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Reviewed work(s):
Source: *The Bryologist*, Vol. 67, No. 4 (Winter, 1964), pp. 427–431
Published by: American Bryological and Lichenological Society
Stable URL: http://www.jstor.org/stable/3240768
Accessed: 23/07/2012 06:45

THE ORIGIN OF ACIDITY IN *SPHAGNUM* BOGS[1]

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In most cases where the pH of *Sphagnum* bogs has been measured it falls in the range of 4.5-3.3 (0.3-5 milliequivalents/1 of H^+), though there are fluctuations in time, and with species and micro-habitat (Pearsall 1941, Pearsall & Lind 1941, Pearsall 1956, Gorham 1956, and Clymo 1963).

In bogs which are entirely dependent on precipitation for their water there seem to be at least four possibile sources of H^+. There are:

1. Precipitation
2. Activity of sulfur-metabolizing bacteria
3. Secretion by live *Sphagnum* plants of whole organic acid molecules
4. Cation exchange in the walls of *Sphagnum* plants

Precipitation

Measurements of the *p*H of precipitation have been made by a number of workers, for example Gorham (1955), Egner and Eriksson (1955 *et seq.*), and Barrett and Brodin (1955).

At some times of the year in areas subject to industrial pollution, the supply of H^+ in rain may form a significant part of the total H^+ accumulating in a bog system. For instance, in 1959 at Malham Tarn, Yorkshire, England, the *p*H of the rain fell to 3.8, (1.6 m.eq./1) in March, but the average concentration of H^+ in that year was 0.5 m.eq./1. In March, 1964 there was about 2.5 m.eq./1 of H^+ present in water from Malham Moss.

In bogs in areas with no great pollution the supply of H^+ in rain seems unlikely to exceed 30% of the total accumulating in a given time, but the effects of evaporation are not at present predictable.

Activity of Sulfur-metabolizing Bacteria

A polished silver wire pushed into a bog will usually show a black deposit after ten minutes or so. The deposit appears to be due to AgS, the $S^=$ deriving perhaps from the breakdown of sulphur-con-taining proteins or from the reduction of $SO_4^=$. The depth at which this can be first detected varies from 9-20 cm below the surface during a year in two bogs examined.

It has been shown (Gorham 1956) that $SO_4^=$ and H^+ concentra-tions in bog pools rise during dry periods and it seems possible that both these increases are due to the activities of sulphur-oxidising bacteria.

This source of H^+ may be important at some times, but there seems to be little quantitative evidence. It cannot in any case ac-count for the immediate large fall in pH of rain after passing over

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Sphagnum plants. It might also be expected that the lowest pH values would be recorded in pools rather than on hummocks, but this is not usually so (Clymo 1963).

Secretion by Sphagnum *Plants of Whole Organic Acid Molecules*

There do not seem to be sufficient organic acid anions in natural conditions to account for much of the H^+. Samples of bog water collected from two bogs on seven different occasions were concentrated under vacuum at 25°C. The concentrates were yellow or brown with no peaks of absorption in the visible region. They resembled the "yellow organic acids" of Shapiro (1957) in following Beer's Law, and in the optical density depending on the *p*H, but they were dissimilar in that the colored material was almost insoluble in ethyl acetate.

If all the material combustible below 500°C were oxalic acid (which has the highest possible proportion of acid H^+ in a given weight), then the organic matter present could just account for the observed *p*H of the solutions. The infra-red spectrum, however, showed that at least the bulk of the material was not oxalic acid. Using the absorption peak at 1705-1725 cm^{-1} as an estimate of $>C=O$ groups, (Bellamy 1958) and supposing that all such groups are in $-COOH$, then the equivalent in H^+ is 0.01-0.05 m.eq./l which is 10-28% of that actually present in these samples. Some at least of these $>C=O$ groups may have come from the breakdown of dead plants in which the $-COO^-$ might be neutralized by cations other than H^+, in which case the amount of excreted $-COOH$ would be over-estimated. It is, however, equally likely that easily metabolizable organic acids might be broken down, with complicated effects on the amount of H^+ and other cations in solution.

Cation Exchange in the Walls of Sphagnum *Plants*

When *Sphagnum* plants are placed in rainwater of about *p*H 5 there is usually a drop in *p*H of one or two units within a minute or so. This would be easily explained by cation exchange. Other evidence (Clymo 1963) also supports this view. About 10-25% of the dry weight, depending on species and vigor, is in the form of un-esterified polyuronic acid. The exchange groups behave as if they had a *p*H of about 3.3 and as if they were at concentrations of about 1 eq./l. At equilibrium the concentrations of cations in the plant walls and the external solution can be largely described by an extension of Donnan theory (though some marked deviations from this remain unaccounted for).

If a solution of about *p*H 5 and containing other cations in addition to H^+ is passed continuously over a *Sphagnum* plant killed by steaming, the *p*H of the effluent will at first be much below that of the influent. The effluent *p*H will gradually rise until, when most of the H^+ in the exchange phase has been replaced by other cations, the influent will be in equilibrium with the plants and the *p*H of the influent and effluent will be nearly the same.
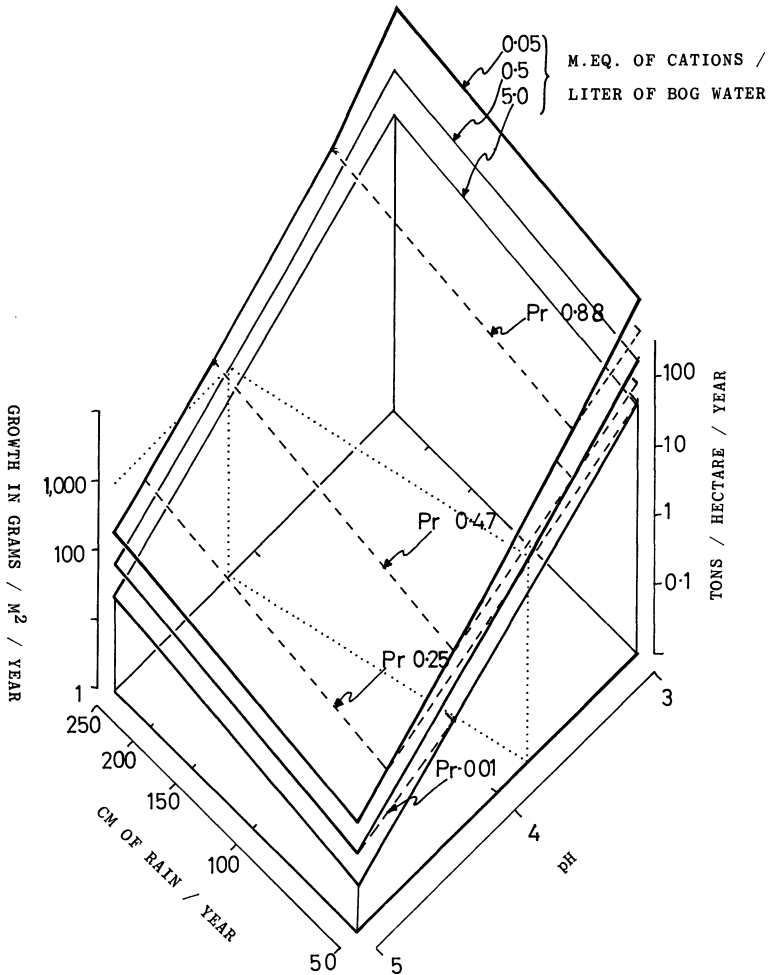
FIG. 1. The calculated relations of growth of *Sphagnum*, rainfall, equilibrium concentration of cations other than H⁺ in the bog water, proportion (Pr) of cations in the exchange phase, and pH, for monovalent cations. Full lines delimit iso-cation concentration planes. Broken lines delimit iso-proportion planes (Pr.) Dotted lines show conditions with 10 tons/hectare/year and 0.5 milliequivalents/l of cations other than H⁺.

In a bog system the *p*H continues to be low, and if cation exchange is to account for much of the H⁺ one must suppose either that the existing cation exchange sites are regenerated by H⁺ produced metabolically, or that entirely new exchange sites are produced in the acid form.

That metabolic activity is involved is also suggested by the ob-

servation of pH values in green clumps of S. *papillosum* consistently about 0.2 units lower than in clumps of yellowish plants in similar microtopographic situations.

It is possible, using the modified Donnan theory, to calculate the pH which would result if given amounts of *Sphagnum* with exchange sites in the acid form were equilibrated with known volumes of solution of known cation composition. If the growth rate of the plants, and the quantity and composition of rainfall were known, one could then calculate the pH to be expected in the bog water. This assumes a closed system going to equilibrium which is, of course, not true, but the results should give some idea of the average values to be expected.

Growth rates of *Sphagnum* plants have been measured by four methods:

1. In a few cases, for example ploughed drainage furrows of known age in which *Sphagnum* plants have subsequently grown, the total mass of material left after a known time can be measured. This will be an underestimate of the true rate and refers only to a special microhabitat. Values of 1-9 metric tons/hectare/year have been found in three situations examined.

2. Periodicity in the length and spacing of branches may sometimes be seen, and these periodicities may be annual. The pattern is, however, more often obscure. Five estimates by this method gave values in the range 5-12 tons/hectare/year.

3. Minimum estimates can be derived from C^{14} dating of horizons in peat. A good example of such dates is given in Turner (1964). Using the conversion 10 grams dry weight/100 ml volume of peat (which is based on 20 samples of widely varying humification), the highest average value in Turner's peat profile of about 3 tons/-hectare/year occurred between 2354-2646 years ago.

4. Plants may be cut to a known length and replaced in the bog. Later they can be recovered and the increase measured. There are a number of difficulties with this method but it is the most widely applicable. Estimates by this method of 1.5 to 12 tons/hectare/year have been found.

In methods 1, 2, and 4 the density of plants must also be known.

These are all average values. Fig. 1 shows that with 0.65 m.eq./1 of monovalent cations and 125 cm/year of rain, an average pH of about 4.0 might be maintained at the faster rates of growth. Even at 3 tons/hectare/year a pH of 4.2 could be maintained by this mechanism.

LITERATURE CITED

BARRETT, E. & G BRODIN. 1955. The acidity of Scandinavian precipitation. Tellus 7: 251-257.
BELLAMY, L. J. 1958. The Infra-red Spectra of Complex Molecules. London.
CLYMO, R. S. 1963. Ion exchange in *Sphagnum* and its relation to bog ecology. Ann. Bot. Lond., n.s. 27: 309-324.
EGNER, H. & E. ERIKSSON. 1955. Current data on the chemical composition of air and precipitation. Tellus 7: 134-138.

GORHAM, E. 1955. On the acidity and salinity of rain. Geochim. & Cos-
    mochim. Acta 7: 231-239.
———. 1956. On the chemical composition of some waters from the Moor
    House Nature Reserve. Jour. Ecol. 44: 375-382.
PEARSALL, W. H. 1941. The "mosses" of the Stainmore district. Jour. Ecol.
    29: 161-175.
———. 1956. Two blanket-bogs in Sutherland. Ibid. 44: 493-516.
———. & E. M. LIND. 1941. A note on a Connemara bog type. Ibid. 29:
    62-68.
SHAPIRO, J. 1957. Chemical and biological studies on the yellow organic
    acids of lake water. Limnol. & Oceanogr. 2: 161-179.
TURNER, JUDITH. 1964. The anthropogenic factor in vegetational history.
    I. Tregaron and Whixall mosses. New Phytol. 63: 63-73.

PHYSIOLOGY OF THE REPRODUCTION OF BRYOPHYTES

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That the periodicity of vegetative and sexual reproduction in bryophytes is conditioned by external factors has now been demonstrated by many authors. Some of the earlier work has been reviewed in a previous paper by Benson-Evans (1961). Other contributions have been made by Gorton and Eakin (1957); Mitra, Allsopp, and Wareing (1959); Bopp (1963); Kofler, Dutel, and Nurit (1963); and Vaarama and Tarén (1963), all of whom have investigated factors controlling germinating spores, protonemal growth, and bud formation in mosses. Rhythms in later stages of vegetative growth leading up to production of sexual branches have been described by Tallis (1958, 1959), and the effects of day length on the development of the sporophyte have been shown by Hughes (1962).

Mohr (1963), Steiner (1963), and Schwabe and Nachmony-Bascomb (1963) have added useful information on factors controlling early development of young thalli and gemmae in liverworts, and Anthony (1962) on the production of gametangia.

It is the purpose of the present article to demonstrate the main environmental factors conditioning sexual reproduction in the bryophytes, with particular reference to the liverworts, by presenting data derived from field observations and laboratory experiments carried out at Cardiff.

MATERIALS AND METHODS

Material of all the species investigated was collected from localities in the counties of Glamorgan, Monmouth, and Brecon. Seasonal field observations of the developmental stages of the bryophytes, and weather records have been made in each locality over a period of years.

Material for experimental work in the growth chambers was from two sources. For direct comparison with field observations, portions of a thalloid mat or turf where the liverwort or moss formed an almost pure stand were potted up in soil from the same habitat and transferred to the growth cham-

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