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THE ORIGINS, SPREAD, AND CONSOLIDATION OF A FLOATING BOG IN HARVARD POND, PETERSHAM, MASSACHUSETTS[1]

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Abstract. The mode of development of an extensive floating bog (400 m by 400 m) at the north end of Harvard Pond, an artificial lake, was studied by careful examination and local dissection of the bog mat within a 32-m by 16-m plot. Excavations were also made at the bog margin. The origins, spread, and consolidation of the floating mat are largely explained by the growth characteristics of one ericaceous shrub, *Chamaedaphne calyculata* (L.) var. *angustifolia* (Ait.) Rehd. A wetland forest was cut about 1830, and *Chamaedaphne* first invaded the tree stumps between 1830 and 1890 (when they were located in a sedge meadow). Harvard Pond was formed about 1890, and the floating mat has developed between 1890 and 1968 (by the lateral spread of *Chamaedaphne* across the water surface to occupy the intervening spaces between stumps). Bog-advance rates were estimated from photographs and from annual growth increments for the shrub. Expansion appears to have been rapid (up to 6.3 cm/year or 2.5 inches/year).

INTRODUCTION

Zones of encroaching vegetation about the margins of a lake have long been viewed by ecologists as classical examples of vegetational succession (Transeau 1903, Dachnowski 1912, Cooper 1913, Chouard and Prat 1929, Conway 1949, and many others). An important step in this succession is thought to be the development of a bog, initiated as a floating mat on the lake surface. This mat is often consolidated by peat accumulation, largely from the decay of sphagnum and heath species. It is finally invaded by forest (Gates 1942, Conway 1949, Dansereau and Segadas-Vianna 1952, Shelford 1963, Ketchledge 1964, Moizuk and Livingston 1966, Daubenmire 1968). Unfortunately, descriptions of succession are often derived only from observations of vegetational "zones" at one point in time: space is substituted for time in the description. Too easily, these zones can be linked to form plausible hypotheses of development. We believe insufficient emphasis has been placed on tests of the proposed hypotheses and that detailed and critical examinations of bog development are needed.

We had at our disposal an area of floating bog formed around an artificial lake—Harvard Pond, Petersham, Massachusetts, the history of which can be traced from historical records. This paper is devoted to our findings about the origins, spread, and consolidation of the floating mat bordering the pond.

Where no authority is cited, taxonomic nomenclature is after Fernald (1950).

STUDY AREA

Harvard Pond is located at 42°30′N, 72°12′W at an elevation of approximately 252 m (756 ft). It is situated in a valley of pre-glacial origin, in the Tom Swamp Tract of the Harvard University Forest.

The bedrock is acidic granite, gneiss, and schist. The valley floor is lined with outwash and there are gravel terraces along the slopes. The valley is oriented north-south, is about 2.5 miles long, and drains in both directions from the center. In the central part of the valley, a forest dominated by *Picea mariana* stands on peat up to 8 m deep. From these organic sediments and the clay and silt beneath, a post-glacial vegetational history has been worked out in some detail (Davis 1958). Dams, placed at the north and south ends of the valley, have formed lakes; the lake at the south end is Harvard Pond.

The climate of the Petersham area is continental (Rasche 1958). The mean January temperature is —6°C (21°F) and the mean July temperature 21°C (69°F). The mean annual precipitation for the area is 102 cm (40 inches). The microclimate of Harvard Pond is somewhat different from that of the surrounding upland. Cold air drainage into the valley results in a shorter growing season and lower night temperatures. (For the year August 1947 through July 1948, Rasche recorded 191 days at or below 32°F for the study site and 163 such days for the Harvard Forest Headquarters at 360 m elevation.) In summer the day temperatures tend to be higher than in the surrounding uplands. (For the same period, 98 days at or above 77°F were recorded for the study site and 89 such days at the Harvard Forest Headquarters.)

The vegetation zones in and about the pond are outlined in Fig. 1. The deepest part of the lake at the southern end is relatively open. Proceed-

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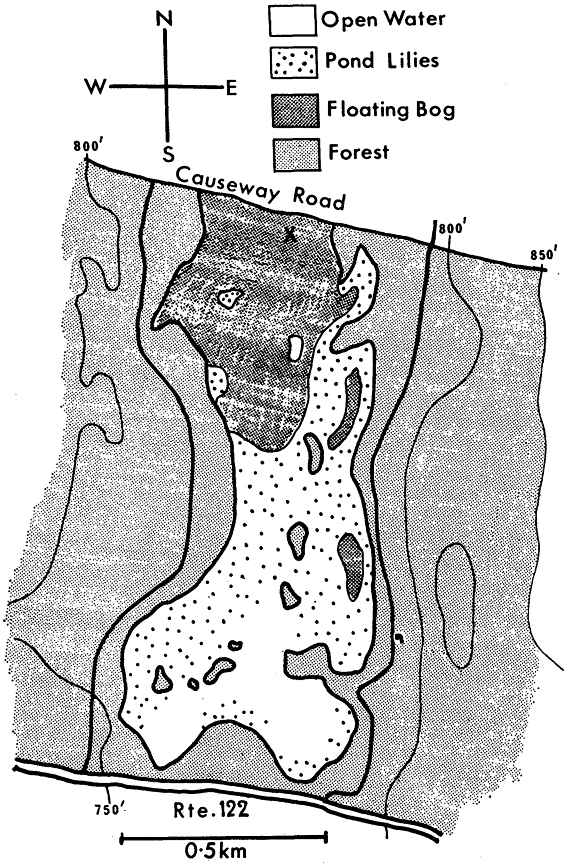

FIG. 1. The study area in Harvard Pond. Data are chiefly from the floating bog at the north end of the lake. The bog mat was dissected in a study plot located at X.

ing northwards, the water surface is increasingly covered with vegetation. Obvious aquatic species are *Nymphaea odorata, Nuphar variegatum,* and *Brasenia schreberi. Utricularia minor* and *Potamogeton* spp. are also abundant. Dense fields of these species are interspersed with patches of mud and plant remains floating at the surface of the lake.

The bog at the north end of the lake—the study area—is a large and therefore remarkable floating mat (about 400 m by 400 m) bounded on the north by a causeway crossing the peat-filled valley. Its appearance is largely determined by one shrub, *Chamaedaphne calyculata* var. *angustifolia* (leatherleaf, cassandra), which produces a dense cover over practically the entire bog surface. Other shrub species are scattered throughout the leatherleaf matrix. Common shrubs are *Alnus rugosa, Pyrus melanocarpa, Kalmia angustifolia, Myrica gale, Rhododendron canadense,* and *Vaccinium corymbosum.* At the bog margin *Decodon verticillatus* is locally abundant. Within the bog and beneath the shrub crown is a dense, undulating mat of *Sphagnum* which includes *S. capillaceum* (Weiss) Schrank, *S. fuscum* (Schimp.) Klinggr., *S. papillosum* Lindb., and *S. recurvum* P.-B. *Sphagnum cuspidatum* Hoffm. floats in water pools within the mat. Although elastic, the surface of the bog supports human weight. Locally, it is sufficiently firm to support the weight of trees such as *Larix laricina* and *Picea mariana.*

Water level, apparently an important factor in the distribution of vegetation in the pond, is not static. By the fall of 1968 the water level had dropped 30 cm below the peak level of spring. A seasonal drop in water level is observed every year, although the 1968 value may be extreme since the spring and early summer were unusually wet while the summer and fall were unusually dry.

Enduring water-level changes have occurred in the pond's history. Part of the area now covered with water was a wet hay meadow in the early 1880's (Benninghoff 1947). By 1887 a dam at the south end of the meadow produced a lake having the same shape as the present one (USGS map based on 1887 survey). The water level was raised in 1939 to accommodate and preserve logs salvaged after the 1938 hurricane. These logs were almost all removed by 1946. Beaver have periodically altered the lake level. At present, most of the lake is less than 1 m deep with the deepest portions to 3 m.

METHODS

The material

Since *Chamaedaphne calyculata* is everywhere present in the bog and at its margins and forms its visual character, it seemed that the nature of mat development might be determined from a study of the growth behavior of this species. This approach proved fruitful and the nucleus of our analyses are based on the behavior of *Chamaedaphne calyculata.*

Chamaedaphne calyculata is a circumpolar ericad, commonly represented in North America (including our study area) by var. *angustifolia* (Ait.) Rehd. This form extends from Alaska to Newfoundland, its southernmost range dipping southeast across the United States from northern Illinois to Georgia. *Chamaedaphne* fits into Pease's (1917) category of shrubs that retain their leaves until next season's leaves have matured. Leaf loss is not pronounced at any one time (Lems 1956), but leaf age rarely exceeds 1 year. Because the shrub retains its leaves throughout the winter, it may best be regarded as an evergreen (Lems 1956). Diverse studies have been made on subjects that relate to the morphology and growth of the shrub (Judd 1966, Sorsa 1966, Dana 1967). Lems (1956) studied the correlation between vigor (vegetative growth) and vitality (seed production) in young shoots which he tentatively related to site in southern Michigan.

Chamaedaphne has been described as an important component of bogs in northern North America (Gates 1942, Conway 1949, Segadas-Vianna 1955), sometimes dominating thousands of acres and often in pure stands. It is usually mentioned in text examples of succession (Shelford 1963, Daubenmire 1968) and is always described as an invader of the established bog mat (Gates 1942, Conway 1949, Dansereau and Segadas-Vianna 1952, and others). Segadas-Vianna (1955) calls it a constructive, conserving, and consolidating species of the sphagnum-heath association (sensu Braun-Blanquet 1932).

Procedures

The methods, which can be placed in four main categories, are outlined below. For continuity, the details of each procedure are given with the appropriate results.

Mat origin.—Patterns of shrub growth and excavations within the bog were used to determine the origins of the existing mat. Shrub growth about the lake margin was examined to indicate the early stages of mat development.

Mat advance.—Morphological and anatomical methods were used to estimate ages, growth rates, and patterns of advance for stems excavated from the mat margin.

Mat consolidation and maintenance.—The age structure of the stem populations in the body of the community was studied by harvesting stems inserted in the basal moss carpet and estimating age by counts of annual length increments. Deductions about live stem turnover were made from these data.

Historical record.—To assess the accuracy of conclusions drawn by other means and to provide additional data, an historic synopsis was made for the site. Data were derived from old photographs and maps as well as the researches of others.

RESULTS

Origin of the Chamaedaphne *mat*

The *Chamaedaphne* mat forms a continuous layer of vegetation in which separate plants cannot be distinguished. However, this sheet of vegetation must have originated from one or more plants that initially invaded the area. To locate the positions of the original plants, stem orientations were mapped to see if they reflected directions of growth. A study plot approximately 32 by 16 m (100 by 50 ft) in area aligned east-west was established (X in Fig. 1). It incorporated a small area of open water in its northeast corner. The boundaries of the plot were marked with string and subdivided into a grid of squares approximately 3 m (10 ft) on a side. Then each square was traversed and stem directions visually noted and recorded with arrows on a map. A stem-direction map for the plot was produced by laying out the data for adjacent squares. The diagram was simplified and reduced in scale by drawing a smaller number of arrows to summarize the patterns for visual presentation. Several levels of detail were tried. All levels produced the same basic patterns. Hence, we believe other observers would have summarized our data to a pattern similar in major respects, and differing only in the precise locations of the arrows.

Stems radiate in all directions from many centers (Fig. 2A). The pattern is consistent with the view that the *Chamaedaphne* sward is formed by the confluence of individual plants from many points of origin.

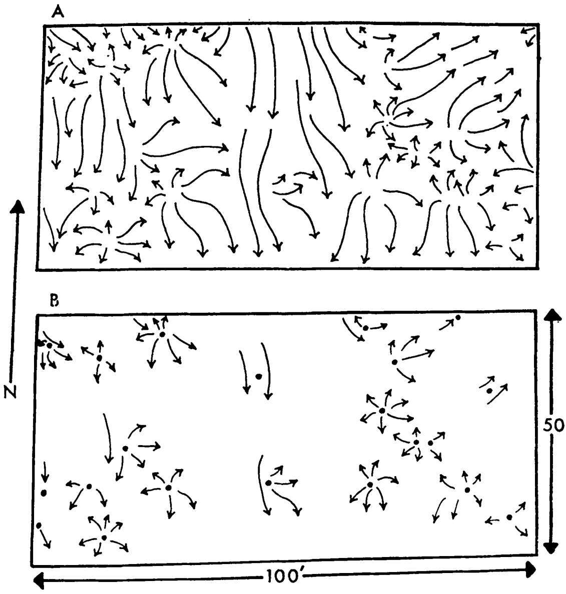

FIG. 2. The origins of the floating bog in Harvard Pond. A: Arrows illustrate the orientations of *Chamaedaphne calyculata* stems within the plot at X (Fig. 1). B: Dots are the locations of tree stumps on the lake bed beneath the plot. Directions of *Chamaedaphne* stems are superimposed on this diagram to show the locational correspondence between shrub centers and stumps beneath.

Three centers in the western half of the plot were excavated. First, a metal rod was probed into each center to locate solid objects beneath. These were encountered in all cases and excavation showed them to be tree stumps (Fig. 3). Fragments of wood taken from the outside of these stumps possessed a sheath of fine roots as might be expected if shrub vegetation had initially become established there.

Probes were made into all other centers and a

FIG. 3. An excavated tree stump beneath the origin of a *Chamaedaphne calyculata* shrub in the study plot at X (Fig. 1). The stump projected 8 cm (3 inches) above the water level (September 1968). The shrubs on the excavated mound about the stump are *Chamaedaphne calyculata* and *Myrica gale*.

solid object was found beneath each one. In addition, probes were made on lines spaced 1.5 m apart from north to south across the plot. Five probes spaced at 3-m intervals were made along each line. In this manner five more solid objects were located beneath the mat. Because (1) two stumps were raised from the open water in the northeast corner of the plot; (2) all three excavated centers were above stumps; and (3) the distribution of solid objects in the plot (Fig. 2B) is reminiscent of the distribution of tree stems in a forest, we propose that these solid objects are all stumps. To indicate the close relationship between *Chamaedaphne* stem patterns and stump locations, arrows representing shrub-stem orientations are superimposed on Fig. 2B in the immediate location of the stumps.

Since a stump origin for the *Chamaedaphne* sward seemed plausible, we assembled more detailed information on the invasion and growth of shrubs on stumps projecting above the water along the east shore of the lake in the fall of 1968. Only stumps with an exposed surface of 15 cm in diameter or more were included in the tally. (Stumps with an exposed surface smaller than this offer little purchase for woody plants). The survey was commenced at the north end of the lake, and all stumps along the eastern shore were examined until we judged (arbitrarily) that the sample was adequate to estimate the woody species to be found on stumps and the approximate frequency of occurrence for the common species. Fifty-seven stumps were examined. The area sampled was a strip about 183 m by 46 m (200 yards by 50 yards).

Seventy per cent (40 in 57) of the stumps had some woody vegetation growing on them. Eleven of the 17 stumps without vegetation projected less than 15 cm above the water level at the time of measurement. Since the lake level drops more than 15 cm each season and since most plants growing on stumps were anchored 30 cm or more above the water, immersion in spring and early summer may be sufficient to make these lesser stumps unsuitable for shrub establishment. Woody species growing on stumps were *Chamaedaphne calyculata, Myrica gale, Kalmia angustifolia, Apocynum androsaemifolium, Vaccinium corymbosum, Cephalanthus occidentalis, Spiraea latifolia,* and *Betula populifolia.* The first three species were most frequently recorded. *Chamaedaphne calyculata* occupied 98% (39 of the 40) of vegetated stumps. *Myrica gale* occupied 63% (25 in 40) and *Kalmia angustifolia* occupied 25% (10 in 40). All the other species together occurred on only 13% (5 in 40) of the vegetated stumps.

Chamaedaphne calyculata plants found on stumps in the water near the margin of the lake vary in size from seedlings less than 2 cm high to shrubs 45–61 cm (2 ft) tall and densely covering the stump; stump invasion is actively continuing at this time. Small seedlings are either single stemmed shoots or have a number of branches at the surface of the substrate. Larger plants (15 cm or more high) are abundantly branched close to the substrate. This abundantly branching habit is necessary if the plant is to spread radially from the stump on which it has become established.

Roots are located only at the rotting surface of the stumps, often in a moss carpet that coats the outer surface. The root system is not extensive. It consists of a mass of fibrous roots, their extremities usually no more than 30 cm distant from the stem base in any direction. The entire root system can be peeled from the stump surface largely intact. On one stump a cap of organic material had formed. This cap contained most of the roots of a shrub growing on the stump. The cap was easily separated from the stump by tipping the plant. It seems that a stump may serve only as a point of initial purchase for the shrub and has a limited role as a growth medium.

Plot excavations and the lake margin stump survey both suggest a stump origin for the *Chamaedaphne* sward.

Mat advance

The spread of *Chamaedaphne calyculata* from the initial points of invasion must depend on the growth habit of the plant. We therefore outline the morphological character of the shrub.

Shoot growth.—The current increment of the shoot, produced in spring, remains unbranched in the first year. In the curved apical region of this shoot flowers are formed in axillary positions; vegetative growth the next year takes place from the buds of the middle to lower portions of the increment. The apical segment, short circuited in this sympodial growth, withers and dies. Usually only one or two of the branches produced from the middle and lower buds of an increment survive for more than 3 or 4 years. A single length of stem may be formed from a number of branches borne laterally one upon another (Fig. 4). Lateral branches arise at an angle to the parent shoot and because these angles persist, annual increments are readily recognized as the relatively straight stems between the "knees" created by growth from a lateral bud (Fig. 4). Hence, the age of any part of the shoot system is readily determined by counting the number of growth increments that separate it from the apex of growth.

Not all branches are formed on the current increment. As the stems within the mat increase in age, their main axes become depressed horizontally. Eventually each stem is buried by leaf litter and *Sphagnum*. Epicormic shoots are often produced on depressed stems close to the substrate. The parent shoots die, and the origin of the epicormic shoot is obscured by the basal mat: an apparently independent plant is formed. The growth of the epicormic shoot is often very vigorous in the first year and, as no flowers are formed, regrowth takes place from the apical bud. However, the new shoot assumes the growth pattern of the parent increment in subsequent years and ensures the continued occupation of the terrain vacated by the dead parent branch.

Root growth.—When the stems become buried numerous adventitious roots are formed. These arise at the nodes, four or more occupying each position. The roots are of small diameter and length and branch repeatedly to form a dense brown tangle about the stem.

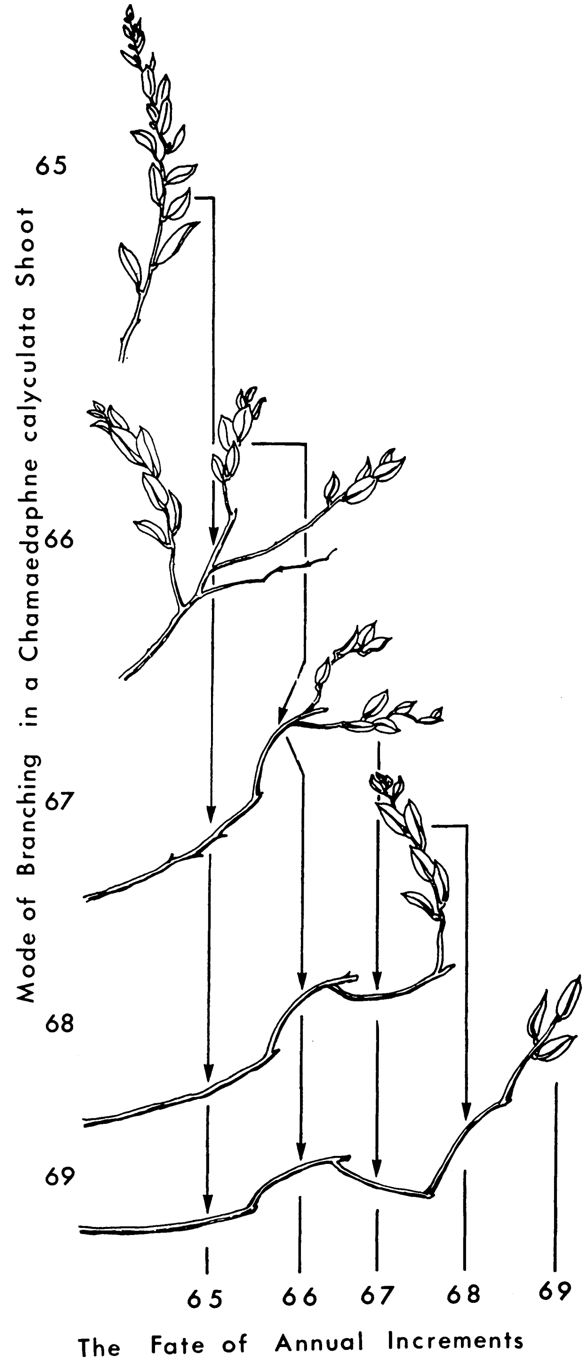

FIG. 4. The pattern of shoot growth in *Chamaedaphne calyculata* traced over 5 years: a sequence of lateral branching by which a shrub spreads from its origin (details in text).

The mat margin.—The mat margin is a mass of intertwining stems. As examples of their growth, two shoot systems were excavated from the edge of the mat (Fig. 5). Because of excavation difficulties only 3-m (10-ft) lengths could be dissected from the mass of other material in the same zone. The excavated shoots had nu-

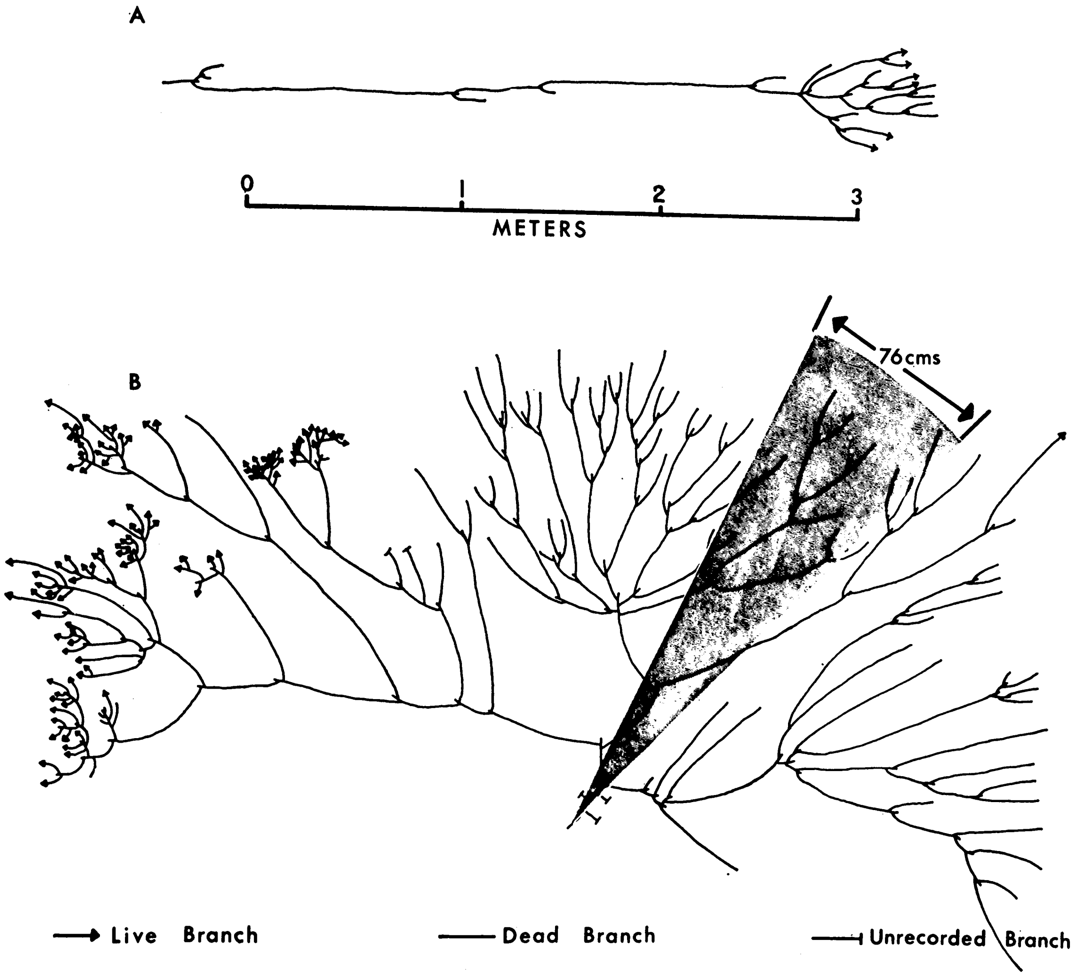

FIG. 5. Two *Chamaedaphne calyculata* shoot systems excavated from the margin of Harvard Pond Bog. A *Chamaedaphne* shoot system may have few (A) or many (B) branches. In B, the entire shoot system was beneath a surface area equivalent to the dark slice. Live branches were above the water surface, dead branches below it.

merous adventitious roots along the greater part of their horizontal length, but these are not indicated in the figures. Both excavated stems (Fig. 5A and B) had similar diameters over their 3-m length. Each axis was never more than 8 mm in diameter even at the end closest to the point of origin (proximal end). One of the excavated stems (Fig. 5A) had few branches, but the other (Fig. 5B) had branched repeatedly. The branches were spread apart for graphic purposes although they were originally included beneath a small surface area in the bog (represented by the hatched sector of the figure). About one-third of them were alive at the time of excavation. Much of the elaborately branched system was dead and below the surface of the water. Hence each branch often has but a short life and the two stems indicate that considerable variation in branch proliferation can occur.

The rate of advance of the bog margin can be measured from the excavated stems. Annual growth increments for the two stems illustrated in Fig. 5 were recorded in different length classes. The modal pattern is closely similar for both shoot systems. For each, 67% of the annual growth increments are between 5 and 15 cm (Table 1). A very small percentage of stems have an annual elongation greater than 20 cm. Since each shoot system lies in an almost horizontal position at right angles to the mat margin, these growth increments can be interpreted as annual advance rates for the edge of the mat. Because the stems do not advance in a straight line but tend to wander, an average horizontal advance of slightly more than 5 cm per year is a conservative estimate.

Although many stems sink and die (Fig. 5B), some stay close to the lake surface, survive and grow here for considerable distances (Fig. 5A).

TABLE 1. Growth rate of two shoot systems of *Chamaedaphne calyculata* in Harvard Pond Bog, expressed as percentage distribution of annual growth increments among length classes

Length (cm)	Shoot system 1 (73)[a]	Shoot system 2 (703)[a]
1–5	15	16
5–10	37	39
10–15	30	28
15–20	12	13
20–25	6	3
25–30	0	1
30–35	0	0

[a] Number of increments counted per shoot system.

TABLE 2. Number of growth rings compared with shoot age determined from growth habit for *Chamaedaphne* stems in Harvard Pond Bog (each column represents a single stem)

Age by growth habit	Age by growth rings							
1	0	0	0	0	0	0	0	0
2	1	1	1	1	1	1	1	1
3	2[a]	2	2	2	1	2	2	2
4	2	2[a]	3	3	3	3	3	3
5	3	1	1[a]	1[a]	3[a]	4	3	4
6	4	1	1	1	4	2[a]	4	5
7	4	2	1	1	3	3	5	6
8	6	2		3	4	2	7[a]	7
9	4	3		3	5	3	6	8
10	5	4		2	6	3	5	9
11	4	3		2	7	3	4	10
12	7	3		3	8	2	6	11
13	9	3		2			4	12
14	6	5		4				[a]
15	5	4						
16	7							

[a] All stem segments below this mark were submerged and usually bore adventitious roots along their submerged length.

No large air spaces are apparent in sections of stem tissue. However, *Chamaedaphne* branches float if cut and placed on the water. Yet, a branch with leaves and flowers does sink and some external means of support at the water surface is indicated. Support for horizontally spreading stems seems to be provided by other plants growing in the water along the bog margin. Plants locally abundant at the margin are *Decodon verticillatus, Nymphaea odorata, Nuphar variegatum,* and *Sphagnum cuspidatum.* In particular, *Sphagnum cuspidatum* may play an important role in mat advance. Although we have not investigated this question we justify our statement as follows: (1) Stems of *S. cuspidatum* tend to form a carpet which, when depressed, rises slowly to the water surface once more, due to trapped gases. (2) The vigorous production of *Chamaedaphne calyculata* shoots at the bog margin frequently correlates with the abundant presence of *Sphagnum.* Dead marginal shoots are often seen where *Sphagnum* is not present. (3) Abundant adventitious roots of *Chamaedaphne* are produced on stems surrounded by *S. cuspidatum* at the bog margin and in the established bog where the stems are surrounded by other *Sphagnum* species. We were unable to induce roots on *Chamaedaphne* stem cuttings in water, and few roots were observed in open water at the bog margin. (4) Excavations beneath the surface of the established bog frequently yielded *Sphagnum cuspidatum* remains where this species did not occur at the bog surface.

Some interesting details of shrub growth can be added. First, the only dead portions of the main axes of the excavated shoots were at their extreme proximal ends (nearest their point of origin). Living lengths greater than 3 m are probably uncommon. Secondly, ring counts of the stem in Fig. 5B were made at intervals along the branch system. Incomplete rings were common, but more than two of these were never encountered in one section. Complete rings were also few. Most sections had two or three rings and 11 was the maximum observed. The number of visible annual increments suggested an age of 40 years for the proximal region of the shoot. Since few rings were observed, the period of active secondary growth for each annual increment is limited.

Eight shoots were removed from the bog to study secondary growth in more detail. For each shoot all annual increments were sectioned and the rings counted (Table 2). Ring counts do not increase sequentially in successively older buried material although exact correspondence between age and ring count is apparent in aerial portions. The change in ring production pattern (in 7 of 8 cases) occurs immediately below the substrate or water surface. Apparently the subaerial environment inhibits ring formation, and ring counts of submerged stems indicate the age at which submergence first took place. For stems at the bog margin, the period of active growth-ring production usually occurs within the first 4 years, after which the stems become submerged. A longer period of active growth seems to occur in stems behind the bog margin where they are supported above the substrate by other stems.

Mat consolidation

Behind the advancing margin of the mat, *Chamaedaphne* stems still dominate the bog. These stems may arise either from epicormic shoots or seedlings.

All stems excavated in the study arose from buried portions of other stems and none from seedlings. Abundant seed is produced, however, and many small seedlings are often found in the bog. In particular, an abundant crop of *Chamaedaphne* seedlings was observed in the bog (up to 8 per 10 cm^2) in mid-July 1967. At one location in the bog, this crop was manipulated to estimate seedling growth under different conditions of shade and moisture. A *Sphagnum* mound 45 cm above water level and densely shaded by *Chamaedaphne* was half cleared of stems to provide two square plots each about 30 cm on a side, one in deep shade and one unshaded. A second site at water level with a mud substrate was similarly prepared. Finally a square plot, 30 cm on a side, was established in an unshaded *Sphagnum* moss carpet at water level. By the end of the summer of 1967 all seedlings on the dry mound had died. Seedlings at water level, but in the shade, had survived but showed no significant growth; many had died by the following summer (1968). Seedlings in unshaded *Sphagnum* close to the water table appeared healthy, had grown to about 4 cm, and had a similar length of root by the fall of 1968. Apparently *Chamaedaphne* seedlings (consistent with their abundance on stumps in the open water) will grow on moist unshaded sites, but no establishment occurs within the *Chamaedaphne* mat.

The build-up of organic matter at the bog surface must largely depend on the "turnover" of *Chamaedaphne* stems. Three features that relate to this subject were investigated: (1) stem age at time of death, (2) stem death rate per year, and (3) the rate of stem replacement per year. Three plots (one 60 cm by 60 cm and two 60 cm by 30 cm), each with about 70 stems, were located in the immediate neighborhood of the study area. All stems arising from the substrate surface within a plot were harvested and aged at the base (0–1 cm above the substrate). Stem age at the time of death was determined from the age of dead stems in the plot and from the age of the oldest living stems present. There were no living stems older than 16 years. Dead stems in the same plots averaged 13 years and the population of dead stems largely fell within two years of this. The death rate is difficult to determine in a rapid survey. However, if the population is in equilibrium so that the same number of stems die and are replaced each year, the death rate will equal the rate of replacement. The three plots had 70, 75, and 67 stems. If the average age of death is 13 years, the replacement rate per year would have to be 5.4, 5.8, and 5.2 stems, respectively. The average replacement was 6.1, 4.8, and 5.2 stems per year respectively for the first 10 years. Replacement and death rates are similar and the sample population appears to be in equilibrium.

Historical synopsis

Stratigraphy and living vegetation indicate that parts of the bog in the vicinity of the study plot have different specific histories, although shrub growth on stumps seems to have been widespread. Hence, our treatment is here limited to the historical background associated with the immediate area of the study plot.

The causeway beside the study area had been constructed by 1830 (Benninghoff 1947, Spurr 1956). This road was built on a bed of logs and it seems probable that tree stems immediately adjacent to the road were cut for the purpose. Hence, the stumps beneath the mat in and about the study plot may date from this time.

The composition of the cut forest was determined by microscopic identification of wood sections from six stumps within the plot. It was probably coniferous. Two *Tsuga canadensis,* three genus *Picea* Dietr., and one *Pinus* L. were recorded. Because the area was a lowland site, the *Picea* were probably *P. mariana.* One stump removed from the bog beside the causeway rested on an interface between clay (below) and 3 inches of sedge peat (above). There was also a sedge layer on the lake bottom towards the western end of the study plot; after the forest was cut, a sedge meadow seems to have developed. This view is supported by historical records which indicate that Fever Creek, which once flowed in the lake bed, was dammed at the southwest end of the valley to produce a wet meadow where hay was harvested about 1880 (Benninghoff 1947). The dam probably raised the water table sufficiently to favor sedge growth in the area of the study plot.

The lake was formed shortly before 1890 (Benninghoff 1947, Spurr 1956). Presently, none of the stumps in the plot are exposed sufficiently to permit shrub colonization, and the contours of the lake match those of the first accurate outline made in 1907. Presumably establishment took place between 1830 and 1890 before the lake level was raised. Stumps in a sedge meadow should provide an ideal habitat for the establishment of the shrub. It probably spread from these points of invasion to form a floating mat between 1890 and the present (1969).

Historical photographs permit a visual estimate of the rate of advance at the bog margin. The two photographs in Fig. 6 were taken from the same point in the winters of 1938 and 1968–69. From them and our knowledge of the area we estimate that the mat has locally advanced about 2 m during this period. This rate, about 6–7 cm per year, agrees well with previous estimates de-

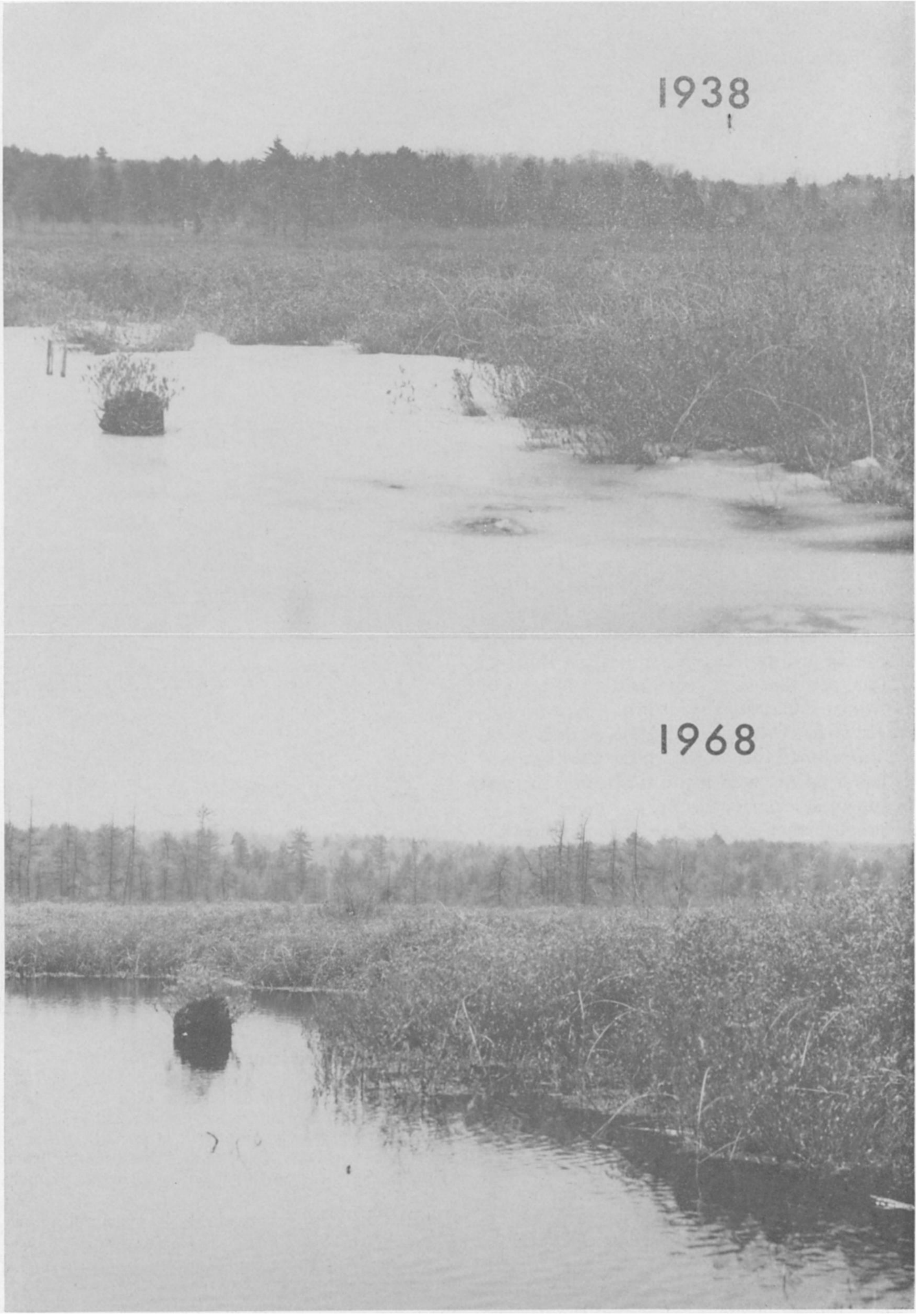

Fig. 6. Advance of a bog margin into Harvard Pond. Both photographs were taken from the same point on the peninsula east of the large floating bog (Fig. 1). In 30 years the margin has advanced approximately 2 m towards the stump.

rived from growth-flush measurements, although the rate of change of the bog margin appears quite variable in the photographs.

Discussion

A model of bog mat development

From the available evidence a simple visual model of mat development and consolidation for Harvard Pond can be constructed (Fig. 7). In Fig. 7A a plant has become established on a partly submerged stump, and one branch has spread laterally across the water surface. The advance of the shrub into the interstump area can be explained in terms of the growth habit of the plant (Fig. 7B and C). In Fig. 7B the branch has become partially submerged. (Horizontal branches near the water surface are usually submerged after 4 years' growth.) Adventitious roots are produced on the submerged portion of the stem and an epicormic shoot has formed proximally to replace the submerging apex. Figure 7C depicts the profile after several years. All the growth-habit characteristics have been repeated. The branches on the parent shoot have produced further branches, the lower ones have been depressed beneath the water surface, and fresh adventitious roots have been formed. The epicormic shoot of Fig. 7B has assumed the normal pattern of branching for the *Chamaedaphne* crown. A new epicormic shoot has formed behind the growth front. Figure 7D shows the pattern after this cycle of events has been repeated many times, and the mat has begun to thicken vertically.

We propose that this thickening occurs as follows. Epicormic shoots from one parent shoot can each develop into an independent shoot system with the same growth features as the parent. Each stem is gradually depressed horizontally by successive loads of snow and ice as the crown enlarges. In this way fresh epicormic shoots come to lie above the parent shoots. Eventually, the parent stems are pressed close to the substrate surface and become overgrown with moss obscuring the origin of the daughter epicormics. In turn the epicormic shoots go through the same cycle as the parent shoots, each cycle lasting approximately 13 years. This unidirectional layering of stems was found to the bottom of the mat in all of 15 holes made through the mat surface in the plot. Thus, the *Chamaedaphne* mat becomes established by successive accumulations of branches, and an equilibrium develops at the bog surface where the number of new shoots appearing equals the number dying. Thus it seems that the vertical thickness of the mat is gradually increased as branches are continually added at the surface. As the mat increases in weight, it presumably sinks lower in the water, eventually coming to rest at the bottom of the lake.

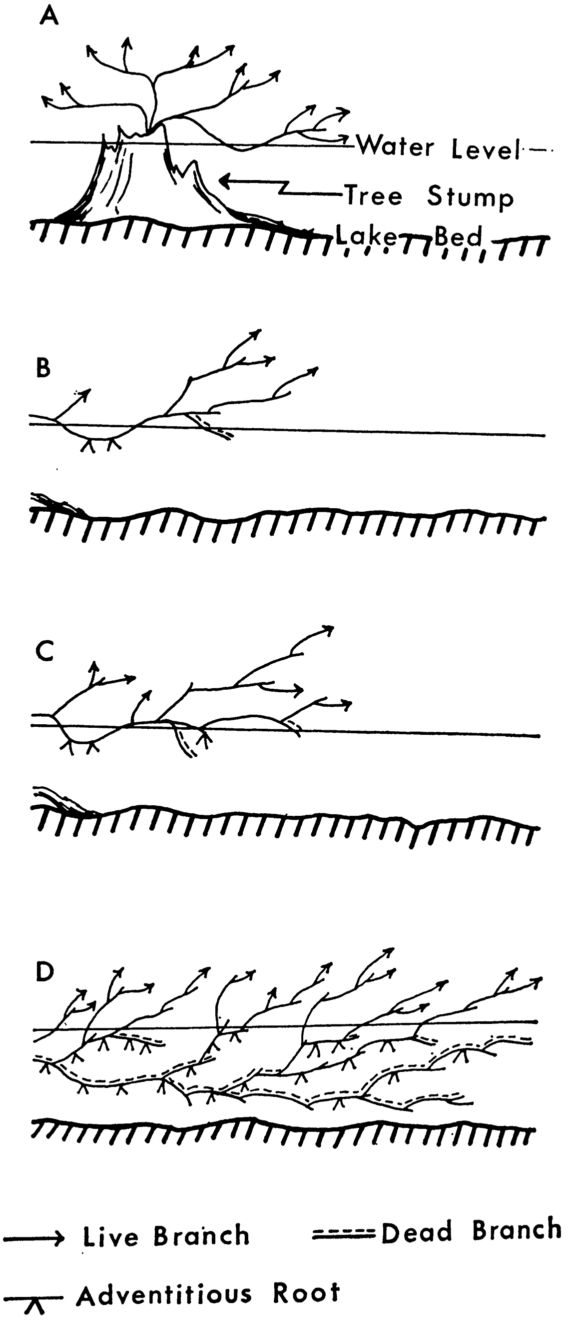

FIG. 7. A model for the growth of a floating bog on Harvard Pond. A, B, C: the growth pattern by which *Chamaedaphne calyculata* spreads across the water surface (details in text); D: the probable vertical structure of the bog if this growth pattern continues indefinitely.

According to the model (Fig. 7D), shoots at the margin of the mat should arise from stems beneath those behind the advancing front. In fact, the two excavated shoot systems (Fig. 5) had their outermost living branches attached to stems at a depth of 45–60 cm beneath the water surface. These stems were definitely at the lower margin of the mat.

No allowance has been made in the model for the possibility that the mat may be built partly from seedlings because these did not appear to be important in our study.

Mat solidarity arises not only from the accumulation of stems but also from the extensive production of adventitious roots which serve to bind many of the buried stems together. In addition, the growth of *Sphagnum* and the accumulation of shed *Chamaedaphne* leaves add to the consolidation of the mat.

The Harvard Bog in perspective

Our data suggest that the development of a floating mat on Harvard Pond can be largely understood in terms of the growth of one shrub, *Chamaedaphne calyculata.* Other species are apparently of greater importance in other areas. Species thought to initiate a floating mat are *Menyanthes trifoliata,* members of the Cyperaceae, and *Myrica gale* (Gates 1942, Conway 1949, Janssen 1967, Daubenmire 1968). *Chamaedaphne* is considered an invader of the established mat in Michigan (Gates 1942). Conway (1949) notes the occurrence of *Chamaedaphne* in Minnesota at an intermediate stage in the succession from bog mat to bog forest. Similarly Dansereau and Segadas-Vianna (1952) deduce an intermediate successional role for the species in both the deciduous and spruce-fir regions of the northeastern United States. Even in Massachusetts, Moizuk and Livingston (1966) have noted *Chamaedaphne* as a sedge invader. In eastern Canada, *Myrica* not *Chamaedaphne,* is credited with a creeping habit and the invasion of a mat margin. In Harvard Pond *Myrica* invades exposed stumps but does not spread more than a meter from these centers of origin. *Myrica* clumps actually provide locational "markers" for the stumps beneath the bog.

Measures of the rates of bog expansion are few. Buell, Buell, and Reiners (1968) note that the margin of a floating mat in Cedar Creek Bog, Minnesota, has remained essentially unchanged in the last 30 years. In contrast, certain parts of the Harvard Pond mat have spread quite rapidly. Our estimates of advance rate for the mat margin indicate a horizontal advance of 5–7 cm per year. If these rates applied in the area now a *Chamaedaphne* mat, the maximum interstump distance of 9 m in the plot would be covered in 65–90 years. Since the pond has been in existence for 80 years, our estimates appear to be reasonable.

Climate has long been held responsible for the expansion and retreat of bogs. It certainly does not limit the expansion of the bog on Harvard Pond. No doubt multiple stump origins can permit a rate of advance far exceeding that possible from a single shoreline. Multiple origins have been suggested by Dansereau and Segadas-Vianna (1952) who note that a solid object such as a rock or a stump is necessary as an anchorage from which vegetative spread can take place. We cannot say how common this form of mat development may be. Yet, in the immediate vicinity of the study area there are numerous artificial lakes with stumps projecting above the water surface.

Floating mats are often illustrated as relatively narrow zones of advancing vegetation at a lake margin. The mat studied here is extensive. It forms a "roof" over the lake buttressed by tree stumps. It may seem surprising that a large and dense mat can develop on the surface of a body of water and remain supported there. A gradual settling of a floating mat is to be expected as peat accumulates at the surface (Dansereau and Segadas-Vianna 1952, Ketchledge 1964), but its buoyancy may, in part, be explained by trapped gases.

The growth habit of *Chamaedaphne* is intriguing. Lems (1956) states that older stems are buried in *Sphagnum* and produce adventitious roots. This growth habit permits the shrub to spread considerably in southeastern Michigan. In New York State, Ketchledge (1964) notes: "It is the highly branched trailing stems and roots of leatherleaf more often than any other plant that form the supporting network of the mat and hold the vegetation together." This seems to hold true for our study. However, Dansereau and Segadas-Vianna (1952), in a simplified bog profile, illustrate *Chamaedaphne calyculata* as numerous individual plants having a limited spread to the stem and root systems. Highly complex branching stems beneath the *Sphagnum* mat are not noted.

The growth habit of this shrub in our study area is similar to that of other bog shrubs. Conway (1949) noted that one runner of *Vaccinium macrocarpon* was 13.5 ft (4.1 m) long, that 2 ft had been added in the last year of growth and that all live roots were on this distal 2 ft (0.3 m) of horizontal stem. This is very similar to the growth behavior of *Chamaedaphne.* The adventitious rooting of decumbent stems is recorded for other bog shrubs, for example, *Myrica gale* (Dansereau and Segadas-Vianna 1952). Trailing stems of *Aronia melanocarpa, Alnus rugosa,* and *Vaccinium corymbosum* also produce adventitious roots abundantly in our study area.

From our work, we cannot agree with Segadas-Vianna (1955) that *Chamaedaphne* prohibits the entry of other species because of its frequent "purity" in stands. Rather, succession seems to depend upon the initial establishment of a *Chamaedaphne* bog mat. On top of the *Chamaedaphne* sward other species are becoming established. In particular, the mat provides a purchase for *Sphagnum* spp., including *S. fuscum, S. recurvum, S. capillaceum, S. papillosum,* that often form a dense layer on its surface.

Our findings have implications for future wetland studies. Perhaps detailed studies of bog development have lagged because of the apparent vegetational complexity of peatlands, perhaps because of the practical difficulties in obtaining direct records of succession. We suggest that the stages and rates of floating bog development may be explored by a critical examination of the growth behavior of key bog species (such as *Chamaedaphne calyculata*) in different areas.

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