x	x	x	.
<i>Oxypolis rigidior</i> (L.) Raf.	.	.	.	.	x	.	.
<i>Parnassia glauca</i> Raf.	.	.	x	x	x	.	.
<i>Pedicularis</i> spp.	.	.	.	x	x	.	.
<i>Peltandra virginica</i> (L.) Kunth.	x	x	.	.	.	.	.
<i>Picea mariana</i> (Mill.) BSP	.	.	.	.	.	x	.
<i>Pinus Strobus</i> L.	.	.	.	.	.	x	.
<i>Pogonia ophioglossoides</i> (L.) Ker.	.	x	.	.	.	x	x
<i>Polygonum coccineum</i> Muhl.	x	.	.	.	.	.	.
<i>Polytrichum juniperinum</i> Hedw. var. <i>alpestre</i> (Hoppe) BSG	.	.	.	.	x	.	.
<i>Pontederia cordata</i> L.	.	x	.	.	.	.	.
<i>Populus tremuloides</i> Michx.	x	.	.	.	.	x	.
<i>Potentilla fruticosa</i> L.	.	.	x	x	x	.	.
<i>Potentilla palustris</i> (L.) Scop.	x	x	.	.	.	x	x

	1	2	3	4	5	6	7
<i>Prunella vulgaris</i> L.	.	.	.	.	x	.	.
<i>Pycnanthemum virginianum</i> (L.) Durand & Jacks.	.	.	x	.	x	.	.
<i>Quercus alba</i> L. (seedling)	.	x	.	.	.	.	.
<i>Quercus borealis</i> Michx. f.	.	.	.	.	.	x	.
<i>Rhus typhina</i> L.	x	.	.	.	.	.	.
<i>Rhus Toxicodendron</i> L.	.	.	.	.	x	.	.
<i>Rhus Vernix</i> L.	x	x	x	.	x	.	x
<i>Rhynchospora alba</i> (L.) Vahl.	x	x	.	.	x	.	x
<i>Rhynchospora capillacea</i> Torr.	.	.	.	x	x	.	.
<i>Rhynchospora macrostachya</i> Torr.	.	x	.	.	.	.	.
<i>Rosa</i> spp.	.	x	x	x	x	.	.
<i>Rudbeckia hirta</i> L.	.	.	x	.	x	.	.
<i>Sagittaria latifolia</i> Willd.	.	x	.	.	.	.	.
<i>Salix</i> spp.	.	.	.	x	x	.	.
<i>Salix candida</i> Fluegge	.	.	.	.	.	x	x
<i>Salix lucida</i> Muhl.	.	.	.	.	.	x	.
<i>Salix pedicellaris</i> Pursh.	.	.	.	.	.	x	.
<i>Sarracenia purpurea</i> L.	x	x	x	x	x	x	x
<i>Scheuchzeria palustris</i> L.	.	.	.	.	.	x	.
<i>Scirpus acutus</i> Muhl.	.	.	x	x	x	x	.
<i>Scirpus americanus</i> Pers.	.	.	.	x	x	.	.
<i>Scirpus atrocinctus</i> Fern.	.	.	.	.	.	x	.
<i>Scirpus cyperinus</i> (L.) Kunth.	x	.	.	.	.	.	.
<i>Scirpus rubrotinctus</i> Fern.	.	.	.	.	.	.	x
<i>Scleria verticillata</i> Muhl.	.	.	.	x	x	.	.
<i>Scutellaria galericulata</i> L.	x	.	.	.	.	.	.
<i>Selaginella</i> spp.	.	.	.	.	x	.	.
<i>Sium suave</i> Walt.	.	x	.	.	x	.	.
<i>Smilacina racemosa</i> (L.) Desf.	.	.	.	x	.	.	.
<i>Smilacina trifolia</i> (L.) Desf.	.	.	.	.	.	.	x
<i>Solanum Dulcamara</i> L.	x	.	.	.	.	.	.
<i>Solidago graminifolia</i> (L.) Salisb.	.	.	.	.	x	.	.
<i>Solidago ohioensis</i> Riddell.	.	.	.	.	x	.	.
<i>Solidago Patula</i> Muhl.	.	.	.	.	x	.	.
<i>Solidago Riddellii</i> Frank.	.	.	.	.	x	.	.
<i>Solidago spathulata</i> DC.	.	.	x	.	.	.	.
<i>Solidago speciosa</i> Nutt.	.	.	.	.	x	.	.
<i>Solidago uliginosa</i> Nutt.	.	.	.	.	x	.	.
<i>Sphagnum capillaceum</i> (Weiss) Shrank var. <i>tenellum</i> (Schimp.) Andr.	x	.	.	.	.	.	.
<i>Sphagnum fuscum</i> (Schimp.) Klinggr.	.	.	.	.	x	.	.
<i>Sphagnum magellanicum</i> Brid.	.	.	.	.	x	.	.
<i>Sphagnum recurvum</i> P.-B.	.	x	.	.	.	.	.
<i>Sphagnum</i> spp.	.	.	.	.	.	x	x
<i>Spiraea alba</i> Du Roi	x	.	.	x	x	x	.
<i>Spiraea tomentosa</i> L.	x	x	.	.	.	.	.
<i>Spiranthes</i> spp.	.	.	.	.	.	x	.
<i>Steironema quadriflorum</i> (Sims) Hitchc.	.	.	.	x	x	.	.
<i>Taenidia integerrima</i> (L.) Drude	x	.	.	.	.	.	.

	1	2	3	4	5	6	7
<i>Thelypteris palustris</i> Schott.	x	x	x	x	x	x	x
<i>Thuidium delicatulum</i> (Hedw.) Mitt.	.	.	x	.	x	.	.
<i>Thuidium recognitum</i> (Hedw.) Lindb.	.	.	.	.	x	.	.
<i>Thuja occidentalis</i> L.	.	.	.	.	.	x	.
<i>Tofieldia glutinosa</i> (Michx.) Pers.	.	.	.	x	x	.	.
<i>Tomenthypnium nitens</i> (Hedw.) Loeske	.	.	.	.	x	.	.
<i>Triadenum virginicum</i> (L.) Raf.	x	x	x	x	x	.	x
<i>Trientalis borealis</i> Raf.	.	.	.	.	.	.	x
<i>Triglochin maritima</i> L.	.	.	.	.	.	.	x
<i>Triglochin palustris</i> L.	.	.	.	.	x	.	.
<i>Typha latifolia</i> L.	x	x	x	.	x	x	.
<i>Utricularia cornuta</i> Michx.	x	.	.	.	x	.	.
<i>Vaccinium angustifolium</i> Ait.	.	.	.	.	.	.	x
<i>Vaccinium corymbosum</i> L.	x	x	.	.	.	.	.
<i>Vaccinium Lamarckii</i> Camp.	.	.	.	.	.	x	.
<i>Vaccinium macrocarpon</i> Ait.	x	x	.	.	.	x	x
<i>Vaccinium myrtilloides</i> Michx.	.	.	.	.	.	x	x
<i>Vaccinium Oxycoccus</i> L.	.	.	.	.	.	x	x
<i>Viola</i> spp.	.	.	.	x	x	x	.
<i>Viola pallens</i> (Banks) Brainerd	.	.	.	.	.	x	.
<i>Woodwardia virginica</i> (L.) Smith	x	x	.	.	.	.	.
<i>Xyris caroliniana</i> Walt.	x	x	.	.	.	.	.

Table II. pH readings of 5 Sarracenia bogs and of surface water of 4 lakes, taken by inserting the electrode of a portable Beckman meter directly into the substrate, on August 26 and 27, 1961. Those in asterisks were measured by the Soil Testing Laboratory of Michigan State University from oven-dried soil samples taken in August, 1962.

	PURDY	OTIS	McKAY	DEEP N.E.	DEEP S.E.
Lake water	6.5	7.9	9.1	8.9	8.9
Open water:					
Surface moss					
at base of					
<u>Sarracenia</u>	5.2	6.0	8.9	7.8*	8.4
	(<u>Sphagnum</u>)	(<u>Sphagnum</u>)	(<u>Thuidium</u>)	(no moss)	(<u>Thuidium</u>)
Depth of 10 cm.					
at root-level					
of <u>Sarracenia</u>	6.1	7.1	8.5	7.8*	8.0
Under tamaracks:					
Surface moss					
at base of					
<u>Sarracenia</u>		6.6			6.5
Depth of 10 cm.					
at root-level					
of <u>Sarracenia</u>		7.0			7.5

SECTION II. SARRACENIA PURPUREA
AND
FACTORS OF ITS ENVIRONMENT

SECTION II. SARRACENIA PURPUREA AND FACTORS OF ITS ENVIRONMENT

A. INTRODUCTION

Sarracenia purpurea has been universally recognized to be a characteristic plant of Sphagnum bogs of eastern and mid-western North America. Waterman (1926) in his work on Sphagnum bogs of Illinois, considers it as one of the indicator plants of a bog, thus: "A bog is characterized in general by a xerophytic vegetation containing such specialized forms as pitcher plant, sundew, cranberry and sphagnum, accompanied by an acid substratum." He goes on to say that Sarracenia purpurea is one of eight or ten typical bog species, the others being Sphagnum spp., Drosera rotundifolia, Vaccinium Oxycoccus, Andromeda polifolia, Chamaedaphne calyculata, Ledum groenlandicum, Kalmia glauca, Betula pumila and possibly Larix laricina. He reports that where bog plants are present, the substratum is always acid, and where no bog plants are found, the substratum is neutral or alkaline.

Gates (1942) in his extensive work on the bogs of the Northern Lower Michigan, lists Sarracenia purpurea as among the most striking plants of a Chamaedaphne association. Similarly, Curtis (1959) considers Sarracenia purpurea as a spectacular member of insectivorous plants present in the bogs of Wisconsin. Obviously then, whenever any of these bog plants are found outside their usual habitat, it is to be assumed that the local environmental

conditions closely resemble those of the bog habitat.

Reports of the presence of Sarracenia purpurea outside Sphagnum bogs began to appear in print in the 1920's. Kurz (1928) found that in Baroda Bog, near Baroda, Michigan, this plant grew under alkaline or neutral conditions.

Wherry (1929) discovered three areas where, although the soil tests showed neutral or alkaline reactions, Sarracenia purpurea was nevertheless present. One was at Junius, Seneca Co., N. Y., where the plant was growing over marl. A second area was at Sauble Beach on the east shore of Lake Huron in Ontario, where pitcher plants were growing under neutral conditions in damp hollows between small sand dunes. The third non-acid locality supporting Sarracenia purpurea was a bog in Porter Co., Indiana. Here the plants grew in hummocks of decaying vegetation that were completely impregnated with alkaline water.

In a popular article in "The Flower Grower" (July, 1940), W. E. Curtis, a widely known wild flower specialist of Boston reported: "Sarracenia purpurea is plentiful in bogs where lower soil horizons, at least, support Cypripedium spectabile, and these are definitely neutral. At Junius, N. Y., there are many fine specimens in a swamp where extensive marl deposits dominate the area.

It had been supposed that the acidity of Sphagnum bogs was the factor determining the distribution of Sarracenia purpurea. On the basis of the above evidence, however, it became apparent that acidity as a factor in the distribution of this plant did not deserve the prominence accorded to it in the past. At least, it could be assumed that this plant is able to tolerate a wider range of acidity and alkalinity than previously had been supposed. What, then, are the factors in an alkaline environment that are similar to those of an acid bog? In other words, if the acidity of the soil is to be accorded a secondary role, then what are the soil conditions that support the growth and development of pitcher plants? Obviously, if an acid bog and an alkaline bog, both supporting Sarracenia purpurea, could be compared with each other, we would have some idea about the factor or factors that exercise a selective influence on the distribution of this plant.

The southeastern shore of Deep Lake presented a unique opportunity for this study because it has both acid and alkaline zones with pitcher plants growing in each area. The open lake water is alkaline (pH of 8.9 in August, 1961), containing marl-encrusted Chara on the bottom. The bog covers an area of about two hundred square meters, bounded on the west by the lake and on the east by a tamarack zone standing at the foot of a steep

hill. On the north, a low shrubby belt separates the bog from a public fishing area and on the south is found a pool with bubbling spring water that empties into the lake.

A visual survey of the bog (Fig. 1, p. 52) shows four distinct vegetation zones stretching from a narrow band of tall plants (Potentilla fruticosa, Asclepias incarnata, etc.) at the margin of the lake on the west, to the tamarack association (Larix laricina, Osmunda regalis, O. cinnamomea, Sarracenia purpurea, etc.) on the east. These vegetation zones are:

- (1) A wet and partially submerged area of tall Scirpus acutus over a mat of basicolous Carex aquatilis var. substricta.
- (2) Cladium mariscoides and scattered clumps of Potentilla fruticosa over bare, marly areas, with the basic soil-inhabiting Rhynchospora capillacea and Scleria verticillata and a few plants of Sarracenia purpurea.
- (3) Potentilla fruticosa zone, characterized by extensive tall shrubby growths of this plant, together with a few pitcher plants and the basicolous Tofieldia glutinosa and Parnassia glauca.
- (4) Carex lasiocarpa zone, forming an extensive mat typical to acid bogs with a few quaking areas and Sphagnum and pitcher plants growing along its southern and eastern margins.

The following more important environmental factors were considered for comparison in this study:

(1) insolation, (2) temperature, (3) aeration, (4) water supplying power of the substrate, (5) H-ion concentration and (6) selected macronutrients.

In this bog the acid and alkaline areas supporting Sarracenia were so close together that some of the environmental factors that were obviously common to both could be safely eliminated from consideration. Insolation and air temperature, both of which affect the aerial portion of the plant, were considered about the same in the two areas since there were no shading effects on either site. Similarly, no records of soil temperatures were kept because the microclimates of the two areas were considered to have essentially the same temperatures. Aeration and water supplying power of the substrate were considered together because they are closely interrelated. The H-ion concentration of the substrate was studied in its proper perspective as a factor but not the sole factor, as was done in the past, in influencing the distribution of Sarracenia. Nutrient availability was studied in regard to the major nutrients rather than the trace elements.

B. MATERIALS AND METHODS

To characterize the bog thoroughly, a detailed study was made of the structural aspect of the plants in the bog. Ten continuous linear transects, each one-half meter wide and separated from each other by 3.5 meters, were laid out across the zones of vegetation from the edge of open water to the tall shrub border. (See Fig. 1, p. 52). These transects were lettered A through J, beginning with the northern boundary of the bog and ending at the pool on the south. Each transect constituted a series of $\frac{1}{2} \times 1$ meter quadrats. In each of these quadrats a presence list was made for all the vascular species and the major bryophytes.

Also, at 10-meter intervals along each transect stations were established for sampling the substrate. These stations designated A-10, A-20, etc., to J-10, J-20, etc., were marked with green bamboo stakes driven into the ground with only a foot showing above the surface to avoid disturbance by campers and fishermen.

At each station equal volumes (a $10\frac{1}{2}$ oz. tin can) of soil samples were lifted from each profile, to a depth of 20 cm. It soon became apparent that there were only two horizons to consider in most stations: an upper layer of organic matter and a lower layer of marl. In Transects A and B, the upper organic layer was about 4 cm. deep at M-10 near the lake shore. It gradually increased in depth

until at Station 50, at the foot of the tamaracks, marl could not be reached at a depth of 20 cm. In all the remaining stations, the upper organic layer varied from a trace to about 5 cm. in thickness. The soil samples were oven-dried at 70°C. and percentage of moisture determined. Then the samples were used in measuring texture and nutrient contents of the soil.

The texture of the soil, which may influence aeration as well as water holding capacity, was classified according to its content of clay, silt or sand by the Bouyoucos method (1936).

The pH of the soil at surface level and at 10 cm. below the surface, the depth to which roots of Sarracenia penetrate, was taken by inserting the electrode of a portable Beckman pH meter directly into the substrate. This was done at each of the four vegetation zones, on August 27, 1961, and the average of five readings was used.

Oven-dried samples taken from all the stations over the A-J transects were processed for content of nitrogen and phosphorus with the Sudbury Soil Testing Kit. This is a method by which oven-dried soil samples are placed in specific reagents and the resulting color compared with a color chart. A rating of "A" indicates that the particular nutrient tested is present in a minimum amount needed for plant growth in general. "B" through "E" mean deficiencies. Since these values have little

ecological meaning for bog species, they are useful only for relative values among the sites. In order to get more precise concentrations of these nutrients, seventeen samples from critical stations of the bog were given a complete chemical analysis by the Soil Testing Laboratory of Michigan State University.

All work was done in July and August, 1962, except the pH determinations by the Beckman meter, which were done in August, 1961. The soil samples were taken during the first two weeks of August, 1962.

C. RESULTS

1. Vegetation. Deep Lake is an alkaline lake with a pH reading of 8.9 (surface water) taken in August, 1961. The submerged aquatic plants of the lake along the bog are Chara spp., Potamogeton natans, P. pectinatus, P. zosteriformis, Elodea canadensis, Utricularia spp. and Ceratophyllum demersum. The emergent zone consists of Nymphaea odorata, Scirpus americanus, S. acutus and Eleocharis Robbinsii.

The bog is separated from the lake by a band of firm sod, 1-2 meters wide. This shoreline was about 30 cm. above the lake water level in the summers of 1960-1962, showing no signs of erosion except where the slough trickled into the lake. On this band were found the following herbaceous and shrubby plants: Potentilla fruticosa, Asclepias incarnata, Eupatorium perfoliatum, Solidago spp., Parnassia glauca, Scirpus acutus, Eleocharis Robbinsii, E. Rostellata, Lobelia Kalmii and Sium suave.

Beyond the margin, the zones of plant associations do not fall in a definite order of succession such as water lily, bog sedge, bog shrub and tamarack. The calcareous nature of the spring water on the south, seeping into the bog has probably interfered with the natural progression toward successive bog associations. Instead, we find the following vegetational zones:

(a) Carex aquatilis var. substricta and Scirpus acutus zone: This is primarily a Carex aquatilis mat extending from the shoreline eastward for about 10 meters. (See Fig. 1, p. 52). Where the Carex mat has gaps, Scirpus acutus, which roots in the marly bottom below the mat, produces stems that rise well above the Carex sod. In other gaps in the mat, or where Carex cover is low, Nuphar advena and Nymphaea odorata exist, suggesting an earlier floating stage in succession. In still other gaps where the sod mat is intact but slightly submerged and Carex cover is low, Utricularia and Chara are present.

As secondary species in this community, we find Scirpus americanus and Eleocharis rostellata. Both of these are usually found in calcareous waters and together with Carex aquatilis var. substricta are indicators of a marsh rather than a bog formation (Fernald, 1950).

(b) Cladium mariscoides zone: This zone is quite extensive in this bog, spreading from Meter 5 to 40 on all transects. The topography here is fairly flat except for a few hummocks which were probably formed by ice action. The dominant species is Cladium mariscoides whose roots and rhizomes are extensively developed like most other bog plants such as Carex aquatilis and C. lasiocarpa. It grows into a very dense mat, often to the exclusion of other species. It has a wide moisture range. At Station 30 it grows stunted and sparse over bare marl,

while toward the lakeward limits of its range, it penetrates into the Carex aquatilis mat and at the opposite edge it joins up with Carex lasiocarpa.

Secondary species in this zone are Rhynchospora capillacea and Scleria verticillata, both basicolous plants.

According to Gates (1942), Cladium mariscoides is usually succeeded by Chamaedaphne calyculata which will give way to Larix laricina. In this bog, however, because of the calcareous nature of the substratum, the shrubby Potentilla fruticosa will probably succeed it. The hummocks have already been occupied by this plant.

(c) Potentilla fruticosa zone: This is located at the southeastern margin of the bog. Potentilla fruticosa shrubs form a rather large and continuous growth so dense that practically all other vegetation is excluded. Solidago spp. and Andropogon scoparius grow in the sun with the shrubby plant, while Parnassia glauca and Tofieldia glutinosa, both natives of calcareous habitats (Fernald, 1950) occupy the shade of the taller plants.

(d) Carex lasiocarpa zone: This sedge grows in tufts from long horizontal rhizomes and stolons. It is the most important plant in the filling up of many lakes (Gates, 1942). In acid bogs it is usually found associated with Dulichium arundinaceum. However, in Deep Lake, Carex lasiocarpa forms almost a pure stand for several square

meters, extending from Stations 40 on up to 60 over transects A to G. (See Fig. 1, p. 52). The sod is nearly level with no hummocks anywhere. It was mostly grounded during the four summers of this study but there were still some quaking areas as well as submerged spots.

Juncus spp. is a secondary species in this zone. As the mat becomes more and more solid, more secondary species enter the association. For example, Glyceria striata, Rhynchospora alba, Triadenum virginicum and Andropogon scoparius have already invaded its borders toward the pool.

Carex lasiocarpa, the dominant plant in this association, has the ability to grow into open water and to form a floating mat. Its rhizomes do not decay in the water and thus rhizomes and their roots interlace to form the mat. The plants grow vegetatively and season after season as the accumulated dead tops cover the rhizomes, new ones are formed above, increasing the thickness of the mat. Finally, the mat and the accumulating bottom ooze meet, the mat becomes grounded and Carex lasiocarpa gradually gives way to the next association (Gates, 1942).

As already noted, the Carex lasiocarpa mat at Deep Lake bog is overrun on its lakeward border by Cladium mariscoides. On the opposite border, on fairly firm ground the invading representatives of the Iris association have already entered the Carex mat. These are herbaceous species

such as Thelypteris palustris, Eupatorium perfoliatum, Solidago uliginosa and Lysimachia terrestris. These plants are adapted to survive occasional flooding and will remain for a time as relicts when the more permanent shrub association takes over (Gates, 1942).

In acid bogs in northern lower Michigan, the shrub association that usually replaces Carex lasiocarpa is a Chamaedaphne calyculata-Andromeda glaucophylla association (Gates, 1942). This change results in the formation of less hydrophytic conditions that encourage the growth of bog forest species such as Larix and Picea. At Deep Lake, however, there are no signs of Ericaceae at this time. Instead, the bog shrub stage here is poorly developed and is mainly represented by Spiraea alba, Rhus Vernix, Salix and Rosa, which blend into the tamarack society at the foot of the hill. This latter is a very narrow zone but quite conspicuous. The tamarack forms the upper layer, the foregoing shrubs, the second, and Sarracenia purpurea, Sphagnum, etc., form the ground cover. The hill is occupied by a number of deciduous forest elements such as species of Ulmus, Quercus and Carya.

2. Soil Factors

(a) Soil texture and soil moisture content:

Only mineral soil material was examined by the Bouyoucos method as this type of granulometric analysis does not apply to the muck or peat of the upper horizon of organic soils. Thus no hydrometer analysis could be made at Meter 50 of Transects A, B, C and D, and at all 60-meter stations since these were organic soils. Results are listed in Table III, p. 53. Station E-5 showed the lowest percentage of sand, namely 60%, and the highest percentage of silt, namely 30%. In all other stations the amount of sand varied between 74 and 82%; of silt, between 12 and 19%; of clay, between 4 and 11%.

The data in Table IV, p. 54, show that at all the stations of Deep Lake bog, the soil moisture content, expressed as per cent of dry weight, measured during the first and second weeks of August, 1962, was high, namely 75 to 109 1/4% for the upper horizon and 42 to 129 1/4% for the lower. Station J-40, a dry marly substrate, had a moisture content of 9%.

(b) Acidity and Alkalinity: The figures in Table V, p. 55, represent pH values obtained in the field on August 26 and 27, 1961, with a portable Beckman meter. They also include pH values of soil samples removed from seventeen selected stations during the first and second weeks of August, 1962, and measured by the Soil Testing

Laboratory. In the following paragraphs values from the Soil Testing Laboratory will be placed in parenthesis.

Lake surface water was found to be distinctly alkaline with a pH of 8.9 measured in 1961. The spring pool was also alkaline, with a pH of 8.5. Station E-5, which is a submerged area close to the lake water, was alkaline, with a pH of (7.4) in the mucky upper layer and (7.8) in the lower marly layer.

At I-10, another submerged area, where some water seeps from the spring pool, the lower marly layer showed a pH of (7.9). At F-20, which is an exposed marly area with very little vegetation, there was a pH of 8.5 in the upper layer and 8.0 in the lower.

At C-30, the pH readings for the upper layer under Potentilla fruticosa were 7.8 and for the lower layer, 7.9. The pH values for D-30, a marly station, were almost similar to those of C-30, namely, (7.6) for the upper and (7.9) for the lower horizons. At I-30, again a marly area, close to the pool, the upper layer had a pH of (7.8) and the lower, (8.0).

At B-40, where pitcher plants were growing close to Potentilla fruticosa or Sphagnum moss, the pH values were (7.6) for the upper and (7.8) for the lower layers. At D-40 and F-40, again with pitcher plants and Potentilla fruticosa growing close together, the lower layer had a pH of (7.7) and 7.8, respectively. At G-40, an exposed

marly surface, the lower horizon had a pH of (7.9).

At C-50, the Carex lasiocarpa mat surface vegetation, which here included a large patch of Sphagnum and a few pitcher plants, had a pH of 6.3 and the lower layer a pH of 6.8 and (7.0).

At Station F-50, at the border of the Carex lasiocarpa mat, with Sarracenia growing over soil classified as marl, pH values were (7.6) and (7.7) for the upper and lower layers, respectively. At F-60, where many pitcher plants and Sphagnum were growing over muck soil, the pH values for the upper layer were 6.5 and (7.1). The lower horizon had a pH of 7.0 (7.0).

At Transect I, all stations checked had various degrees of alkalinity (7.8-8.0).

At J-60, the marly lower layer showed a pH of (8.0) under Potentilla fruticosa.

(c) Nutrients: The values for nitrogen taken from all the stations over the A to J linear transects, and measured by the Sudbury Soil Testing method, showed that the entire bog was extremely low in available nitrogen (mostly values of C and D, Table VI, p. 56). There was no appreciable difference in the quantity of this nutrient in acid (C-50 and F-60) or alkaline zones (B-40, D-40, F-40 and F-50), where Sarracenia purpurea was growing.

As to phosphorus, the Sudbury Soil Testing method showed various degrees of deficiency of this nutrient

over the stations tested (values of B to E, Table VII, p. 57). These findings were supported by the Soil Testing Laboratory which reported only 13-13 pounds per acre-furrow-slice (13-13 lbs/A) in the upper horizon and 4-25 lbs/A in the lower horizon of the non-Sarracenia areas. In the Sarracenia areas, both acid and alkaline, it gave 3-12 lbs/A in the upper layers and 1-21 lbs/A in the lower.

Chemical tests for potash showed that the Carex aquatilis and Cladium mariscoides zones (roughly Stations 10 to 30 on all transects), had a rather small amount of this compound, namely, 32-80 lbs/A in the upper layer and 16 lbs/A in the lower. These are represented in Table VIII, p. 58. The amount increased somewhat in both the acid and alkaline zones supporting Sarracenia purpurea, namely, 83-132 lbs/A in the upper layers and 20-35 lbs/A in the lower. The Sudbury Soil Testing Kit showed minimum to adequate amounts of this nutrient over most stations tested.

As to calcium, the figures in Table IX, p. 59, indicate that in the upper horizon from the seventeen selected stations this nutrient varied from 4750 lbs/A to 8400 lbs/A. In the lower horizon the variation was greater, namely, 1103 lbs/A to 7060 lbs/A. At C-50 and F-60, both with the lowest pH values in the bog, the lower layers which contain no marl, gave the lowest values of calcium, namely 1680 lbs/A and 1103 lbs/A, respectively.

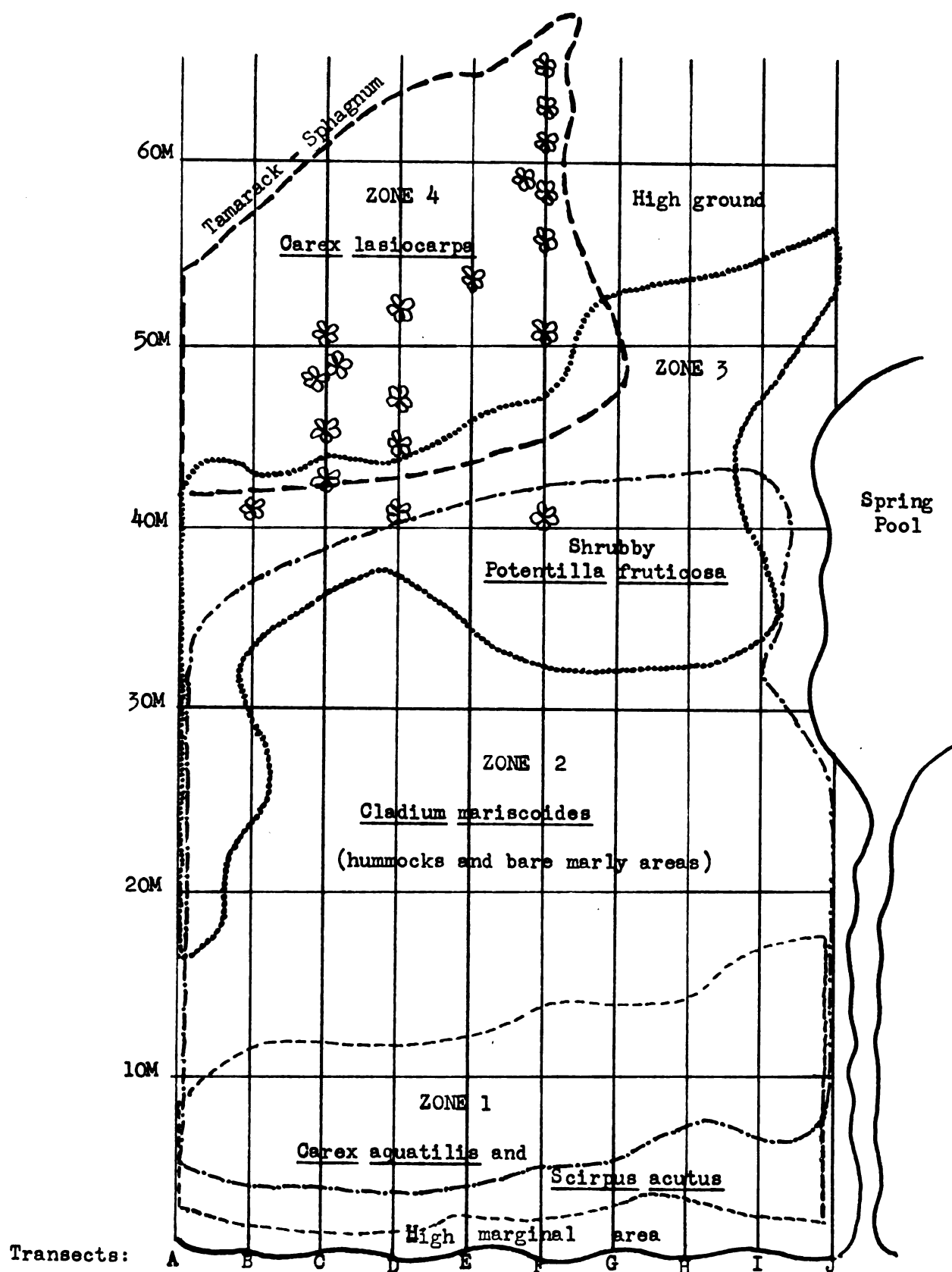


Fig. 1. Sketch map of southeastern bog of Deep Lake.

☼ = *Sarracenia purpurea*

Table III. Soil texture, expressed as percentages of sand, silt and clay (recorded in that order) in the lower horizon using Bouyoucos hydrometer method. Values are for stations spaced 10 M apart (except E-5) along 10 Transects (A to J) on the southeastern shore of Deep Lake. Stations lacking mineral soil to a depth of 30 cms. were not subjected to textural analysis. Sarracenia purpurea areas are underlined.

Transects	A	B	C	D	E	F	G	H	I	J
Meter 5					60-30-10					
" 10	76-16-8	77-16-7	76-17-7	78-18-4	78-16-6	79-16-5	78-14-8	78-15-7	79-15-6	77-17-6
" 20	78-16-6	78-17-5	76-18-6	76-18-6	76-18-6	76-17-7	78-15-7	80-16-4	77-16-7	76-18-6
" 30	79-13-8	79-14-7	75-18-7	77-18-5	79-16-5	78-16-6	78-16-6	80-15-5	75-19-6	80-12-8
" 40	75-19-6	<u>75-17-8</u>	74-15-11	<u>75-18-7</u>	78-15-7	<u>76-16-8</u>	76-17-7	81-14-5	80-15-5	80-15-5
" 50					79-15-6	<u>79-14-7</u>	80-14-6	82-12-6	80-15-5	82-13-5

Table IV. Water content in percentages determined from oven-dry soil samples, removed from the upper and lower horizons (to a depth of 30 cms.) of all Stations, during the first and second weeks of August, 1962. Stations are spaced 10 M apart (except E-5) along 10 Transects (A to J) in the southeastern bog of Deep Lake. Sarracenia purpurea areas are underlined.

Transects:	A	B	C	D	E	F	G	H	I	J
Meter E-5										
upper					1110					
lower					589					
M-10 upper	268	209	<u>141</u>	161	170	118	185	157	259	<u>494</u>
lower	64	52	98	70	66	61	65	78	74	100
M-20 upper	158	150	182	<u>146</u>	126	131	122	119	178	<u>144</u>
lower	55	61	86	60	63	60	56	73		65
M-30 upper	493	396	302	229	188	163	320	167	98	75
lower	100	85	<u>49</u>	58	<u>49</u>	58	56	58	<u>54</u>	53
M-40 upper	720	574	502	313	399	598	467	190	149	9
lower	189	<u>234</u>	242	<u>55</u>	139	<u>78</u>	66	58	63	
M-50 upper	649	833	903	1003	573	367	75	141	288	55
lower	689	882	<u>1110</u>	758	99	<u>121</u>	229	42	52	
M-60 upper				1094	1089	704	666			159
lower				1294	1276	<u>1167</u>	838			46

Table V. pH values of the upper and lower soil horizons (to a depth of 30 cms.) of representative stations in the 4 vegetation zones of the southeastern bog of Deep Lake, measured by a portable Beckman meter on August 26 and 27, 1961. Values in parenthesis were measured by the Soil Testing Laboratory of Michigan State University from oven-dried soil samples removed in the first two weeks of August, 1962. Stations are spaced 10 M apart (except E-5) along 10 Transects (A to J). Sarracenia purpurea areas are underlined.

Transects:	A	B	C	D	E	F	G	H	I	J
Meter 5 upper lower					(7.4) (7.8)					
Meter 10 upper lower									(7.9)	
Meter 20 upper lower						8.5 8.0				
Meter 30 upper lower			7.8 7.9	(7.6) (7.9)					(7.8) (8.0)	
Meter 40 upper lower		(7.6) (7.8)	7.7	(7.7)		7.8	(7.9)			
Meter 50 upper lower			6.3 6.8	(7.0)		(7.6) (7.7)				
Meter 60 upper lower					6.6 7.0	6.5 (7.1) 7.0 (7.0)				(8.0)

Table VI. Content of available N, of oven-dried soil, measured with the Sudbury Soil Testing Kit (A indicates minimum requirement, B to E, deficiencies). Soil samples removed from the upper and lower horizons (to a depth of 30 cm.) in the first and second weeks of August, 1962, along 10 Transects (A to J), in the southeastern bog of Deep Lake. Sarracenia purpurea areas are underlined.

Transects:		A	B	C	D	E	F	G	H	I	J
Meter 5	upper					C					
	lower					D					
Meter 10	upper	C	C	C	C	C	C	C	C	C	C
	lower	D	D	D	D	D	D	D	D	D	D
Meter 20	upper	C	C	C	C	C	C	C	C	C	C
	lower	D	D	D	D	D	D	D	D	C	D
Meter 30	upper	A	C	C	B	C	D	C	C	C	D
	lower	C	D	C	D	D	D	D	D	D	D
Meter 40	upper	B	C	B	B	B	D	C	C	C	D
	lower	C	<u>D</u>	C	<u>C</u>	D	<u>D</u>	C	D	D	
Meter 50	upper	C	B	C	C	B	B	B	C	A	C
	lower	C	B	<u>C</u>	C	C	<u>C</u>	C	C	C	
Meter 60	upper				C	B	C	C			B
	lower				C	C	<u>C</u>	D			C

Table VII. Content of available P of oven-dried soil, in pounds per acre-furrow-slice, measured by the Soil Testing Laboratory of Michigan State University, and with the Sudbury Soil Testing Kit (A indicates minimum required, B to E, deficiencies). Soil samples removed from the upper and lower horizons (to a depth of 30 cm.) in the first and second weeks of August, 1962, from Stations spaced 10 M apart (except E-5), along 10 Transects (A to J), in the southeastern bog of Deep Lake. Sarracenia purpurea areas are underlined.

Transects:	A	B	C	D	E	F	G	H	I	J
Meter 5 upper					C 18					
lower					C 23					
Meter 10 upper	C	C	C	C	C	C	C	D	C	D
lower	C	C	C	C	C	C	C	C	C 11	C
Meter 20 upper	B	B	C	B	B	C	C	C	C	B
lower	C	C	C	C	C	C	C	C	C	C
Meter 30 upper	E	C	C	C 17	C	C	C	C	C 13	C
lower	E	C	C	C 18	C	C	C	C	C 24	C
Meter 40 upper	C	D 12	C	D	C	D	C	C	C	C
lower	E	<u>D 21</u>	D	<u>D 12</u>	D	<u>C</u>	C 25	C	B	
Meter 50 upper	C	D	C	D	C	D 7	C	D	E	C
lower	E	D	<u>D 5</u>	D	D	<u>C 1</u>	D	C	C	
Meter 60 upper				D	D	3	D		E	
lower				E	E	<u>5</u>	E		C 4	

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Table VIII. Potash content of oven-dried soil in lbs/A, measured by the Soil Testing Laboratory of Michigan State University. Soil samples were taken from the upper and lower horizons (to a depth of 30 cms.) in the first two weeks of August, 1962, at Stations spaced 10 M apart (except E-5), along Transects A to J, in the southeastern bog of Deep Lake. Sarracenia purpurea areas are underlined.

Transects:	A	B	C	D	E	F	G	H	I	J
Meter 5 upper lower					A 32 A 16					
Meter 10 upper lower	AA AA	AA AA	A AA	A AA	AA AA	AA AA	A AA	A AA	A AA	A AA
Meter 20 upper lower	AA AA	A AA	A AA	A AA	A AA	A AA	AA AA	AA AA	AA AA	AA AA
Meter 30 upper lower	AA AA	AA AA	A AA	AA80 AA16	A A	AA AA	A AA	AA AA	AA64 AA16	AA AA
Meter 40 upper lower	A AA	AA132 AA 20	A AA	A AA32	A AA	A AA	AA AA16	A AA	A AA	AA
Meter 50 upper lower	A AA	A A	A A 35	A A	A AA	AA104 AA 24	AA A	A AA	A AA	AA
Meter 60 upper lower				B A	A AA	AA 88 AA 24	A AA			AA AA 24

AA indicates adequate amounts; A, minimum amount; B, deficiency.

Table IX. Calcium content of oven-dried soil in lbs/A, measured by the Soil Testing Laboratory of Michigan State University. Soil samples were taken from the upper and lower horizons (to a depth of 30 cms.) in the first two weeks of August, 1962, at Stations spaced 10 M apart (except E-5), along Transects A to J, in the southeastern bog of Deep Lake. Sarracenia purpurea areas are underlined.

Transects:	A	B	C	D	E	F	G	H	I	J
Meter 5 upper					8230					
lower					4800					
Meter 10 upper										
lower									4750	
Meter 20 upper										
lower										
Meter 30 upper				6550					4750	
lower				4708					5370	
Meter 40 upper		8150								
lower		<u>5964</u>		<u>7060</u>			4800			
Meter 50 upper					8400					
lower			<u>1680</u>		<u>6050</u>					
Meter 60 upper					4870					
lower					<u>1103</u>				5716	

D. DISCUSSION

While digging for soil samples at Dee Lake, it became apparent that there were actually only two distinguishable horizons in the profile of the soil. These were various thicknesses of peat or muck on top and a uniform cover of marl underneath. Presence of marl indicates that the area had been under water because this compound is formed only under aquatic conditions (Hale 1903). It is composed largely of calcium carbonate derived mainly from precipitation by plants, remains of calcareous shells of animals and remains of calcareous plants (Welch 1952). A large number of marl-encrusted Chara are seen floating in the hard waters of the lake, which would indicate that marl is still being actively deposited here. This fact, as well as the presence of numerous mollusk shells in the marl bed of the bog, would seem to show that these organisms were probably the ones most actively involved in the formation of marl at this bog.

Normally, as marl accumulates to water level in the shallower shores of a lake, it becomes gradually covered over with bog or marsh vegetation which stops its deposition. In this particular bog, this process of accumulation was apparently speeded up by a drop in water table. The physiography of the bog gives every indication that the lake basin originally extended to the

tamarack zone and became exposed rather suddenly because there are no signs of erosion between the tamarack area and the lake shore. Signs of such receding can be seen all around this and many other lakes in this part of Michigan.

It would also appear that the basin of the lake forming the bog at this point was not level. Thus, the higher parts of the bottom became exposed to the air first, forming the marly Cladium mariscoides zone, while the depressions remained filled with water for a time. The depression by the lake shore appears to have been shallow as was suggested at E-5, where marl was reached at about 10 cm. Here marsh plants such as Carex aquatilis and Scirpus acutus took over, the alkaline condition of the soil being maintained by the lake water.

The second depression, near the tamarack zone, was much deeper, as is suggested by the lack of marl in the upper one meter. Here, the surface water began to be occupied by Carex lasiocarpa which is the forerunner of a typical bog (Rigg 1916). This zone when completely built up, should become an acid bog, provided spring water does not reach it. Already there are many patches of Sphagnum here.

1. Texture of the Soil: Under conditions of good drainage, texture of the soil may greatly influence aeration. In coarse-textured soil where the spaces

between the soil particles are relatively large, gas exchange can take place freely. However, under conditions of very low water table, this type of soil will lose water through percolation very rapidly and become dry. In clay soils where the particles are tightly packed, water loss through percolation is minimized. However, here there is less space for gases, and therefore under conditions where oxygen is being continually removed, the concentration of oxygen is lower. The best type of soil would be one containing both large and small pore spaces which permit adequate drainage of excess water and insure good aeration, at the same time retaining some water through capillary action of its smaller pores.

In water-logged soils, such as found in bogs, this relationship between soil texture and pore space is completely disrupted. In such soils water fills the spaces between soil particles regardless of texture.

At Deep Lake bog, as stated on p. 48, the Bouyoucos test was applied only to the lower or marly layer of Stations 10 to 40 along the transects. A study of the data in Table III, p. 53, indicates that no great variations were demonstrated in the amount of sand, silt and clay over the entire bog. In the stations supporting Sarracenia (B-40, D-40, F-40, F-50), the amount of sand varied only between 75 and 79%, that of silt, between 14 and 18% and clay, between 7 and 8%. In any event, as

discussed above, the high water table here would have minimized any influence soil texture might have had on aeration or loss of water through percolation except under conditions of extended drought.

2. Water content of the soil: The data in Table IV, p. 54, indicate an extremely high water content during the first two weeks of August, 1962. In the alkaline stations supporting Sarracenia purpurea (B-40, D-40, F-40 and F-50), the amount of water held by the soil varied between 313 and 598% for the upper horizons and between 55 and 234% for the lower. In the two acid stations supporting Sarracenia (C-50 and F-60), the water content was even greater, namely 704 and 903% for the upper and 1110 and 1167% for the lower. Too much water in the soil may do as much damage to a plant as too little water, because it restricts the space available for air (Leeper 1957). Oxygen itself, necessary for the respiration of the roots may become deficient. This may lower the metabolic functions that the roots perform, such as absorption (Kramer et al. 1960). Whitney (1942) reports a reduction in water absorption by tomato, corn and other plants in the near absence of oxygen. Poor aeration also results in an accumulation of CO₂. Although plants differ in their tolerance of CO₂ and poor aeration, generally the root systems suffer from this situation. Kramer et al. (1954) report wilting of herbaceous plants by a high

concentration of CO_2 because this gas produced an immediate decrease in permeability to water. The response of Sarracenia purpurea to its water-logged habitat appears to be a reduced root system which further reduces the rate of absorption and also restricts the soil volume from which nutrients are absorbed by the plant.

Another effect of lack of oxygen in the soil is a reduced rate of microbiological activity that transforms complex organic compounds into available nutrients for plant use. According to Alexander (1961), a large number of soil organisms are involved in the step by step degradation of nitrogenous matter into amino compounds, ammonium salts (ammonification) and then to nitrite and nitrate forms (nitrification) of nitrogen. Ammonification seems to proceed best in well-aerated soils but due to the great number of different organisms capable of bringing about these changes, it can take place to some extent under almost any conditions. Nitrification, however, is an oxidation process and only aerobic bacteria can accomplish it. Thus, in soils with a high moisture content and poor aeration, there is a reduction in the production of nitrates which are the most available form of nitrogen for higher plants. Furthermore, it is known that in poorly drained and aerated soils the process of nitrification may be reversed. Nitrates, nitrites and ammonium

may be reduced into molecular nitrogen (Lyon, Buckman and Brady 1952). This process known as denitrification is thought to be due to the action of anaerobic bacteria (Hutchinson 1957).

3. Acidity and alkalinity: The lake water and spring pool were found to be distinctly alkaline in 1961, the former having a pH of 8.9 and the latter a pH of 8.5. The substrate near the pool was alkaline as was the area adjacent to the lake. The pH values gradually decreased as distance from these two bodies of water increased, until they became acid in the tamarack zone (See Table V, p. 55). There were Sarracenia purpurea growing in two acid stations (C-50 and F-60) and four alkaline stations (B-40, D-40, F-40 and F-50).

Many scientists (Darwin 1884, Lloyd 1942, Zahl 1961, 1964), have presumed that the insectivorous habit in plants was developed as a device to supplement the short supply of nutrients in the soils in which these plants live. That bogs are so deficient in nutrients has been known for some time. In his "Summary of Bog Theories", Rigg (1916) cites deficiency of available nitrogen as one of the characteristics of bogs. Transeau (1906) makes the statement: "Bog soils are notably deficient in available nitrogen."

Bog soils in which insectivorous plants grow, have also been known to be acid in reaction (Rigg 1916,

Dachnowski 1908, 1909, Livingston 1905, and others). Thus when Sarracenia purpurea was reported thriving in neutral or alkaline situations, some explanation had to be sought for this phenomenon. In order to explain the presence of these plants in such soils, Wherry (1929) advanced a theory which is explored in this study. He suggested that this plant, having developed a means of obtaining nitrates, phosphates, and other nutrients through digestion of insects, requires soils in which these compounds are lacking or at a minimum. Usually only Sphagnum bogs meet fully this need of the plant. He concluded that Sarracenia purpurea is rarely found in neutral or alkaline soils not because of the H-ion concentration but because in many such soils nutrient elements are available in such quantities that injury occurs. At Deep Lake, as will be shown in the next paragraphs, both acid and alkaline areas supporting Sarracenia purpurea are almost equally deficient in nutrients.

4. Nutrients: Plants extract many elements from the substrate for their use. Out of these, nitrogen, phosphorus, potassium and calcium were selected for study because they are used in relatively large quantities and are the ones which most frequently receive attention in soil nutrient studies. It is well known that certain nutrient elements may be plentiful in a particular soil and yet be unavailable to plants because they may be in a

fairly insoluble form or may be bound up in organic matter that has not fully decomposed (Lyon, Buckman and Brady 1952). Thus, a complete chemical analysis of soils will not give a true picture of the amount of nutrients that are available for utilization by plants at a particular time. In this study, therefore, only nutrients that are in available form were measured.

As stated earlier, the water-logged conditions of Deep Lake bog greatly retard the biochemical processes that transform organic matter into available form of nitrogen compounds such as nitrite and nitrate salts. Data listed in Table VI, p. 56, indicate that soil samples from both the upper and lower horizons show a high degree of deficiency in available nitrogen over practically the entire bog area. Of the four alkaline stations supporting Sarracenia purpurea, two (D-40 and F-50) are only slightly less deficient than the acid stations supporting this plant (C-50 and F-60). The other two alkaline stations (B-40 and F-40) are even poorer in this nutrient than are the acid stations.

As to phosphorus, in the acid areas (C-50 and F-60), Sarracenia purpurea was found growing in much overlying marl containing a very small amount of this nutrient detectable with the procedures used, namely 3 pounds per acre-furrow-slice (3 lbs/A) in the upper layer and 5 lbs/A in the lower (See Table VII, p. 57). In the alkaline

stations (B-40, D-40 and F-50), this species was growing in peat or muck over marl with a phosphorus content varying from 7 to 12 lbs/A for the upper horizon and 1 to 21 lbs/A for the lower. These amounts are rated from "very low" to "low" in fertility level for field crops by the Department of Soil Science of Michigan State University (Bull. E-159, 1963), but are probably adequate for the needs of Sarracenia at this time of the year (first and second weeks of August) when practically all growth had ceased. Plummer (1963) found that soils in the moist pine barrens in the Middle Coastal Plain region of Georgia, which support several species of Sarracenia, show a definite decrease in productivity and in certain nutrients, particularly P_2O_5 , from April through September. He reported that the amount of available phosphorus for the five areas studied dropped from an average of 19 lbs/A on April 1, to 12 lbs/A on June 1 and to 10 lbs/A on October 1. It would therefore seem reasonable to assume that at Deep Lake bog, the amount of available phosphorus was somewhat greater in the spring and early summer (when Sarracenia purpurea produced its seeds and most of its leaves) than the figures in Table VII, p. 57, would indicate.

As to potash, the Sudbury testing method showed an adequate amount of this compound over most of the stations tested, indicated as "AA" in Table VIII, p. 58.

All other stations rated at least the minimum amount required for crop growth, namely "A". Likewise, the laboratory results in the same table with 88 to 132 lbs/A in the upper organic layers are rated from "low" to "medium" in fertility level for field and vegetable crops by the Department of Soil Science of Michigan State University (Bull. E-159, 1963). The lower marly layers, with 20 to 35 lbs/A are rated "very low" in fertility level. In these stations the organic layers were quite thick and Sarracenia purpurea roots did not penetrate below them into the marly layers. One would therefore conclude that the supply of potash was quite adequate for the growth of this plant even as late as the middle of August when practically all active growth had ceased.

The calcium content in peat soils of Michigan varies from 0.16% (800 lbs/A) in low-lime muck and 6.8% (34,000 lbs/A) in high-lime muck (McCool et al. 1925). The figures in Table IX, p. 59 indicate that Deep Lake is to be counted somewhere in between these two extremes. The over-all figure of about 5000 lbs/A for the lower horizon of the Carex aquatilis and Cladium mariscoides zones (Stations D-30, E-5, I-10 and I-30), may be explained by the large amount of calcium carbonate in the marl. The lowest amounts of calcium are found in the lower horizon of C-50 (1680 lbs/A) and F-60 (1103 lbs/A). As expected, these are the two stations supporting Sarracenia

purpurea, which have the lowest pH of all the stations tested. (See Table V, p. 55). But even here the pH does not fall below 6.5 which is considered the upper limit of soils requiring liming by the Soil Science Department cited above. One may conclude, therefore, that the amount of calcium is not a limiting factor in this bog for the growth of higher plants.

E. SUMMARY AND CONCLUSIONS

1. At Deep Lake, Sarracenia purpurea grows both in acid and alkaline areas.
2. Of four essential nutrients measured in both acid and alkaline substrates supporting Sarracenia purpurea, one was found to be in such low quantities as to be regarded as a limiting factor. This was nitrogen. Calcium was abundant; potash was adequate while phosphorus was in very short supply but probably adequate during the growing season.

SECTION III. VARIATIONS IN THE LEAF
OF
SARRACENIA PURPUREA

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As we have already noted in the Literature Survey, p. 3, the separation of the Sarracenia of North America into species is based almost entirely on leaf morphology, the flower playing a very minor role. The over-all leaf form is thus generally considered as a constant characteristic, controlled by genetic rather than environmental factors. Therefore, from a taxonomic viewpoint, any variation in leaf form warrants careful consideration.

The present study was undertaken to determine whether or not some of the variations in leaf form that could be noted in this part of the country were due to genetic differences or whether they were due to environmental influences. Two acid bogs (Purdy Lake and Otis Lake) and two alkaline bogs (McKay Lake and the alkaline area of the southeastern bog of Deep Lake) were selected for this study. Map coordinates of these bogs are given on pp. 14-18).

The problem was attacked from three angles:

- (1) A study of size of pitcher leaves was made in the field.
- (2) Reciprocal transplants were made from the two acid bogs to the two alkaline bogs, and vice versa.
- (3) Variation in leaf shape was induced in the laboratory.

III-1 STUDY OF SIZE OF PITCHER LEAVES

A. INTRODUCTION

A preliminary examination of the pitcher plants in the four bogs (description of these bogs was given on pp. 14-18) under study showed that the plants in the acid bogs had rather large but fewer leaves, while those in the marly or alkaline bogs had numerous small leaves; some of the plants had a single flower while others had two or more flowers. No sooner was an examination of these variations undertaken, however, when it became clear that the plants with numerous leaves and more than one flower were not single plants but several plants formed by vegetative reproduction of the rhizome. Each had its own growing point, with its own rosette of pitcher-leaves and in no instance was there more than a single flower on a single plant, despite Hooker's (1874) assertion that "they send up at the end of the flowering season one or more slender stems bearing each a solitary flower."

With this information in mind the quantitative study of the variations was continued as originally planned because the variations still existed--some of the "plants" or colonies did have larger but fewer leaves, while others had a large number of smaller leaves. No attempt was made to select plants of the same age for this study because there seems to be no way of determining

the age of pitcher plants. They are perennials but form no annual rings which might serve as an indication of their age. The number of leaf bases on the rhizome were also of no value because it was known from studies of seedlings by the author that the number of leaves produced each year is highly variable.

B. METHODS

To select a method for comparing the pitcher leaves of Sarracenia presented a unique problem. It was difficult to decide whether to use their absorptive or their photosynthetic capacity for this comparison, or to use both. If we were to compare the absorptive surfaces, then only the inner surface area of the leaf cone would have to be measured. Those of the hood and wing would have to be excluded. However, the pitchers are not always full to capacity with fluid and insect material, so their volume may not form a sound basis for comparison. Also, not the entire inner surface of a pitcher is actively engaged in absorption (Hooker 1874, Russell 1919, Lloyd 1942). Whether this absorptive area varies in proportion to the size of the leaves, is not known. It is reasonable to assume that a large leaf would have a large absorptive surface. However, it is also possible that a younger leaf might have a larger absorptive surface in comparison to its size than a larger, more mature leaf. For these reasons, it was decided to eliminate the absorptive surface of the cones from consideration and to measure only the photosynthetic capacity of the leaves by the following methods.

Ten mature "plants" were selected that were typical for each of the four bogs under study, and the length and width of the leaves were measured with a

flexible plastic ruler the end of which was placed against the point of insertion of the leaf into the rhizome. In situations where Sphagnum was deep and the pitcher-leaves were almost completely submerged in it, the solid petiole at the base of the pitcher was rather long and it was not possible to determine where it ended and where the hollow part began. For this reason the length of the entire leaf was measured from its point of insertion to its tip and no attempt was made to distinguish between the solid petiole and the hollow pitcher. The width was measured across the widest part of the leaf, including the wing. A leaf area index was used based on the formula two-thirds length x width used by Cain et al. (1956) for tropical rain forest species and adopted by Cooper (1960) for all species of temperate vegetation. In the present study the area index was selected as a simple procedure for comparing relative leaf areas and not for the purpose of placing the leaves in definite Raunkiaerian leaf-size classes as in the two cited studies. The results are summarized in Table X, p. 79.

C. RESULTS AND DISCUSSION

A study of the figures in Table X will show that Sarracenia purpurea "plants" growing at Purdy Lake, which is a well established Sphagnum bog (pH of 5.2-5.4 at the surface and 5.9-6.4 at the root-level of Sarracenia) have an average of 17 leaves per "plant", but the pitchers are unusually large, having an average LW value of 65.

Likewise, Otis Lake, another Sphagnum bog (pH of 5.9-6.0 at the surface and 7.0-7.2 at the roots of Sarracenia) had fewer (12) but larger pitchers per "plant" (LW value of 51).

McKay Lake, an alkaline bog, (pH of 8.3-9.1 at the surface and 8.3-8.6 at the roots of Sarracenia) had a greater number (30) but smaller pitchers per plant (LW value of 15).

Deep Lake (the alkaline area of the southeastern bog) with a pH of 8.3-8.4 at the surface and 8.0 at the roots of Sarracenia, supported plants that had a greater number (27) but smaller pitchers per colony (LW value of 21).

D. CONCLUSION

Sarracenia purpurea in the two acid bogs (Purdy Lake and Otis Lake), produce fewer but larger pitchers per "plant" or colony than those growing in the two alkaline bogs (McKay Lake and the marly zone of southeastern Deep Lake bog).

Table X. Number and average 2/3 LW values of pitcher leaves for 10 plants in 4 bogs, recorded in August, 1961.

PURDY L. (acid)		OTIS L. (acid)		MCKAY L. (alk.)		DEEP L. (alk.)	
(a)*	(b)	(a)	(b)	(a)	(b)	(a)	(b)
13	43.1	24	35.7	24	8.0	72	20.0
15	78.9	6	45.2	44	22.0	25	17.2
24	39.0	15	37.5	46	17.6	20	22.2
33	54.9	17	47.7	46	20.8	62	20.3
9	99.0	7	68.0	25	23.5	9	22.8
13	52.0	9	47.9	17	19.4	8	27.7
5	78.0	16	43.3	25	8.4	20	16.2
11	91.5	6	62.5	25	9.0	10	18.4
6	44.5	9	59.5	22	9.8	25	15.9
39	65.3	12	62.6	25	14.8	15	23.7
$\bar{x}$ =	16.9	64.6	12.1	51.0	30.0	15.3	26.6
$s_{\bar{x}}$ =	± 3.64	± 6.71	± 1.87	± 3.57	± 3.45	± 1.93	± 6.52

*(a) shows number of pitcher leaves per plant

(b) shows average 2/3 LW value of pitchers per plant

Table XI. Number and average 2/3 LW values of pitcher leaves of transplants from acid to alkaline bogs and vice versa, recorded in August, 1963, two years after the transplants were made.

OTIS L. (acid) to DEEP L. (alk.)		DEEP L. (alk.) to OTIS L. (acid)		MCKAY L. (alk.) to PURDY L. (acid)		
(a)*	(b)	(a)	(b)	(a)	(b)	
26	32.1	23	24.9	18	37.6	
26	22.9	35	27.5	13	34.7	
		9	36.7			
$\bar{x}$	26	27.5	23	29.7	15.5	36.2
$s_{\bar{x}}$	0	±4.58	±7.47	±3.56	±4.29	±1.44

*(a) shows number of pitcher leaves per plant

(b) shows average 2/3 LW value of pitchers per plant

III-2 RECIPROCAL TRANSPLANT EXPERIMENTS

A. INTRODUCTION

The existence of significant differences in leaf size and number could be due to the plants being from genetically different stock or it could represent an environmental response of the same basic genetic stock. Reciprocal transplants have long been used in helping to discriminate between these two alternatives (Bonnier 1920, Clements 1929, Turesson 1922, Clausen et al. 1940, McMillan 1959 and Mooney et al. 1964). If plants from acid bogs transplanted into alkaline bogs continued thereafter to produce long pitchers, it would be reasonable to assume that the variation was genetic in nature and not induced by environmental factors. The same conclusion would be drawn if plants from the alkaline areas continued to produce smaller pitchers when transplanted into acid bogs.

B. METHODS

During the week of August 10, 1961, three mature plants of about the same size were selected in Otis Lake bog and transplanted into the marly zone of Deep Lake bog into the holes left by the removal of similarly selected three plants which were in turn transplanted into Otis Lake bog in the holes left by the three previously mentioned plants. Mutual transplants of three plants each were also made in the same manner between McKay bog and Purdy bog.

C. RESULTS AND DISCUSSION

A year later, these twelve plants were examined for any change in general appearance, particularly in the size of new leaves produced. Eleven of the twelve transplanted plants had survived. The plants transferred from the alkaline bogs (McKay and Deep Lake) into the acid bogs (Otis Lake and Purdy Lake) had produced some longer leaves, close to the size of the neighboring plants. However, their flower stalks and size of flower and capsule remained small, like those of their former habitat.

Similarly, the plants that had been brought from the two acid bogs had produced somewhat smaller leaves than the older ones. Their flower stalks were quite long and the floral parts and capsules were much

larger than those of the surrounding plants. Thus, in both instances, the flowers had remained true to the old form, at least during the first season, but the leaves had begun to be affected by their new environmental conditions.

Incidentally, the transplants in Deep Lake had accidentally brought with them several cranberry plants (Vaccinium macrocarpon) and a single orchid (Pogonia ophioglossoides), all of which bloomed and formed fruit.

In the second spring following transplanting, a sudden drop of temperature on May 21, 1963, to 27°F. resulted in extensive frost damage to pitcher plants. Many leaves, both young and old, had their hood and the upper part of the pitcher frozen and these parts became necrotic. The transplants suffered more damage by this freeze than the other plants. All three transplants at McKay Lake and one each at Deep Lake and Purdy Lake began to die soon after this date. The surviving individuals were examined again on August 30, 1963, at which time the leaves were counted and measured. The results are summarized in Table XI, p. 79.

None of the plants in these bogs, either in the natural populations or among the transplants, bloomed in 1963. It is presumed that the flower buds which had already been formed on May 21st were killed by the freeze.

The orchid and cranberry transplants at Deep Lake bloomed and formed fruit for the second year.

A comparison of the figures in Table XI with those in Table X, p. 79, brings out the fact that the transplants show significant departures in leaf size and leaf number from those of plants of their former habitat. The most spectacular change occurred in the transplants to the marly zone of Deep Lake of plants from the acid bog at Otis Lake, where the number of new leaves of the transplants (26) is more than twice the average number of leaves on plants growing in Otis Lake. This increase in leaf number brings the count about identical to the number of leaves (26.6) on plants normally growing in Deep Lake. Similarly, the LW value of the transplants (27.5) has been reduced considerably from the average figure (51.0) for the plants in Otis Lake, and is close to the LW value (20.5) of the plants of Deep Lake.

The least modification in number of leaves of all transplants was obtained in the reciprocal of the above transplanting, i. e., from Deep Lake to Otis Lake. However, even here, a definite trend toward a smaller number of leaves (from 26.6 to 23) and greater LW value (from 20.5 to 29.7) is to be noted.

The second set of transplants from an alkaline bog (McKay) to an acid bog (Purdy) shows this trend to a greater extent. Leaf number has been reduced from 30 to

15.5 and LW value increased from 15.3 to 36.2.

The gradual manner in which these transplants became morphologically adjusted to their new habitat is reminiscent of a phenomenon that has attracted considerable attention (Clements 1929, Went 1959, Mooney et al. 1964, Rowe 1964). The fact that it took two full growing seasons to make the adjustment has two possible interpretations. First, the root systems were not thoroughly washed free of soil and the lag may simply reflect the attenuation of the small mass of original substrate. Secondly, the metabolic pools within the plants take time to attenuate as Went (1959) has shown for potatoes, Highkin (1958, 1961) for peas and Rowe discusses generally. The earlier habitat appears to leave a gradually attenuating impression. It would be useful to learn whether both or only one of these mechanisms was involved. The fact that death and freeze damage of the transplants exceeded that of the indigenous population suggests that metabolic pools were out of balance.

D. CONCLUSION

It may be concluded from these transplant experiments that leaf size and number are highly variable in Sarracenia purpurea and that these variations are determined by ecological factors. This is not to imply, however, that the capacity to make a response of leaf size to substrate chemistry might not itself be the product of adaptation. It is possible that many small leaf cones would result in a high internal surface area to leaf mass ratio and partially accommodate for a reduction in availability of some nutrient such as iron in the marly bog.

III-3. INDUCED VARIATIONS IN LEAF SHAPE

A. INTRODUCTION

While taking measurements of pitcher-leaves for the preceding experiments, it was noted that some of the leaves were flat, having a very narrow pitcher and a very wide wing (Fig. 2, p. 90). Robinson (1908) reported that plants of Sarracenia purpurea kept under glass for a year at the New York Botanical Garden showed a marked tendency to form blade-like structures instead of pitcher-shaped leaves. Shufeldt (1918) made the observation that the leaves of pitcher plants changes very materially in several respects when the plants were kept in the house and did not receive much light, and that "the most curious and interesting thing was to see the hollow pitcher-part gradually becoming absorbed, almost disappearing in some specimens." The idea seemed fantastic, especially as several plants kept in a Detroit classroom during the school year had produced normal leaves.

About the first of July, 1962, while the problem was being considered, three plants brought into a Detroit classroom in April and transferred to the Kellogg Biological Station in June, suddenly sprouted flattened leaves. Obviously, there was some factor in the new location that hindered the normal development of pitcher leaves. Since

the plants in question had been kept indoors in two different locations and it was already known that the Detroit site had not induced the formation of flat leaves in these and several other plants, it was obvious that the variation was due to conditions in the second location. In Detroit, the plants had been kept in front of a window facing west, with strong fluorescent lighting during the day. At the Station, they were placed on an open window sill of a study room facing south, with practically no artificial lighting.

The environmental conditions in the Detroit classroom, subject to severe temperature changes during week-ends, were thought to be too complex for use in this study. On the other hand, Purdy Lake bog and the study in the Biological Station which are located only about five miles apart, presented relatively simpler conditions for comparison. The study room was practically never used so any effect that fluorescent lighting might have on the morphology of leaves could safely be eliminated from consideration. Further, the window was open for long periods during this study and thus deficiency of ultra-violet light could probably be eliminated from any consideration. Temperature and relative humidity at both locations were considered essentially similar, leaving total amount of incident light as the most likely variable that might effect a change in leaf form. Thus three plants

were freshly dug out of Purdy Lake, placed on the study window sill and light intensity measured both in the bog and in the window location.

B. METHODS

Light readings were made in foot/candles with a Weston Illumination Meter, Model 756, between 12 Noon and 12:15 P.M., from June 28 to July 28, 1963. Altogether 22 readings were taken. For the study room the light meter was held parallel to the wing of a particular pitcher leaf, facing south, measuring light falling directly on the leaf. At the bog, the meter was similarly held facing south, parallel to the wing of the same pitcher-leaf each day. The results are summarized in Table XII.

Table XII. Average of 22 readings of light intensity in foot/candles, taken around noon time, at the study window sill of the Biological Station and at Purdy Lake bog, from June 28 to July 28, 1963. A Weston Illumination Meter, Model 756, was used.

Study window sill	Average of 755 f/c	(100-1400 f/c)
Purdy Lake bog	" 1396 "	400-2600 "

C. RESULTS AND DISCUSSION

In a study of light three values are of paramount importance: quality or wave length of the light, duration or time of illumination and intensity of illumination. In this study quality and duration of light were considered constant in the two areas under comparison. Only intensity remained as a variable to be compared. It was found that light intensity values for the study were considerably lower than those for the bog (See Table XII, p. 88). All new leaves of the three experimental plants in the study were flat in shape (Figs. 3, 4 and 5). The older leaves remained normal and their pitchers were not "absorbed" during the experimental period.

D. CONCLUSION

In view of the above observations it does not seem unreasonable to conclude that for Sarracenia purpurea which lives mainly in open sunny places, light intensity is an important factor in the normal development of its leaf form, and that low intensity of illumination is a major cause for the production of flattened leaves.



FIG. 2. Plant removed from the bog to photograph the flattened leaf.



Fig. 3. Plant No. 1, showing blade-like leaves.



Fig. 4. Plant No. 2, showing blade-like leaves.



Fig. 5. Plant No. 3, showing blade-like leaves.

SECTION IV. POLLINATION IN
SARRACENIA PURPUREA

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A. INTRODUCTION

Scientists in the past have assumed that Sarracenia must depend upon insect agency to effect pollination of its flower (Jones 1908). James (1883) in comparing pitcher plants to water lilies, says: "With its broad, flat table-like expansion, most effectively concealing the stamens behind it, the stigma is utterly incapable of self fertilization."

Higley (1885) states that "all the species of the genus Sarracenia are constructed in such a manner that in fertilization they are absolutely helpless without the aid of insects."

Macfarlane (1908) too, regards the structure of the flower as a device to encourage cross-pollination. He explains that a bee attracted to the flower by nectar has only one way to get inside, the orifice below the stigma. Thus it must rub against the stigma as it enters the flower, brushing on it any pollen that may have adhered to its body. He states that upon leaving the flower, the bee does not use the same orifice, but may tip over the side of a petal to make its exit.

Jones (1908), who has done extensive work on insect associates of Sarracenia, reports that insects not

only enter but also leave through the five entrance holes where the stigmas are located, as mentioned above, but that self-fertilization does not occur because there is no pollen in the floral cavity at this time. He explains that the flower sheds most of its pollen soon after opening, while it is in an inverted position. It then begins to tilt again and by the third day it takes a vertical position, so the pollen spills out. He states further that "as the blossoms remain fresh and continue to be attractive to insects for more than two weeks (here he is speaking about S. flava), it would seem that this change in the position of the flower and the consequent spilling of pollen would decidedly favor cross-pollination."

Insects have been known to frequent the flowers of Sarracenia for some time. Jackson (1880) reports seeing the floral cavity filled with flies "all busy as could be eating the pollen." James (1883) suggests that perhaps there is something in the pollen or in some secretion of the flower which has an intoxicating effect on the flies which then fall into the pitchers below. Higley (1885) disagrees with James as to the reason for the presence of flies. He states that they are attracted to the flower to aid in its fertilization.

The "flies" mentioned above are not identified by any of these observers. Higley (1885) later on his article describes a fly, Sarcophaga sarraceniae Riley,

which drops its larvae into a pitcher tube where they feed upon dead insects. He adds, however, that this insect has nothing to do with the flower, intimating that the "flies" previously mentioned by Jackson, James and himself in connection with the flower, are different from Sarcophaga sarraceniae.

Jones (1908) lists this same fly, Sarcophaga sarraceniae Riley, as among the insect pollinizers of S. flava. He states that this fly is associated not only with the pitchers but also with the flowers of this plant. He describes the insect as bristly and often yellow with pollen, and of suitable size almost necessarily to touch the stigma in entering and leaving the flower.

It will be noted that in the above discussion none of the various workers mention the possibility of self-fertilization ever taking place. Also, there is no record of any experimental work done by any of them to support the contention that cross-pollination is the only means of fertilization in this plant.

This portion of the study was therefore undertaken with three goals in mind: 1. To follow the sequence of development of the flower of Sarracenia purpurea from bud to seed formation, 2. To ascertain the type of pollination, and 3. To determine the agent or agents of pollination.

A portion of the experimental work was done at Rose Lake bog (Clinton Co., Michigan, T5N, R1W, Sect. 26)

during the spring of 1962. This is a Sphagnum bog located on the grounds of Michigan Wildlife Experimental Station on the western shore of Rose Lake, about seven miles north-east of East Lansing, Michigan. The experiments were repeated the following year at a bog along the eastern shore of Bridge Lake, near Clarkston, (Oakland Co., Michigan, T4N, R8E, Sect. 14). Change of site was necessary because flower buds of Sarracenia purpurea at Rose Lake and many other bogs of southern Michigan were frozen by a sudden drop of temperature on May 21, 1963.

B. FLORAL STRUCTURES AND THEIR DEVELOPMENT

The flowers of Sarracenia purpurea are regular, perfect, with 3 imbricate bracts at the base. There are 5 sepals, imbricate at the base, ovate, persistent and reddish purple. Petals are 5 in number, obovate, incurved, deciduous and reddish purple in color. Stamens are numerous and hypogynous; the filaments are short and filiform; the anthers are versatile, introrse and two-locular. Ovary is five-locular and globose, with axile placentation; ovules are numerous; style is simple below, branched above into a five-rayed umbrella-shaped disk, bearing a small hooked stigma beneath the notched tip of each ray. Fruit is a five-valved, loculicidal capsule. Seeds are small, numerous and anatropous; the embryo is minute and is located near the hilum.

The flowers are about 4-7 cm. long and about 9 cm. wide. They are solitary, borne at the end of a scape which may attain a length of up to 58 cm. The entire surface of the ovary is covered with tiny tubercles which exude nectar as the flower opens. This secretion continues long after the flower has been pollinated and the stamens and petals have been shed. According to Russell (1919), the nectar is secreted by glands situated at the bases and along the sides of the tubercles. These glands are more numerous over the lower half of the ovary than over the upper. In addition to the ovary, various

parts of the flower, such as the bracts, sepals and petals, also contain nectar glands.

Dehiscence of the anthers takes place as soon as the flower opens. At this time the flower is in an inverted position and the umbrelloid part of the style forms the floor of the floral cavity. As the pollen falls into the style, it becomes coated with nectar from the ovarian wall. This gives it an adhesive quality which enables it to stick to the body of visiting insects and to the stigma. The latter organ, although dry, is nevertheless provided with long, curved hairs which effectively trap pollen grains and hold them. The umbrelloid style, also, contains many long hairs to which the pollen grains may adhere until brushed off by insects.

The pollen grain is barrel-shaped in longitudinal view (Fig. 6, p. 100). Three or four grooves extend from pole to pole. In polar view, it appears round, and 5-8 grooves can be seen on the outer surface. Shrive (1906) states that there are no germinal pores in the pollen grain, the tubes growing directly from the grooves.

According to Macfarlane (1908), the flower buds form in August and September but remain concealed among the leaf bases until next spring. At Rose Lake there was no outward sign of bud formation on April 14th, 1962. A plant taken indoors on that date, however, produced a bud in four days. Fifteen days later, on May 3rd, the

flower had fully opened. In the bog itself, buds began to appear on May 1st. On May 19th only a single flower could be seen in the entire bog, but by May 24th, practically all flowers had opened. A week later, on June 1st, all stamens and petals had been shed. Gradually, the bracts, sepals, together with the broad style, turned greenish and remained attached to the ovary. As the seeds ripened, the ovary as well as the style grew considerably in size. Dehiscence of the capsule took place early in October, about four and a half months after fertilization.

In the following photographs the main stages in the development of the flower have been recorded. At first, the bud is round (Fig. 7, p. 101). Soon the flower stalk starts to lengthen, the round bud standing erect on its tip (Fig. 8, p. 102). Then the stalk bends at its tip (Fig. 9, p. 102) and the bud becomes inverted in position and somewhat flattened (Fig. 10, p. 103). At anthesis, the flower hangs downward, with the ovary and stamens above. The style below forms the floor of the floral cavity (Fig. 11, p. 104).

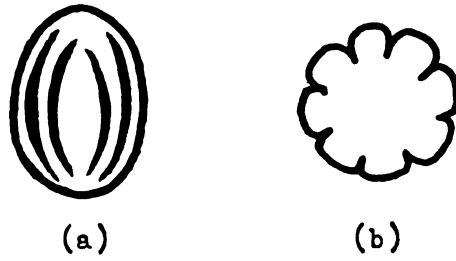


Fig. 6. Hydrated pollen grain of Sarracenia purpurea.

(a) longitudinal view
(b) polar view



Fig. 7. Emergence of the flower bud.



Fig. 8. Globular bud on top of peduncle.



Fig. 9. Peduncle bending at tip.

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Fig. 10. More advanced stage; the bud flattening out.



Fig. 11. The flower at anthesis.

C. MATERIALS AND METHODS

1. Flowers deantherved and cross-pollinated by hand. To determine the effectiveness of cross-pollination, 20 flower buds were deantherved at a very early stage (before the anthers had dehisced) and cross-pollinated by hand with pollen obtained from other Sarracenia flowers in the same bog. Signs of bud formation were noted on May 1st, 1962, at the Rose Lake bog, and the buds deantherved on May 19th. Cross-pollination of each flower was continued daily until June 1st, a total of eight times. On this date no pollen was available for this purpose. Each bud was protected by a polyethylene bag which was perforated with a fine needle to permit free exchange of gases.

The deantherving process was a very delicate and time-consuming operation because of the fact that 70 to 80 stamens had to be removed before anthesis of the flower had taken place. This was accomplished by inserting a pair of forceps in-between the tightly folded sepals and petals of the bud, taking care not to prick the ovary or tear the umbrelloid style in the process. If such damage was noticed, the bud was discarded.

2. Flower buds bagged and left undisturbed. Twenty very young buds were bagged and left undisturbed for the entire experimental period. Any seed formation in these flowers would be interpreted as an indication that self-pollination takes place under these conditions.

3. Flowers self-pollinated by hand. A third set of 20 buds were bagged and repeatedly self-pollinated by hand until June 1st, altogether eight times each. A separate camel's hair brush was placed alongside each flower within the plastic bag in order to eliminate any accidental entry of pollen from outside through a contaminated brush.

4. Study of Insect Pollinizers. Insects visiting the interior of free flowers were trapped between May 24th and June 2nd. By this latter date, practically all insect activity around the flowers had terminated, even though the weather was bright and sunny. An eight-hour watch on June 1st netted only two insects. Method and site of entry of these visiting insects and their behavior while within the floral cavity were observed. The body and pollen collecting apparatus of insects trapped leaving the flower were studied and presence of Sarracenia pollen noted.

The same procedure was followed the second year at Bridge Lake bog with some modifications. The experimental work here was started on May 30th instead of the 19th because the buds had not reached the deanthering stage at the earlier date. Instead of polyethylene bags, fine-mesh cotton organdy was used to cover the buds, in order to provide free exchange of gases and to prevent condensation of moisture inside the bag.

Twenty Sarcophaga sarraceniae flies were removed from the floral cavities of pitcher plants near the southern end of the bog. They were then daubed with red nail polish on the dorsal surface of the thorax, chilled in a portable icebox until inactive, and placed back in the flowers. Twenty other flies were similarly colored blue and placed in flowers in the center of the bog. A third group of 20 flies was colored orange and placed near the northern end of the bog. The movement of these flies from flower to flower was followed to ascertain their role as pollinating agents.

D. RESULTS AND DISCUSSION

1. Flowers deanthed and cross-pollinated by hand. At Rose Lake, of the 20 flowers that were de-anthered and cross-pollinated by hand, 14 survived. The others were stepped on, broken or otherwise destroyed. All of these 14 capsules, except one, formed seeds, ranging from 8 to 613 in number.

At Bridge Lake, 17 capsules survived of the 20 deanthed and hand-cross-pollinated flowers. All of these set seed, ranging from 69 to 1021 in number. Thus, of an over-all total of 40 deanthed flowers in the two bogs, 31 survived, 30 of which, or 97%, formed seeds, with an average yield of 319 seeds per capsule. The above results are shown in Table XIII, p. 115).

2. Flower buds bagged and left undisturbed. Of the 20 flower buds that were bagged at Rose Lake and left completely alone, 16 survived. All had formed capsules but only two of these contained seeds. One had 13 and the other one had 75 seeds.

At Bridge Lake, of the 20 flower buds similarly bagged, only 5 survived, 4 of which set seed (1, 9, 9 and 74 in number). Thus, of a total of 40 bagged buds in the two bogs, 21 survived, six of which, or 29%, formed seeds. These results are presented in Table XIV, p. 116.

It must be remembered that insects were completely excluded from these flowers and that no pollen from the

outside could reach the floral parts enclosed within the bags. Therefore, barring apomixis, which is not reported for this species, the formation of seed in these flowers would have to have resulted from self-pollination.

3. Flowers self-pollinated by hand. The above conclusion is further strengthened by an examination of the third group of experimental capsules, namely, those that were self-pollinated by hand. Of 20 such flowers at Rose Lake, 18 survived and of these no less than 6 capsules had seeds in them, ranging from 8 to 248 in number. At Bridge Lake, 12 of similarly hand self-pollinated flowers survived the drought of the summer of 1963, and all formed seeds, ranging from 5 to 595 in number. Thus, of a total of 40 flowers in the two bogs, 28 survived, 18 of these, or 64%, formed seeds. These results are shown in Table XV, p. 117.

The data given in Tables XIII, XIV and XV are summarized in Table XVI, p. 118.

The significance of differences in pollination success among the various experiments was determined using the t-test (Steel and Torrie 1960). The probability that the differences between unassisted self-pollination and hand-assisted cross pollination were due to chance is less than .0005. Similarly, the probability that the differences between hand-assisted self-pollination and hand-assisted cross-pollination were due to chance is less than .01 (See Appendix II, p. 160.

It is clear from the results of these experiments that cross-pollination is the most effective method of fertilization in this plant. It results in more capsules with seeds and more seeds per capsule. Of 31 trials attempted, there was only one failure which was probably due to accidental damage to the ovary during the deanthering process. However, the results of these experiments also indicate that the plant is not entirely incapable of self-pollination, although, as observed by earlier workers, the structure of the flower obviously favors cross-pollination. Of the flower buds that were bagged and left undisturbed, nearly one-third, or 29%, produced seeds. When self-pollination was effected by hand, the percentage of flowers setting seed rose to 64%. Thus it may be concluded that cross-pollination is the standard method of pollination in Sarracenia purpurea and that the relative ineffectiveness of self-fertilization appears due to morphological rather than physiological or genetic characteristics.

Seed viability was not tested because the seeds had to be harvested before reaching full maturity for fear they might be destroyed by the curious if left bagged or by parasites if left exposed and unprotected for a period of five months necessary for full maturity.

4. Study of Insect Pollinizers. The Sarracenia fly, Sarcophaga sarraceniae Riley, mentioned by several

scientists as being associated either with the flower or the leaf of pitcher plants, was also trapped abundantly from the flowers of Sarracenia purpurea at both Rose Lake and Bridge Lake bogs.

On cloudy and rainy days, and especially in late afternoons and early evenings, three or more of them could be found within each floral cavity. They were not seen to be feeding at this time. They remained motionless and did not fly from flower to flower unless disturbed.

On the other hand, on sunny days, they could be seen actively flying about Sarracenia plants. They were attracted to the shiny sepals where they lapped up nectar and gradually worked their way into the floral cavity. In the bog it was not possible to observe what went on inside the flower as the slightest disturbance, such as lifting up of a petal, drove them off. Therefore, two plants were brought into a Detroit classroom and placed inside a large terrarium. A dozen Sarracenia flies were caught at the bog and released in the terrarium, and their activity watched for eight hours. During this period the flies completely ignored the flowers and were found dead the following morning. Next day, a fresh supply of flies was brought in and again released in the terrarium. This time a spotlight was turned on one of the flowers. As soon as the sepals and petals reflected the light, the flies quickly landed on them and started feeding. Subse-

quently, they entered the floral cavity where they stood at the base of the ovary lapping up nectar. A petal was removed at a strategic location so that their activity could be observed without alarming them. Five or six of the flies were seen standing in a row, sticking out their probosces and actively lapping up nectar. When the light was turned off, they again lost interest in the flower. Whether the reflection of light on the flower attracted them, or whether more nectar was produced under the stimulus of light, was not determined.

It seems possible that the report by Jackson (1880) that he saw flies eating pollen grains in the floral cavity was the result of inaccurate observation. The flies in the terrarium were seen moving among the filaments while the pollen-filled stamens were still present, but at no time were they observed eating pollen. On the contrary, they inserted their probosces in-between the filaments in order to reach the ovary wall where nectar was present in abundance. It was sticky to the touch and tasted sweet.

None of the marked flies were found anywhere in the bog the day following the marking, but an examination of the flowers in which they were placed revealed that they were no longer there. Two days later, two marked flies were recovered. One was in a flower about 150 meters south of its original site and the other had

moved 50 meters south from its original flower. The third day a third marked fly was recovered about 50 meters north of its original location. This would indicate, therefore, that Sarracenia flies move from flower to flower over a rather wide range. The bodies of all flies captured from both the Rose Lake and Bridge Lake bogs were laden with Sarracenia pollen and therefore it may be concluded that these flies are effective agents of cross-pollination of this plant.

The more spectacular visitors to the Sarracenia flower were the bumble bees, Bombus impatiens Cresson, B. griseocollis (Degeer), B. terricola Kirby and B. vagans Smith, which were extremely active through most of the day, moving incessantly from flower to flower, never staying long inside a flower. In spite of their large bodies they seemed to have no difficulty entering or leaving the flower. They entered through the openings where the stigmas project, but usually emerged from the side of the flower in-between two petals. Because of their rapid and incessant moving from one flower to another, and because of the large amount of pollen they carried, it is reasonable to consider them as effective pollinizers of Sarracenia purpurea.

Another group of insects that were most active about the flowers were the honey bees (Apis mellifera Linn.) Like the bumble bees, they usually entered through the

stigmatic openings and left from between two petals. They are probably the most effective pollinizers of all the insects visiting the flowers because they are of the right size to brush against the stigma as they enter the flower.

In addition to the above, a large number of ants were seen in the flowers at all times. They were at the base of the ovary in-between the filaments when the flower was young, and on the walls of the bare ovary, in the older flower. Their activity continued long after the stamens and petals had been shed. However, because of their small size, and because they were seen crawling in and out of all parts of the flower, the chances that they might touch the minute stigmas were considered very small.

Several other species of insects were also trapped from the flower but because of their small number their visits appeared to be accidental. Therefore, they were not considered to have an important role in pollination.

Table XIII. Production of seeds in deantherved and hand-cross-pollinated flowers at Rose Lake bog (1962) and Bridge Lake bog (1963).

Location	Number of Seeds
Rose Lake	87
" "	261
" "	115
" "	8
" "	518
" "	423
" "	539
" "	0
" "	326
" "	281
" "	613
" "	84
" "	59
" "	42
Bridge Lake	773
" "	674
" "	189
" "	1021
" "	238
" "	212
" "	256
" "	230
" "	290
" "	302
" "	100
" "	658
" "	670
" "	422
" "	325
" "	109
" "	69

$$\bar{x} = 319*$$

$$s_{\bar{x}} = \pm 45.78$$

Percentage of flowers setting seed: 97%

* Average seed count of 10 field grown capsules was 812.

Table XIV. Production of seeds in buds that were bagged and left completely undisturbed at Rose Lake bog (1962) and Bridge Lake bog (1963).

Location	Number of Seeds
Rose Lake	0
" "	0
" "	0
" "	0
" "	75
" "	0
" "	0
" "	0
" "	0
" "	0
" "	0
" "	0
" "	0
" "	0
" "	13
" "	0
Bridge Lake	9
" "	0
" "	1
" "	9
" "	74

$$\bar{x} = 9$$

$$s_{\bar{x}} = \pm 4.83$$

Percentage of flowers setting seed: 29%

Table XV. Production of seeds in flowers that were self-pollinated by hand at Rose Lake bog (1962) and Bridge Lake bog (1963).

Location	Number of Seeds
Rose Lake	8
" "	0
" "	248
" "	216
" "	0
" "	0
" "	0
" "	17
" "	0
" "	0
" "	0
" "	19
" "	0
" "	0
" "	0
" "	65
Bridge Lake	16
" "	5
" "	210
" "	299
" "	357
" "	106
" "	370
" "	595
" "	106
" "	9
" "	74
" "	204
$\bar{x}$	= 105
$s_{\bar{x}}$	= ± 29.62
Percentage of flowers setting seed: 64%	

Table XVI. Summary of data from Tables XIII, XIV, XV.

	Capsules Survived	Capsules with seeds	Range of seeds per capsule	Mean of seeds per capsule	Percent of capsules with seeds
Hand-cross- pollinated (Tables XIII)	31	30	8-1021	319	97
Hand-self- pollinated (Table XV)	28	18	5- 595	105	64
Self-pollinated bagged, untouched (Table XIV)	21	6	1- 75	9	29

E. SUMMARY AND CONCLUSIONS

1. In Sarracenia purpurea five months are required from emergence of flower bud to ripening of seeds.
2. The flowering of Sarracenia purpurea is almost simultaneous in a particular bog. Less than two weeks elapse between the appearance of the first flower and the shedding of the last petal.
3. The flower is visited not by just one species but by several species of insects. Among the most numerous visitors are Sarcophaga sarraceniae Riley, Bombus impatiens Cresson, B. griseocollis (Degeer), B. terricola Kirby, B. vagans Smith, Apis mellifera Linn. and several species of ants.
4. Cross-pollination, promoted by the structure of the flower, is the most effective means of fertilization in this plant, producing the largest number of seeds. However, under the experimental conditions of this study, the flower was found to be physiologically and genetically capable of producing seed by self-pollination.

SECTION V. GERMINATION OF SEEDS OF
SARRACENIA PURPUREA

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SARRACENIA PURPUREA

A. INTRODUCTION

According to Baldwin (1942) "knowledge of the proper pretreatment to induce prompt and complete germination can best be gained by a study of the ecological factors affecting the seed in its natural habitat between the time of maturity and germination." Consequently, this series of experiments was carried out in an effort to establish the ecological factors controlling seed germination in nature.

During its period of popularity in Europe as an interesting horticultural plant in the last century, Sarracenia purpurea and its hybrid forms had been raised from seed but no detailed account could be found as to methods used. In Gardeners' Chronicle of 1874, David Moore, speaking of pitcher plants in general and a Sarracenia hybrid in particular, states that "the seed was ripened in 1868. In the following spring the seeds were sown and that the pot was placed in a moderately warm house when the seeds began to germinate about a month after they were sown." It is not stated here under what conditions the seeds were kept over the winter months prior to being placed in the pots in the spring.

There are only two other references of more recent date about germination of Sarracenia purpurea seeds.

Shreve (1906) reports that "seeds of the crop of 1901, which in October of that year were placed in Sphagnum in a loosely covered glass vessel, germinated in July 1902". Macfarlane (1908) in his Monograph on the Sarraceniaceae, states: "The ripe capsule of Sarracenia shed their seeds from July to September in their native haunts. Germination takes place in from three to five weeks, and a small seedling may be formed before winter in the warmer southern states, or germination may be delayed until the succeeding spring in colder states."

The lack or scarcity of pitcher plant seedlings in some of the bogs under study was quite puzzling. In Purdy Lake bog, which is a Sphagnum bog containing a large, well-established Sarracenia purpurea population, only about a dozen seedlings and young plants were found after a thorough search during the summer months of 1960 to 1963. On the other hand, Otis Lake bog, also a Sphagnum bog, contained a large number of seedlings. The seedlings were so crowded that it was not immediately possible to determine which pitcher-leaf belonged to which plant without untangling them from one another. It looked as if a number of seeds had fallen in a certain spot and had all germinated at once. At Rose Lake, another Sphagnum bog, there were hundreds of seedlings. McKay Lake bog, an alkaline bog, had no seedlings at all. Deep Lake had no seedlings in its southeast bog (both acid and alkaline

areas), but in its northeast bog, which is alkaline in reaction, there were almost as many seedlings and young plants as mature ones.

As a result of these observations it would appear that the degree of acidity or alkalinity was not the determining factor controlling germination. It was also apparent that lack or scarcity of seedlings was not necessarily caused by lack of seeds because in Purdy Lake bog 95 "plants" out of 140 had one to four fruits per "plant" in the fall of 1960, and yet, only about a dozen seedlings could be found. Furthermore, the plants were known to have flowered at least in the preceding three years.

At Proud Lake bog (Oakland Co., Michigan, T2N, R8E, Sect. 21), about thirty miles north of Detroit, no seedlings were found in October of 1960 even though at least 300 plants had capsules full of seeds and were mature enough to have flowered in previous years. All the seeds used for the germination experiments in this study were collected at the Proud Lake bog in 1960.

These observations indicate that germination of seeds may be a critical aspect in the ecology of this plant. At the same time, delayed germination reports given by Moore (1874), Shreve (1906) and Macfarlane (1908), point to the possibility that dormancy is involved in the problem. This part of the study was therefore undertaken

to identify factors inducing germination under controlled conditions and to correlate these results with those operative in nature.

B. LITERATURE SURVEY

It is known that many seeds of wild plants, apparently mature, fail to germinate even when all their specific environmental requirements are met. This failure of seeds to sprout because of internal causes is called dormancy (Meyer and Anderson, 1959). This condition is considered to be of survival value to the species through unfavorable seasons. Crocker and Barton (1953) state that dormancy is typically a selective adaptation of plants in temperate regions which prevents seeds from germinating in the fall of the year when the seedlings would be quite vulnerable to severe weather conditions.

Dormancy may be due to many factors. A very important factor may be the impermeability of the seed coat to water. This condition prevents imbibition which is the mechanism that triggers all activity connected with germination. With absorption of water the seed coat becomes more permeable to gases, allowing oxygen to enter and carbon dioxide to leave the seed. The water activates enzymes within the seed, causing digestion of stored foods and their translocation to growing parts. As the embryo grows, the seed coat is ruptured permitting the emergence of the radicle. Without imbibition of water, none of these activities would take place.

A second common cause for dormancy may be the mechanical strength of the coat which may prevent the

expansion of the embryo (Amen 1963). Still another cause for dormancy connected with the seed coat may be the impermeability of this structure to the entry of oxygen and escape of carbon dioxide (Thornton 1943-45).

Methods of breaking dormancy inherent in the seed coat are scratching or cracking of the coat by mechanical means (Crocker and Barton 1953) or by removing some of the external tissues with strong acids (Steinbauer et al. 1954 and Burns 1959).

It is also known that minimal, optimal and maximal temperatures exist for the germination of seeds. In many plants germination occurs only within a very narrow range of temperature (Whitney 1942). Also, it is known that seeds of plants of the temperate regions require a long period of low temperature in a moistening agent before germination may take place (Toole et al. 1956). Stratification in moist peat at 5°C. to 10°C. for two or three months was found effective in breaking the dormancy of certain seeds (Barton 1930). Likewise, Cross (1931) and Steinbauer et al. (1954) found alternating temperatures effective in inducing germination.

Light and darkness, alone or in combination with temperature, are other important factors to be considered in the germination of seeds. Evenari (1956) gives numerous examples of both inhibition and enhancement of germination by light. Certain seeds are known to germi-

nate poorly when held continually in either light or dark, while other seeds respond most favorably to continuous irradiation (Toole et al. 1956) or continuous dark (Meyer and Anderson 1959). Likewise, Toole et al. (1962) found that continuous or repeated exposures of pine seeds to light shortened the period of stratification necessary for complete germination. Photoperiodism was considered by Koller et al. (1962) to be another factor influencing germination of seeds. They noted that some seeds may be "long day" and others "short-day" seeds and that this requirement may be correlated with temperature changes.

Another widespread mechanism of dormancy may be the occurrence in the seed of chemical inhibitors (Randolph et al. 1943 and Went 1957). Evenari (1949) listed many species of plants from the seeds of which germination inhibitors have been isolated. On the other hand, certain other chemicals, such as nitrates and nitrites, are known to be effective promoters of germination in certain seeds (Heit 1948).

C. MATERIALS AND METHODS

Seeds were collected during the first week of October, 1960, from Proud Lake bog. Maturity of the seeds was determined by observing that many of the capsules had dehisced and lost some of their seeds. As flowering of a pitcher plant population in a given bog is almost simultaneous, the seeds would probably never be more than a few days apart in maturity. The capsules were broken off the scapes and the seeds extracted by hand. Almost all of the capsules were heavily infested with the lepidopteran larvae of Endothenia habesana Wlk. and many of the seeds were partially eaten or the seed coat punctured. The seeds were sorted out under a dissecting microscope and only those that showed no injury were retained. The seeds were then stored in a refrigerator at 5°C. in a tightly stoppered glass jar, and removed as needed, for the various experiments.

Before being placed in a moistening agent prior to germination, the seeds were shaken in Arasan in order to prevent the growth of fungi. Then they were placed in one of the following light and temperature conditions and moistened with distilled water, bog water or 0.2% potassium nitrate.

1. At 22°C., in constant light
2. At 22°C., in constant darkness
3. At 22°C., in alternate light (8 hrs.) and darkness (16 hrs.)

4. At 33°C., in constant light
5. At 33°C., in constant darkness
6. At 33°C., in alternate light (8 hrs.) and darkness (16 hrs.)
7. In alternating light (at 22°C., 8 hrs.) and darkness (at 5°C., 16 hrs.)
8. In alternating light (at 33°C., 8 hrs.) and darkness (at 5°C., 16 hrs.)
9. At 28°C., in constant light
10. At 28°C., in constant darkness

A preliminary test indicated that germination took at least nine days. Therefore, counts of germinated seeds were started on the ninth day and were continued every other day throughout the test period. The seedlings were removed when fully germinated. As defined by Baldwin (1942), germination was considered to be "the development of the plantlet from the seed."

EXPERIMENT (A)

To determine the effect of moistening agents on germination of seeds under different light and temperature conditions and different pre-chilling periods.

The Arasan-coated seeds were spread on blotters in 30 Petri dishes in lots of 100 seeds each. Ten of these were moistened with distilled water, 10 with bog water and 10 with 0.2% potassium nitrate. All dishes were then kept in the refrigerator at 5°C. for two weeks.

Three other sets of seeds were similarly started. These were pre-chilled for one month, two months and three months, respectively. Again, 10 dishes of each were moistened with distilled water, 10 with bog water and 10 with 0.2% potassium nitrate.

Whenever necessary, during the pre-chilling as well as the germination period of this and the other series of experiments, bog water was added to the dishes initially moistened with bog water. Distilled water was used for seeds initially moistened with distilled water and also for those moistened with potassium nitrate. Both bog water and distilled water were brought to the same temperature as the dishes, when used.

The bog water used in these and the following experiments was obtained in all cases as follows: a centrally located spot containing typical bog flora was selected in Proud Lake bog. A little pressure on this spot formed a cavity which soon filled with water. The water was dipped in wide-mouth glass jars, subsequently filtered and stored in the refrigerator.

EXPERIMENT (B)

To determine the effect of sulphuric acid on germination of seeds under different light and temperature conditions, without pre-chilling.

Seeds were treated with concentrated sulphuric acid for one minute and spread in 30 Petri dishes over blotters. Ten of the dishes were moistened with distilled water, 10 with bog water and 10 with 0.2% potassium nitrate solution. Each dish was then placed in one of the ten experimental environmental conditions.

Another lot of seeds was treated with concentrated sulphuric acid for five minutes and similarly placed in the ten environmental conditions.

EXPERIMENT (C)

To determine the effect of the substrate on germination of seeds under different light and temperature conditions, with and without pre-chilling.

Arasan-coated seeds were spread over minced Sphagnum, moistened with bog water in 20 Petri dishes, each containing 100 seeds. Ten of these were pre-chilled for two weeks and ten were not. One of each series was then placed in each of the ten environmental conditions listed on page 127.

In a similar manner, seeds were spread over marl, moistened with distilled water, in 20 Petri dishes. Ten of these were pre-chilled and ten were not. They were then placed in the ten environmental conditions as above.

At the same time, seeds were spread in 10 Petri dishes over blotter moistened with distilled water. These were not pre-chilled.

All dishes were kept moist throughout the course of the experiment with their respective moistening agents.

EXPERIMENT (D)

To observe germination of seeds under natural light and temperature conditions in a bog.

Proud Lake bog was chosen for this experiment because of its relative proximity to Detroit and also because all seeds used for the present series of germination experiments were obtained at this bog.

In November of 1960, 800 seeds, untreated in any way, were spread in the bog in-between two quarter-inch layers of glass wool and covered with about half an inch of Sphagnum. The spot was staked and left undisturbed until the following spring.

D. RESULTS AND DISCUSSION

EXPERIMENT (A)

To determine the effect of moistening agents on germination of seeds under different light and temperature conditions and different pre-chilling periods.

The results of these experiments are summarized in Tables XVII to XXII. In the first column are given the moistening agents. In the second through the fifth columns, the percentage of germination is given first; then come in order, the number of days required for initial germination to take place, the number of days required for germination to reach its peak (this number is underlined), and finally, the last day at which germination took place.

1. At 22°C. in constant light

The results summarized in Table XVII indicate that at 22°C., in constant light, the moistening agent made no difference in the percentage or time of germination.

Three-months of pre-chilling produced the highest percent germination and the 2-week pre-chilling the lowest percent germination.

Table XVII. Germination of seeds, pre-chilled for 2 weeks, 1 month, 2 months and 3 months, moistened with distilled water, bog water and 0.2% potassium nitrate, and kept at 22°C. in constant light. 100 seeds used per dish.

	2-wk. prechills		1-mo. prechills		2-mo. prechills		3-mo. prechills	
Dist. water	22%	9-12-24	50%	9-12-27	50%	9-12-18	62%	9-12-24
Bog water	19	9-12-18	43	9-12-24	44	9-12-21	58	9-12-18
KNO ₃	21	9-12-24	50	9-12-21	50	6- 2-21	59	9-12-24
Average	21%		48%		58%		60%	

2. At 22°C. in constant darkness

The results summarized in Table XVIII show that at 22°C. in continuous darkness, the moistening agent, potassium nitrate, increased the percentage of germination in all except the 2-week pre-chills. The 3-month pre-chilled seeds gave the best germination results and the 2-month pre-chills the next best. The 1-month pre-chilling resulted in considerably less germination while the 2-week pre-chills gave the poorest results.

Table XVIII. Germination of S. purpurea seeds, pre-chilled for 2 weeks, 1 month, 2 months and 3 months, moistened with distilled water, bog water or 0.2% potassium nitrate, and kept at 22°C. in constant darkness. 100 seeds used per dish.

	2-wk. prechills		1-mo. prechills		2-mo. prechills		3-mo. prechills	
Dist. water	1%	18	6%	12-15-21	22%	12-12-24	15%	9-12-15
Bog Water	6	21	8	12-15-18	23	12-12-21	39	9-12-24
KNO ₃	2	15-21	19	12-12-24	50	12-12-24	47	12-12-24
Average	3%		11%		32%		44%	

3. At 22°C. in alternate light (8 hrs.)
and darkness (16 hrs.)

The results summarized in Table XIX show that at 22°C., in alternate light (8 hrs.) and darkness (16 hrs.), the moistening agent, potassium nitrate, gave the best germination in all cases. Two-month and 3-month pre-chilling gave equally good germination, and 2-week pre-chilling gave the poorest results.

It will be noted that the 3-month pre-chilled seeds produced on the average the same percent germination as those in constant darkness (Table XVIII).

Table XIX. Germination of S. purpurea seeds, pre-chilled for 2 weeks, 1 month, 2 months and 3 months, and moistened with distilled water, bog water or 0.2% potassium nitrate, and kept at 22°C. in alternate light (8 hrs.) and darkness (16 hrs.). 100 seeds used per dish.

	2-wk. prechills	1-mo. prechills	2-mo. prechills	3-mo. prechills
Dist. water	1% 21	5% 12-12-18	39% 9-12-18	30% 9-12-24
Bog water	2 15-18	10 12-12-18	44 9-12-21	47 9-12-21
KNO ₃	5 12-18	18 12-12-21	56 9-12-21	55 9-12-24
Average	3%	11%	46%	44%

4. At 33°C., in constant light
5. At 33°C., in constant darkness
6. At 33°C., in alternate light (8 hrs.)
and darkness (16 hrs.)

In the environmental conditions No. 4, 5 and 6, listed above, in all pre-chilling series, the primary root broke through the coat in many seeds, but soon turned reddish and shriveled up. In certain other seeds germination progressed up to the partial emergence of the cotyledons, but the entire plantlet was soft and limp, remained flat on the blotter and disintegrated before completion of the germination process. It was therefore concluded that a temperature of 33°C., whether in constant light, in constant darkness or in alternate light and darkness, was too high to permit germination of Sarracenia purpurea seeds. This phase of the experiments in this as well as in the following series was therefore abandoned.

7. In alternating light (at 22°C., 8 hrs.)
and darkness (at 5°C., 16 hrs.)

Results shown in Table XX below indicate that in alternate light and darkness with alternating temperatures of 22°C. and 5°C., all pre-chilled seeds in all moistening agents gave consistently good results. This is extremely interesting when one considers the fact that in nature these are probably the conditions most closely occurring for germination of seeds of this plant.

Table XX. Germination of S. purpurea seeds, pre-chilled for 2 weeks, 1 month, 2 months and 3 months, moistened in distilled water, bog water or 0.2% potassium nitrate, kept in alternating light (at 22°C., 8 hrs.) and darkness (at 5°C., 16 hrs.). 100 seeds used per dish.

	2-wk. prechills	1-mo. prechills	2-mo. prechills	3-mo. prechills
Dist. water	55% 24-33-48	56% 24-36-48	59% 18-24-39	57% 21-27-39
Bog water	54 24-39-51	64 24-30-54	48 21-36-42	60 18-24-39
KNO ₃	58 24-36-48	56 24-30-48	54 18-21-42	66 15-24-39
Average	56%	59%	54%	61%

8. In alternating light (at 33°C., 8 hrs.)
and darkness (at 5°C., 16 hrs.)

As stated in Experiments No. 4, 5 and 6, on page 136, 33°C. was found to be too high to permit germination of Sarracenia purpurea seeds.

9. At 28°C., in constant light

At 28°C., in constant light, all pre-chilled seeds gave excellent results in a shorter germination period than in Experiment No. 7. The 1-month, 2-month and 3-month pre-chilled seeds gave almost equally good germination percentages, the 2-week pre-chills gave the smallest number.

All moistening agents gave about the same results (Table XXI).

A comparison of the figures in Tables XVII, p. 133, to XXI indicates that in constant light seeds germinate equally well at 22°C. and 28°C. in all except the 2-week pre-chills. The 2-week pre-chills had much less germination at 22°C. (21%) than at 28°C. (43%). Type of moistening agent made no appreciable difference in the germination results at these two temperatures under constant light.

Table XXI. Germination of S. purpurea seeds pre-chilled for 2 weeks, 1 month, 2 months and 3 months, moistened with distilled water, bog water of 0.2% potassium nitrate, and kept at 28°C., in constant light. 100 seeds used per dish.

	2-wk. prechills		1-mo. prechills		2-mo. prechills		3-mo. prechills	
Dist. water	42%	12-12-24	56%	9-15-24	60%	9-15-24	72%	9-15-18
Bog water	42	12-12-27	71	9-15-21	46	9-12-24	45	9- 9-18
KNO ₃	46	12-12-24	55	9-12-18	68	6- 9-24	60	9- 9-18
Average	43%		61%		58%		59%	

10. At 28°C., in constant darkness.

As shown in Table XXII, at 28°C., in continuous darkness, germination percentages were considerably lower than in constant light (Table XXI). Apparently light has a stimulating effect on the dormant seeds of S. purpurea.

The 3-month pre-chilled seeds gave the best and the 2-week pre-chills the poorest results. The moistening agent, potassium nitrate, gave the best results in practically all cases.

A comparison of the results shown in Table XVIII, p. 134, with those of Table XXII, will indicate that in constant darkness, the 2-month and 3-month pre-chilled seeds gave about the same results, both at 22°C., and 28°C. The 2-week and 1-month pre-chills gave definitely better results at the higher temperature. Potassium nitrate increased the percentage of germination in most cases, indicating that in the absence of light this chemical may have a stimulating effect on seeds.

Table XXII. Germination of S. purpurea seeds pre-chilled for 2 weeks, 1 month, 2 months and 3 months, moistened with distilled water, bog water or 0.2% potassium nitrate, and kept at 28°C., in constant darkness. 100 seeds used per dish.

	2-wk. prechills		1-mo. prechills		2-mo. prechills		3-mo. prechills	
Dist. water	15%	12-12-24	25%	12-15-30	28%	12-15-15	65%	12-15-18
Bog water	10	12-12-21	31	12-15-30	23	12-15-21	27	12-15-18
KNO ₃	20	12-12-21	41	12-15-30	48	12-15-24	41	12-15-18
Average	15%		32%		33%		44%	

EXPERIMENT (B)

To determine the effect of sulphuric acid on germination of seeds under different light and temperature conditions, without pre-chilling.

Seeds treated with concentrated sulphuric acid for one minute or five minutes, moistened by all three moistening agents and placed in all experimental environmental conditions, failed to germinate. It was concluded that the embryo had been injured by the acid.

EXPERIMENT (C)

To determine the effect of the substrate on germination of seeds under different light and temperature conditions with and without pre-chilling.

The results of the various experiments in this series are summarized in Table XXIII below. It will be seen that the 2-week pre-chills in Sphagnum and marl (2nd and 4th columns) gave about the same results as the 2-week pre-chills over blotters obtained in Experiment A (Tables XVII - XXII). This indicates that the substrate made no appreciable difference in the rate or speed of germination.

In the absence of pre-chilling, there was no germination except in alternate light and darkness at 22°C., (8 hrs.) and 5°C., (16 hrs.), respectively. However, germination was considerably delayed under these conditions, requiring at least 39 days as against

24 days (Table XX, p. 137) or 18-27 days (Table XXIII) for 2-week pre-chills. The percentage of germination, too, was much lower, being less than one-half of the comparable figures (column 1, Table XX; columns 2 and 4, Table XXIII).

Table XXIII. Germination of *S. purpurea* seeds over Sphagnum, marl or blotter, moistened with distilled water, and placed in all environmental conditions. 100 seeds used per dish.

	On <u>Sphagnum</u>		On <u>Sphagnum</u> Prechilled 2-wk.		On Marl Prechilled 2-wk.		On Blotter	
1. 22°C. const. light	0		24% 9-21		0		15% 9-27	0
2. 22°C. const. dark.	0		1		0		2 15	0
3. 22°C. alt. lt/dk	0		3		0		2 12-18	0
7. alt. lt/dk 22°C/5°C	20% 39-69		50% 27- <u>33</u> -48		29% 39- <u>45</u> -66		61% 18- <u>30</u> -57	7% 45-72
9. 28°C. const. light	1% 24		47 12- <u>12</u> -21		1 36		57 12- <u>12</u> -36	0
10. 28°C. const. dark.	0		18 12-21		0		13 12-21	0

EXPERIMENT (D)

To observe germination of seeds under natural light and temperature conditions in a bog.

In May of 1961, an examination of the area at Proud Lake where 800 seeds had been placed the previous November, disclosed only one seedling pushing up through the glass wool. There was no trace left by the remaining seeds. The seedling survived the summer months producing several intensely red-colored small leaves and appeared to be well established. Then, in the fall, it could no longer be found. It is presumed that it was pulled up by some one, as it was not in a location where any one could have stepped on it.

Germination of one seed out of 800 indicates a very high mortality rate. This fact, coupled with the following observations made in this study, may, at least partially answer the question as to why certain bogs contain seedlings and others do not.

The first and most obvious reason for lack of seedlings is, of course, the lack of seeds. In all the bogs, except Rose Lake, the seeds were almost completely chewed up by the phytophagous larva of Endothenia habesana Wlk. during the past two years that these bogs have been under observation. It is not inconceivable to assume that most of the seeds in some bogs are thus destroyed. Also, it was observed that presence of mature plants does not

necessarily insure seed production. In early May of 1963 a number of flower buds had been staked out for pollination experiments at Rose Lake and Bridge Lake. A sudden drop of temperature to 27°F. on May 21st completely wiped out the Rose Lake crop of buds and about 95% of those at Bridge Lake. This may explain why many observers in the past have recorded that Sarracenia purpurea does not flower every year.

It was also observed that seeds, whether pre-chilled or not, remained afloat in distilled or bog water. Those that were not pre-chilled did not germinate and soon became moldy. Those that were pre-chilled germinated while remaining afloat. Since many bogs are subject to periodic flooding, this characteristic of seeds and seedlings to remain afloat may of course be of tremendous advantage to the plant. Seed and seedling may be carried away by the water and may thus find favorable locations for establishment. Or, on the other hand, they may be taken out into open water with no chance of ever reaching a suitable substrate for ecesis. Also, floating seeds, whether in bog or open water, would be exposed to the elements. It will be recalled that 33°C. was not found to be conducive to germination of these seeds. If the seeds remained exposed during the fall and winter months, they would of course be subject to freezing, which too, might prevent germination. Of one hundred seeds, placed in the usual

manner over moistened paper in a Petri dish, none survived the -5°C . temperature of the freezer compartment of a refrigerator.

The experimental results listed in Tables XVII to XXIV are summarized in Table XXV.

Table XXIV. Effect of substrate on germination of *S. purpurea* seeds, moistened with distilled water, pre-chilled for 2 weeks, placed in all experimental environmental conditions. 100 seeds used per dish.

Compiled from Tables XVII to XXIII.

	On <u>Sphagnum</u>	On Marl	On Blotter
From Table XXIII			
1. 22°C. constant light	24%	15%	22% (Table XVII)
2. 22°C. constant darkness	1	2	1 (Table XVIII)
3. 22°C. alternate light/dark.	3	2	1 (Table XIX)
7. Alternate light/dark. 22°C./5°C.	50	61	55 (Table XX)
9. 28°C. constant light	47	57	42 (Table XXI)
10. 28°C. constant darkness	18	13	15 (Table XXII)

E. SUMMARY AND CONCLUSIONS

1. The dormancy of a majority of seeds of Sarracenia purpurea was broken by pre-chilling to 5°C. In most cases the 2-week pre-chilling produced the poorest germination results, the 1-month somewhat higher results and the 2-month and 3-month pre-chilling the best germination results.
2. Treatment by sulphuric acid to break the dormancy of the seeds resulted in injury to the embryo. Consequently, there was no germination in such seeds.
3. The substrate, whether Sphagnum, marl or blotter, had no appreciable effect in the germination of seeds.
4. Peak germination in the shortest possible time (9-15 days) was achieved in constant light at 28°C., with either 1-month, 2-month or 3-month pre-chilled seeds, in any moistening agent.
5. At 22°C., 2-month and 3-month pre-chilled seeds germinated equally well in total darkness and alternate light and darkness. At 28°C., there was somewhat higher germination in constant light than in constant darkness.
6. In the absence of pre-chilling, there was practically no germination over any substrate, with any moistening agent, except in alternate light

and darkness in alternating temperatures (light at 22°C., 8 hrs. and darkness at 5°C., 16 hrs.), in which case germination required at least 39 days. These results substantiate Macfarlane's report that in the south Sarracenia purpurea seeds germinate in three to five weeks after ripening, at least to the extent that pre-chilling is not necessarily a prerequisite for germination of these seeds.

7. With as little as a 2-week pre-chilling period, under the same temperature and light conditions as in No. 6 above, germination time was cut down to 24 days, and germination rate more than doubled.
8. Under the same temperature and light conditions, as in No. 6 above, namely light at 22°C., 8 hrs. and darkness at 5°C., 16 hrs., all pre-chills gave consistently good results in all moistening agents. These experimental conditions roughly approximate natural conditions in a northern bog in the spring and support Macfarlane's and Shreve's findings that in the north Sarracenia purpurea seeds germinate in the spring.
9. Lack or scarcity of seedlings in a bog may be due to any number of factors such as: frost damage to flower buds in early spring, unavail-

ability of pollinating insects during the very short flowering period of this plant, attack by the larva of Endothenia habesana of ripening seeds, the floatability of seeds which may carry them into open water or which may subject them to extreme temperatures, and unavailability of sites suitable for germination and ecesis.

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APPENDIX I. Fixation and Staining Technique
(See text, p. 4)

One to two-day-old vigorously germinating seedlings were selected. These were plunged in a fixative of three parts of absolute alcohol to one part of glacial acetic acid. After six hours in this fixative, the seedlings were removed and hydrolyzed in 2.7N hydrochloric acid for 15 minutes in a 60°C. oven. The seedlings were then placed in Foelgen's solution (Schiff's reagent) for 20 minutes to stain the DNA of the chromosomes. The meristem of the primary root tip was now removed, placed on a slide and macerated with a glass rod, separating the cells from each other. At this time a drop or two of 45% acetic acid was added to wash out excess Foelgen's solution. Pressure over a cover slip further separated the cells of the meristem. The slide was then soaked in tertiary butyl alcohol and mounted in diaphane. An unreduced chromosome number of 26 was counted in cells at the metaphase stage.

APPENDIX II. Application of the t-tests*
(See text, p. 109)

$$P_1 = \frac{6}{21} = .29 \qquad P_2 = \frac{30}{31} = .97$$

$$\sigma_{P_1} = \sqrt{\frac{\frac{6}{21} \times \frac{15}{21}}{21}} \qquad P_2 = \sqrt{\frac{\frac{30}{31} \times \frac{1}{31}}{31}}$$

$$= \sqrt{.0097} \qquad = \sqrt{.001}$$

$$\sigma_{(P_2 - P_1)} = \sqrt{(\sigma_{P_1})^2 + (\sigma_{P_2})^2}$$

$$= \sqrt{.0097 + .0010} = .1034$$

$$t_1 = \frac{P_2 - P_1}{\sigma_{(P_2 - P_1)}} = \frac{.97 - .29}{.1034} = \frac{.68}{.1034} = 6.57$$

$$P_3 = \frac{18}{28} = .64$$

$$\sigma_{P_3} = \sqrt{\frac{\frac{18}{28} \times \frac{10}{28}}{28}}$$

$$= \sqrt{.0081}$$

$$\sigma_{(P_2 - P_3)} = \sqrt{(\sigma_{P_3})^2 + (\sigma_{P_2})^2} = \sqrt{.0081 + .0010} = .0954$$

$$t_2 = \frac{P_2 - P_3}{\sigma_{(P_2 - P_3)}} = \frac{.97 - .68}{.0954} = \frac{.31}{.0954} = 3.26$$

First, data obtained from unassisted self-pollinated flowers were compared with those resulting from hand-cross-pollinated flowers. The table value of t at 50 degrees of freedom at the 5% level was found to be 2.011. This is much smaller than the observed value of 6.57. Therefore, the probability that the results are due to chance was less than .005. Similarly, the data resulting from hand-self-pollinated flowers were

APPENDIX II. (Cont'd)

compared with those of hand-cross-pollinated flowers. The table value of t , at the 5% level, was found to be 2.011. This was again smaller than the observed value of 3.26. Therefore, the probability that the results were due to chance was less than .01.

* Dr. W. D. Baten, Professor of Statistics of Michigan State University, helped me with the t -tests.