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NOTICES OF PUBLICATIONS OF GENERAL BEARING

RECENT WORK ON ECOLOGY OF BRYOPHYTES

- (I) **Maybrook, Annie C.** "Note on the biology of *Fegatella conica*." *New Phytol.*, **13**, 1914, pp. 243-249, 1 fig.
- (II) **Watson, W.** "Xerophytic adaptations of bryophytes in relation to habitat." *New Phytol.*, **13**, 1913, pp. 149-169, 181-189, 3 figs.
- (III) **Cannon, W. A.** "A note on the reversibility of the water relation in a desert liverwort." *Plant World*, **17**, 1914, pp. 261-265.
- (IV) **Skene, M.** "The acidity of *Sphagnum* and its relation to chalk and mineral salts." *Ann. of Bot.*, **29**, 1915, pp. 65-87.
- (V) **Schoenau, K.** "Die Verfärbung der Polytrichaceen in alkalisch reagirenden Flüssigkeiten." *Flora*, **105**, 1913, pp. 246-264.
- (VI) **Boas, F.** "Zur Physiologie einiger Moose." *Hedwigia*, **54**, 1913, pp. 14-21.
- (VII) **Garjeanne, A. J. M.** "Der Einfluss des Wassers auf *Alicularia scalaris*." *Beih. z. Bot. Centralbl.*, **31**, 1914, pp. 410-419.
- (VIII) **Kessler, B.** "Beiträge zur Oekologie der Laubmoose." *Ibid.*, **31**, 1914, pp. 358-387.
- (IX) **Watson, W.** "A Somerset heath and its bryophytic zonation." *New Phytol.*, **14**, 1915, pp. 80-93, 7 figs.

The ecological importance of bryophytes, especially as pioneers—either alone or together with thallophytes—in various plant associations, has become increasingly evident during recent years, and a considerable amount of attention has been paid to the physiology and ecology of these plants. For summaries of various recent contributions, apart from those cited above, reference may be made to this JOURNAL, **1**, 1913, pp. 51, 124, 198, 201.

(I) The authoress has made a careful investigation of the modifications in structure of the thallus of plants of *Fegatella conica* found growing in a moist hole in a hedge bank, with reference to the light intensities to which the plants in different positions in the cavity were exposed. Previous writers had shown that reduction of the air-chambers, in addition to changes in the form and branching of the thallus, occurred in this and other members of the Marchantiales under conditions of moisture and darkness; but the exact relation between these modifications and the external factors had not been investigated. The authoress considers that the absence of air-chambers from the plants in the wettest and darkest positions is due to the combined effect of darkness and moisture, since in thalli growing in decreased intensities of light there is a gradual decrease in the

number of air-chambers per unit of surface area and in the size of these chambers. The final disappearance of the chambers, however, is apparently dependent upon the moisture factor, for only in those forms showing marked adaptations to a moist habitat were the chambers totally lacking.

(II) The author here brings together a large amount of interesting information concerning the morphology of both liverworts and mosses, the chief merit of his contribution being that he has extended Grebe's compilation of the "xerophytic adaptations" of mosses (see this JOURNAL, 1, 1913, p. 124) to the bryophytes as a whole, and has added various facts from his own observations. The various protective arrangements against drought are considered under the following headings. (1) Protective arrangements of the sporophyte:—general protection by the thallus or leaves of the gametophyte and by the calyptra; immersion of capsule; length of seta; curvature of seta; papillosity of calyptra, perianth, seta, peristome-teeth, spores; bell-shaped calyptra; hairy calyptra; position of stomata on capsule; plication of capsule; fleshy or bulbous involucre. (2) Protective arrangements in the gametophyte:—(a) reduction of water output by cushion-forming habit, investments of dead or non-chlorophyllous cells, shape of leaf or thallus, size of leaf-cells, thickenings of leaf-cells, stem structure, arrangement of leaves on stem, capillary structures; (b) water storage methods, as water-sacs, water-storing cells, mucilaginous cells, hypogaeal tubers, succulent tissue. As the author points out, "many of the plants mentioned as exhibiting 'xerophytic' devices are not xerophytes; the devices simply enable the plant to live under less moist conditions than if they were absent."

(III) According to the ways in which the longer-lived plants in the Arizona desert region respond to the great variation in water relation to which they are exposed each year, these plants may be divided into (1) succulent species with a reversible water relation, (2) non-succulent species with a reversible water relation, (3) spinose or sclerophyllous species with an irreversible water relation. To class 1 belong the Cactaceae, to class 2 the woody plants in general, and class 3 consists mainly or wholly of ferns and bryophytes—"resurrection" plants which become dormant on drying and revive on being moistened. Many plants in fairly moist as well as from more or less arid regions have to a greater or less degree a reversible water relation of this kind; for instance, the liverwort *Corsinia marchantioides* was found by Schröder to revive after having been kept in a herbarium for seven months, some mosses after two years; *Sedum elegans* survived a water loss of 90 per cent. Peirce found that the lichen *Ramalina reticulata* when air-dry can absorb so much water that its wet weight is over twice its air-dry weight, and that there was at the end of a long dry summer 14 per cent. water in the air-dry plant. Humphrey found that some Californian liverworts, when air-dry, could yet lose 5 to 12 per cent. of water and survive. Both in California and southern Arizona the rainfall is periodic, with a drought season between the rain seasons, but the California summers are visited by fogs or dew which probably serve to mitigate the severity of the drought, whereas the dry seasons in Arizona are without dew or fog and though shorter are possibly more intensely arid than in California. The response of a liverwort to the more arid desert region has therefore a special interest.

No liverworts have been found in the domain of the Desert Laboratory, Tucson, which is probably too arid for these forms, but a species of *Plagiochasma* was found on the southern face of the Santa Catalina mountains at about 5000 ft.; the rainfall here is about 20 in. and is about equally divided in amount between winter and summer. At the time the liverwort was seen, October, there was no rain, but the humidity was probably not so low as in the fore-summer; it was mainly for this reason that the species was fully expanded, though it was also growing in a protected situation among some mosses at the

northern face of a cliff. Plants kept indoors and given water frequently during winter remained expanded, but early in spring they were given no water for a few days and promptly became rolled up; on being given water they expanded within a few minutes. In a series of experiments the plants were found to lose 80 per cent. of their moist weight in becoming air-dry. The plants were allowed to remain for 25 days without water, in air of very low humidity and at a very high temperature, the glass-house at the time being undoubtedly much more arid than the habitat of the liverwort even in unusually dry seasons; but on being given water the plants promptly unrolled and resumed their active condition. This plant clearly possesses a margin of safety by which it can withstand exceedingly arid conditions, hence it seems doubtful whether aridity in itself is the definitive factor limiting its lower distribution.

(IV) The author points out that in the discussion of the influence of the chemical nature of the soil on vegetation the question of calcium carbonate has always been prominent, since it is one of the soil constituents that can be most easily recognised and estimated and the differences in flora due to its presence or absence are often very striking. Calcicole plants, thriving only on chalk and calcifuge plants, which cannot live in its presence, may be wholly confined to one type of soil or to the other, or their behaviour may change with change in other external factors. Cases are seen in *Achillea atrata* (calcicole) and *A. moschata* (calcifuge)—when the two species occur together in the same valley each is strictly confined to its own type of soil but if either occurs in absence of the other it is non-discriminating—and in *Castanea vesca*, which cannot grow on chalk unless an abnormal high percentage of potassium be present in or added to the soil. Though probably most plants regarded as calcifuge belong to this indeterminate type, in some cases the repugnance to chalk is constant and independent of other external factors, and of these a striking example is afforded by *Sphagnum*, the species of which are rapidly killed by water containing calcium carbonate. The author refers to observations which go to prove that the influence of chalk on vegetation may be indirect—for instance, M. C. Rayner's work on *Calluna* (see this JOURNAL, 1, 1913, p. 59) showed that the presence of chalk interferes with the proper development of the mycorrhiza and promotes the growth of a bacterial sheath on the roots, this interference with the root symbiosis being accompanied by and apparently responsible for symptoms of weakness in the plant; or direct, whether physical or chemical—for instance, Kraus (see this JOURNAL, 2, 1914, p. 256) demonstrated the effect of chalk on the water content and temperature of the soil, the former diminishing and the latter increasing as the amount of chalk present rises, and showed that some plants growing typically on chalk can grow equally well on siliceous soil if its physical properties resemble those of chalk, while the behaviour of *Castanea* already noted indicates that in this case the chalk acts by interfering with the supply of other salts through the roots. Another important effect of chalk is that it alters the reaction of the soil, making it neutral or alkaline; and to this is probably due its noxious effect in many cases, including probably that of *Sphagnum*.

The author then gives a summary, from Paul's memoir (1908), of the earlier observations on *Sphagnum* and its relation to chalk. Oehlmann (1898) found that it dies in a 0.05 per cent. solution of chalk, the time elapsing before death varying with the species used; to produce the same effect with calcium sulphate a 0.1 per cent. solution was necessary, with calcium nitrate a 0.75 per cent. solution. Weber (1900), however, claimed to have grown various species successfully in water containing chalk, even adding powdered chalk to the cultures without harming them; he concluded that the chalk is harmful only in the presence of other plants which by growing more vigorously in the chalky water rapidly supplanted the *Sphagnum*. Graebner (1898–1904) agreed that chalk as such is not harmful, and attributed the failure of the *Sphagnum* to too high a mineral content in

general; according to Ramann (1895) *Sphagnum* can persist only in water containing less than 0.003–0.004 per cent. of mineral substances; Duggeli (1903) from moor experiments concluded that *Sphagnum* was affected adversely not only by the chalk but also by mineral salts in general, but his results are not convincing since his mineral solutions apparently always contained chalk or magnesia in addition to other constituents. Haglund (1912), also from field experiments, found that with addition of lime or phosphate *Sphagnum* died or was severely injured, while addition of potassium fertilisers induced the growth of other mosses and of algae which covered the young *Sphagnum* shoots.

By far the most extensive investigation was that made by Paul (1908), who tested many different salts and many different species of *Sphagnum* and obtained valuable results. Paul first determined the concentrations of calcium carbonate necessary to kill various species, and showed that the number of mg. per litre varied from about 90 in the case of high moor species (*S. rubellum*, *S. papillosum*, *S. molluscum*) to about 200 in that of low moor species (*S. acutifolium*, *S. platyphyllum*) and over 300 in that of the generally distributed *S. recurvum*—that is, the dwellers on the high moor where the supply of salts is normally very low are much less resistant than those on the low moor where minerals are more abundant. He then tried the effects of various salts, and found that all the species grew satisfactorily in an almost concentrated solution (2 gm. per litre) of calcium sulphate; the other salts were tested with *S. medium*, which is moderately sensitive to chalk (fatal chalk concentration 134 mg. per litre), and found that to kill this moss very different concentrations of different salts, acids and alkalis were required, e.g. of calcium nitrate 966 mg. per litre, of potassium bicarbonate 240, of potassium carbonate 149, of potassium bisulphate 720, of potassium sulphate 6480, of sodium chloride 300, of calcium chloride 1100, of sulphuric acid 150, of nitric acid 82, of sodium hydroxide 40. Hence *Sphagnum* is not uniformly adversely affected by the high concentrations of the salts applied to it—some salts it tolerates at high while others are harmful at very low concentrations, the salts of calcium are harmless while phosphates and alkaline salts are very toxic; another important point to be noted is that as the salts were tried alone the antitoxic action of one salt on another which occurs in nature is omitted—this would probably raise considerably the concentration at which harm would result in a culture solution.

Before discussing the most interesting part of Paul's work—his views on the relation of the harmful action of chalk to the "acidity" of *Sphagnum*—reference is necessary to investigations on the nature of the "acidity" of *Sphagnum* and peat. Leiningen (1907), starting from the observation that litmus paper applied to *Sphagnum* turns red, found that the plants require a considerable quantity of alkali for their neutralisation. Baumann and Gully connected this acidity of *Sphagnum* with the acidity of peat and found that the acidity was much the same in *Sphagnum* and the underlying peat, the latter being somewhat higher—e.g. 0.228 gm. acid hydrogen per 100 gm. of *Sphagnum*, 0.260 in the case of peat. In investigating the nature of the acid substances they started from Sprengel's observation that peat can decompose and render soluble tricalcium phosphate, worked out the reaction between this compound and peat and *Sphagnum*, and found that both decompose it in the same way and to about the same extent. In this reaction it would appear that successive small quantities of the almost insoluble calcium compound go into solution and are attacked by the organic compounds of the peat, or *Sphagnum*, part of the phosphoric acid appearing in the solution as such, part as monocalcium phosphate, while part of the calcium is removed by the peat; the reaction consists essentially of a splitting up of the phosphate with removal of the base and liberation of the acid, the formation of the monocalcium salt being regarded as secondary and due to action between the liberated acid and the undecomposed phosphate. The amount of P_2O_5 which went

into solution from tricalcium phosphate with 1200 c.c. water was 158 mg.; with addition of 6 gm. *Sphagnum*, 1383 mg.; with addition of 6 gm. peat, 1561 mg. The observations were extended to other salts and the remarkable result obtained that with the exception of the extremely insoluble calcium oxalate all the salts tried were broken up with liberation of the acid of the salt. Peat and *Sphagnum* possess this property in common, and though the peat is slightly more active the two sets of figures obtained were so closely parallel that the property is evidently referable to the possession of some common compound. Fixing on the fact that *Sphagnum* and peat can break up such salts as sodium chloride, liberating the acid and removing the base, Baumann and Gully argue that if an acid is responsible we must suppose that an insoluble organic acid is capable of breaking up so strong a combination as sodium chloride, producing an insoluble sodium salt and liberating hydrochloric acid. This they consider impossible, and they conclude that the reaction is due to the presence of colloidal substances (see this JOURNAL, 2, 1914, p. 209) which adsorb the base and set free the acid, and they adduce the following considerations in support of their theory. (1) The conductivity of *Sphagnum* and peat is very low, only about one-tenth that of a solution of acetic acid having the same solvent action on tricalcium phosphate. (2) When *Sphagnum* or peat acts on a salt the amount of acid liberated is, relatively to the amount of *Sphagnum* or peat used, less as the concentration of the solution is decreased, greater as the amount of *Sphagnum* or peat acted on by a constant volume of solution is decreased. (3) The activity of *Sphagnum* or peat decreases slowly when it is kept—this would correspond to the slow change in surface of a colloid. (4) The amounts of the acids set free from different salts are widely different, acids being liberated in the following order for a series of salts with the same base:—(a) hydrobromic, hydriodic, hydrochloric, nitric; (b) sulphuric; (c) acetic, the last named in largest quantity. This corresponds to the activity of the acids in various colloidal reactions. (5) As regards the bases, bivalent bases are adsorbed more actively than monovalent, potassium more than sodium. (6) It is possible to wash out a large portion of the adsorbed base with distilled water, especially if it contain carbon dioxide; by this means the original acidity of the *Sphagnum* or peat may be almost completely restored.

Hence Baumann and Gully conclude that the old "humus acids," to which the acidity of acid soils in general and of peat in particular was ascribed, are non-existent, the acidity being in reality due indirectly to the presence of negatively charged colloidal compounds which break up any salts present in the soil, the acid of the salt then producing an acid reaction in the soil. They regard the colloids in question as being chiefly located in the hyaline cells of the *Sphagnum* leaf. The colloidal hypothesis put forward by Baumann and Gully has received the weighty support of Czapek, and other writers have agreed with their deductions, though some chemists have attacked these views and sought to refer the reactions to ordinary chemical processes with typical acids. The matter is really one for the physical chemist, but it may be noted that at any rate there is no evidence of the existence of insoluble alkaline salts of the humus acids, the compounds of the artificial preparations with the alkalis being soluble, and that to account for the retention of bases in the form of such salts by peat or *Sphagnum* some sort of adsorption must be invoked. As a matter of fact, no one denies that the humus acids are colloids, and acids which are colloids will of course act both as acids and as colloids, hence the attempt to explain all their peculiarities on the basis of one only of these two properties is bound to fail. For the purpose of the ecologist it is sufficient to recognise that peat contains compounds capable of breaking up salts and liberating their acids, and that the acid nature of peaty soil is probably due largely to the presence in it of these (mineral) acids. These compounds are already present in *Sphagnum*, and their significance for the life of the

Sphagnum is taken to lie in the possibility it gives of absorbing bases from the very dilute solution in which the moss lives.

Returning to Paul's work on the relation of *Sphagnum* to chalk, he suggests that the chalk saturates the acid compounds of the cell-walls and so prevents the absorption of bases; this does not directly produce death from starvation but it causes the plant to make an effort to replace the saturated compounds, with the result that metabolism is so much increased that death ensues from a sort of exhaustion. In support of this view he adduces the fact that different *Sphagnum* species have different acidities, and that hand in hand with this variation goes the variation in repugnance to chalk, the more acid species being also the more sensitive. The agreement between high acidity and great sensitiveness is in most cases very close when the amounts of chalk are given not in terms of the concentration used but as the number of mg. required to kill 1 gm. of the plant (dry weight); if concentration is taken the agreement though still holding in a general way is not so satisfactory, and though Paul prefers the former method of statement he does not show experimentally that the toxic effect of the chalk takes place when a certain amount is supplied, rather than when a certain concentration of the solution is used.

The author's own work was begun on the publication of Baumann and Gully's paper (1910). The data he presents are arranged under the following six headings. (1) Liberation of acids from their salts. To demonstrate this fundamental effect it is only necessary to soak *Sphagnum* shoots for a few hours in a solution of any salt and test with an indicator—a strong acid reaction is always obtained. That the acid present in the treated salt solution is the acid of the salt used is less easily shown, but the author obtained fairly conclusive results by using solutions of copper chloride, each solution being left standing overnight, with a given amount of *Sphagnum* and then tested with ammonium hydroxide and with silver nitrate and the resulting colour and precipitate respectively compared with those given by control portions of the original solutions—the colour (test for copper) was weakened while the amount of precipitate (test for chloride) was the same before and after treatment, hence a large amount of copper had been removed while the acid radicle was present in undiminished quantity and the solution had acquired a strong acid reaction. (2) Localisation of the acid compounds. Since Baumann and Gully give no experimental evidence for their view that the walls of the hyaline cells are the chief seat of the colloids, this point was investigated, leaves and leafless stems being placed separately in NaCl solution; the stem was found to be slightly more active than the leaves and small branches, probably owing to the greater thickness of the cell-walls. The removal of such substances as chlorophyll and fats by boiling successively in ether, alcohol and water had no effect on the acid reaction; this was reduced to two-thirds by prolonged treatment with chloral hydrate which almost entirely removed the cell contents including the protoplasm, but probably the walls also undergo alteration by this powerful reagent. (3) Occurrence of the acid reaction in other plants. Besides *Sphagnum*, other plants gave an acid reaction, confirming Baumann and Gully's statement that several mosses have the same properties and Wieler's statement that this is the case with the cell walls of vascular plants also; the average acidity of *Sphagnum* is 0.07, and most of the other objects tested are less active and lie in or below the region of the less active species of *Sphagnum*. The acid properties are widely distributed among plants, and to them is certainly to be attributed the acid nature of humus; the action of chalk on the soil, besides the direct neutralisation of acids therein, will be to saturate the acid compounds of the plant remains and so prevent them breaking up salts in the soil solution, i.e. it prevents the souring of the soil indirectly as well as directly. (4) Variation of acidity in different species of *Sphagnum*. To ascertain whether the differences in acidity shown by different *Sphagnum* species were secondary and not primary, on the ground that were all

the species of the same initial acidity then those living in stations with low mineral supply would absorb less base than those in more favourable stations and would retain more unsatisfied acid, i.e. would appear to be more acid, the author washed out the absorbed bases and determined the acid in the washed material. On washing with water saturated with carbon dioxide, which removed about 90 per cent. of the absorbed base, it was found that while the acidity was increased there was no general levelling up between the different species—i.e. the difference of acidity is primary, supporting Paul's conclusion that species living in stations poor in food materials require the highest acidities in order to obtain the necessary amount of bases. (5) *Sphagnum* and chalk. The author discusses the relation to calcium carbonate under two heads: (a) Is the sensitiveness different in the different species? (b) In what does the toxic action of chalk consist? As to a, the author's results confirm Paul's view in principle, i.e. the species studied were sensitive to chalk in different degrees and the more acid species are the more sensitive, but he finds that the correlation cannot in practice be followed out in fine detail—for one thing, the determination of the fatal dose of chalk is a matter of great difficulty. As to b, the theory that the toxic action of chalk is due to saturation of the *Sphagnum* acids and subsequent derangement in metabolism does not appear probable in view of the experimental evidence. If the saturation acts directly, it is difficult to see why high concentrations should kill the highly acid species and not those with low acidity. It is also difficult to conceive the mechanism of an indirect action, for the *Sphagnum* cannot feel the want of fresh absorbed base at once since it is capable of living and growing in distilled water for a long time at the expense of previously absorbed base—a *Sphagnum* supplied with a fatal amount of chalk dies promptly and shows no signs of attempting to manufacture a fresh quantity of acid compound by temporarily increased growth. Since alkalis are found to act in precisely the same manner as does chalk, while acids at low concentrations exercise a decided stimulating effect on growth, the author concludes that the harmful effect of chalk and of alkalis probably lies in the fact that they deprive *Sphagnum* of the acid reaction which is beneficial to it. The method by which *Sphagnum* obtains its supply of food bases entails the liberation of the acids of the salts concerned, hence the plants are normally bathed in an acid solution; the reaction was at first an accidental accompaniment of another process but has now become a necessity for the moss. Those species living in stations where the salts and consequently also chalk are scarce require a large quantity of acid compounds, they are doubly secured from ever encountering an alkaline reaction; those inhabiting the more favoured low moors, both because they are less acid and because chalk is more abundant in their environment, have more chance of being subjected to the influence of a neutral or alkaline medium. It naturally follows that the former are more sensitive than the latter. Whether or not the connexion between acidity and sensitiveness be explainable in some such way as this, it would appear that the preference of *Sphagnum* is for an acid reaction and its repugnance, in the case of chalk as in other cases, for an alkaline one. (6) *Sphagnum* and mineral solutions. Water culture experiments made by the author yielded no data as to the nutrient value of the salts employed, but they showed that the less acid species of *Sphagnum* can flourish in quite high concentrations of mineral solutions, thus far going against the widely accepted view that *Sphagnum* is sensitive to high concentrations, as such, of mineral solutions; but though the more resistant species of *Sphagnum* grow well in solutions of a salt content similar to that offered in water culture to higher plants, it does not follow that these conditions will be equally favourable in nature—it was found that after about two months a vigorous growth of algae occurred, these plants then completely covering the *Sphagnum* and making its healthy growth impossible, and the same thing can be seen frequently in the field with *Sphagnum* growing in ditches.

(V) It has long been known that various mosses and liverworts will continue to grow when submerged in water, the new thalli or leafy shoots produced under aquatic conditions differing more or less markedly from those normally formed under aerial conditions. In this paper, Schoenau deals chiefly with the discolouration undergone by the leaves of species of *Polytrichum* when plants are submerged in ordinary tap-water—the old leaves turn brown and eventually almost black, while the tip of the shoot continues to grow and gives off branches bearing green leaves of simpler structure. The discoloured leaves are not killed, as might be supposed; their cells show normal chloroplasts with starch grains, and are capable of plasmolysis, while these leaves can give off protonema from which new plants arise. The discolouration is confined to the cell-walls. The cell-walls of bryophytes show various chemical peculiarities: they rarely give direct cellulose reactions, and never those of cork or woody substance, but on the other hand they often contain pectic substances, fats, and also two characteristic bodies called sphagnol (a phenol-like substance especially abundant in *Sphagnum*) and “*Dicranum*-tannic-acid,” which apparently occur combined with cellulose, since cellulose reactions are given when these substances are removed from the cell-walls. The cell-walls of the leaves of Polytrichaceae contain cellulose, pectin, fat, sphagnol and tannin, and the browning of the walls is due to the oxidation of the tannin in an alkaline solution. This occurs when the water has been deprived of its carbon dioxide by the carbon assimilation of the submerged leaves, so that the bicarbonates originally present in the water are converted into basic carbonates, while the oxygen given out by the leaves hastens the process which results in the browning of the cell-walls. A similar phenomenon occurs in *Sphagnum rubellum*, which in presence of alkali becomes blue, the colour change being here also attributable to tannin-like substances in the cell-walls; but while in *Sphagnum* this colour change indicates the death of the plant, in *Polytrichum* the leaves remain alive not only in ordinary water but also in dilute alkaline solutions. Like *Sphagnum*, *Polytrichum* gives an acid reaction and is very sensitive to alkalis, alkaline solutions being much more injurious than acids, which the plants can resist in a remarkable degree. For instance, *P. strictum* remained uninjured for over 12 hours when placed in a 0.1 per cent. sulphuric acid solution, which immediately acted injuriously on *P. commune*; Schoenau connects this difference with the different habitats of these two species, *P. strictum* growing along with the acid Sphagna while *P. commune* grows chiefly in woods and only here and there occurs in Sphagneta. When *Polytrichum* plants are killed by treatment with acid the leaves show a yellow colouration due to disorganisation of the chlorophyll, the cell-walls remaining colourless.

(VI) The observations made by Boas also start from the fact that various subaerial mosses grow well when submerged in water. He gives the results of growing a considerable number of liverworts and mosses in tap-water, distilled water, and in various solutions. As to growth in acid solutions, he confirms Schoenau's observation that *Polytrichum* is much less sensitive to acids than to alkalis, and finds that acid solutions strongly promote the growth of the plant, the best concentrations being 0.002 per cent. in the case of sulphuric acid and 0.001 per cent. in that of nitric acid. The effects of various chemical compounds upon different bryophyte species varied very considerably; no conclusions of biological interest are apparent from the data given. It is interesting, however, to note that *Polytrichum*, *Dicranum* and *Hylocomium* were able to survive a long sojourn in water which had been boiled to drive off dissolved air and placed in tubes which were evacuated at about 220 mm. pressure and sealed up; evidently terrestrial mosses resemble aquatic plants in their ability to live and even grow in the absence of an external supply of oxygen if necessary, and doubtless in nature this is a useful faculty in the case of plants liable to be submerged at times.

(VII) As is well known, practically every tissue and every living cell of a liverwort is capable under favourable conditions of giving rise to a new plant; in the case of the leafy Jungermanniales, as in mosses, a filamentous protonema is usually first formed, and from this the new shoots arise. In many cases, however, regeneration takes place by the outgrowth from the stem of adventitious or "innovation" shoots, without the intervention of protonema. In most investigations on these processes of regeneration the different organs or pieces of them have been artificially separated from the plant and cultivated in a moist atmosphere, but since the process is frequently seen in nature the question arises whether the stimulus to regeneration may not come from causes other than injury or decay of parts of the tissue, etc. Garjeanne observed that a patch of *Alicularia* (*Nardia*) *scalaris*, growing in a place flooded by autumn rains and covered to a depth of about 5 cm., showed numerous slender small-leaved ventral branches, such as do not normally occur in this plant; hence submergence evidently induces the formation of those innovation shoots or stolons which may become detached and give rise to new plants. He cultivated the plants under water and found that after some months the tissues became disorganised and decayed, though certain cells remained alive, retaining their green colour and functioning as cysts or resting-cells. The new shoots formed meanwhile under water, though much more resistant to the action of water than the old parts of the plant, showed various modifications in the form, cell-contents and cell-walls of the leaves, some of which are interesting from the fact that they are constant and even diagnostic features of other species of *Alicularia*. For instance, the leaves were very often indented in the middle—a normal feature in *A. breidleri* and sometimes found in *A. compressa* and *A. geoscypha* but not in the type or the described varieties of *A. scalaris*; the oil-bodies were frequently warty, as in *A. geoscypha*, instead of smooth; and the cell-walls were not thickened at the corners—this, however, is a usual feature in varieties of leafy liverworts growing in wet places or under water. The author does not appear to be familiar with the literature of the subject, for many of the modifications which he described as occurring in his cultures of *A. scalaris* are normally found in varieties of this species which grow in wet places, the "type" being connected by intermediate forms with varieties which grow submerged; but these submerged forms have never been fully described, and Garjeanne's paper is of interest as indicating the plastic nature of the leafy as well as the thalloid liverworts and the modifications in form and structure induced by changes in water supply and other conditions of growth, such as they may be exposed to in nature. There is room for much further work on this subject, but it is necessary that those taking it up should in the case of each species investigated be familiar with the characters of the plants found growing under different natural conditions, not merely with those of a single batch of plants found in some one particular habitat.

(VIII) Various observations have been made during recent years on the germination of moss spores under different external conditions of temperature, light, food supply, etc., and it would seem probable that these may have a bearing upon the ecology of mosses, and should be taken into account, for instance, in any attempts to explain the occurrence of certain species on acid and of others on neutral or alkaline substrata, and the apparently sharp distinction between "calcicolous" and "calcifuge" species or varieties. Borodin (1868) found that moss spores would not germinate in darkness on inorganic substrata, but Heald (1898) showed that germination occurred in darkness in culture solution containing sugar or peptone, though stimuli such as increased temperature or etherisation which promoted growth of the mature plant did not induce germination in darkness; Schulz (1902) however concluded from his experiments that light could not be replaced by any other factor—for instance, the spores in his sugar cultures simply swelled up, the sugar not being assimilated but stored as starch. Treboux (1905) found that

good growth of protonema was obtained in darkness in a purely inorganic medium if the spores were first induced to germinate by supplying sugar, and he regarded this fact as being of ecological importance, since in nature moss protonema is probably capable of saprophytic nutrition, while the capacity for germination in weak light might also be an important ecological factor. Laage (1907) cleared up some of the discrepancies in previous accounts by finding that the failure of moss spores to germinate in darkness in inorganic media is due to too high concentration of the culture solutions used; he obtained germination by simply adding traces of sodium chloride and other salts to distilled water. Becquerel (1904) found that for normal development of the protonema of mosses the culture solution must contain the same elements as in the case of higher green plants.

Kessler's investigations were undertaken mainly in order to ascertain whether the influence of the substratum on the growth and distribution of mosses is exerted upon the germinating spore and protonema or only comes into play at a later stage in the plant's life history; but as his work proceeded he encountered and attacked experimentally various other problems. He found that the germination of moss spores is markedly influenced by the reaction of the culture solution. Germination is favoured by alkalinity in the case of mosses normally growing on alkaline substrata (lime-rich schists, limestones), indeed the spores of most of the "calciphilous" mosses experimented with were unable to germinate in even a slightly acid medium. On the other hand, an acid medium gave the best results in the case of species limited to acid substrata (chiefly *Sphagna* and *Polytrichaceae*); in some of the *Polytrichaceae* germination was possible in a slightly alkaline medium but the protonema soon perished without giving rise to adult plants, while in the case of *Sphagnum* no germination took place. In neutral media germination took place in all the species dealt with. In short, most of the species germinated almost equally well in acid, neutral and alkaline media, with the exception of (1) the *Sphagna*, *Polytrichum commune*, *P. piliferum* and *Tetraphis pellucida* which failed altogether to germinate in even slightly alkaline media (other mosses of this "acid" group germinated but feebly, e.g. *Pogonatum aloides* and *P. urnigerum*), and of (2) the pronouncedly "calcicolous" species (*Hypnum commutatum*, *Grimmia pulvinata*, *Orthotrichum sexatile*, etc.) which failed to germinate in an acid medium. Bessler tried the effect of placing spores of "acid" and of "alkaline" mosses in alkaline and acid media respectively, and later reversing the reaction of the solution. For instance, *Funaria hygrometrica*, which germinated only in alkaline and neutral solutions, was sown in acid solution; *Polytrichum commune*, which germinated only in acid solutions, was sown in alkaline solution. After good germination had taken place in control cultures of *Funaria* in alkaline and *Polytrichum* in acid solutions, the reaction was reversed, when the hitherto ungerminated spores at once showed germination; on the other hand, *Funaria* spores allowed to remain in acid solution and *Polytrichum* spores allowed to remain in alkaline solution showed no signs of germination at all even after a month.

In order to ascertain to what extent and in what manner lime content determines the distribution of the typical "silicicolous" or "calcifuge" and the "calcicolous" moss species, Bessler used normal neutral culture solution mixed with equal volumes of varying strengths of calcium bicarbonate solution—the latter prepared by adding 1 gm. of precipitated chalk to 1 litre of distilled water, passing carbon dioxide through for an hour, filtering off the undissolved carbonate, and diluting to 10, 1 and 0.1 per cent. The tabulated results of germination and protonema growth show the existence of the same relation between habitat and the influence of lime as was found to exist between habitat and that of the reaction of the culture solutions. That is, the "acid" mosses—those which grow on acid-reacting substrata and which prefer or require acid culture solutions—

scarcely germinated in dilute and not at all in strong calcium bicarbonate solutions; the species which grow in neutral or weakly alkaline solutions and which occur chiefly or exclusively on lime-free or lime-poor rocks behaved similarly. On the other hand, of those mosses which occur on lime-rich substrata and show in culture a strong preference for alkaline reaction, some germinated both in dilute and strong lime solutions, but others (e.g. *Orthotrichum saxatile*, *Barbula muralis*) failed to grow in dilute solutions and showed increasingly strong growth in solutions of increasing strength. From a comparison of the results obtained with acid and alkaline culture solutions, dilute acids and alkalis, and calcium bicarbonate solutions of different strengths, Kessler concludes that the influence of lime upon the growth of mosses is to be attributed to the alkaline reaction of calcium carbonate and not to the calcium itself. The results of his experiments on spore germination and protonema growth agree with those obtained by Paul and Schoenau as to the behaviour of mature moss plants towards lime-content and alkaline reaction; Paul cultivated various species of *Sphagnum* in water containing calcium carbonate and other alkaline salts of different concentrations and found that in all cases the plants perished (see IV) while Schoenau showed that the Polytrichaceae are also extremely sensitive to alkalis (see V).

Various writers have described the occurrence of an incrustation of calcium carbonate on mosses growing on rocks bathed by water rich in lime. In various species which he cultivated in order to obtain the ripe spores, Bessler observed small white or yellowish masses of calcite crystals on the tips of the leaves; the species showing this grow in nature on lime-free substrata, and it was never observed in species growing on lime-rich rocks or soils. While a general encrusting of lime is attributable to carbon assimilation, this explanation cannot apply to these deposits on the leaf-tips, which are evidently due to actual excretion of lime such as occurs in the chalk-glands of higher plants. The mosses showing this phenomenon (Polytrichaceae, *Dicranum* spp., *Bartramia* spp.) were grown in distilled water, in somewhat "hard" tap-water, and in solutions of calcium bicarbonate, nitrate and chloride; lime excretion was seen only in the plants grown in tap-water, those grown in higher lime concentrations showed the yellow and brown discolouration of the leaves observed by Schoenau (see I, above). Bessler found a similar excretion of lime, in the mosses mentioned, in plants growing in nature, and he suggests that, although as shown by experiment the spores of these mosses germinate poorly in alkaline solutions, their capacity for lime excretion may enable them to establish themselves on the same habitats as mosses which germinate well on alkaline substrata, so that this may afford at least a partial explanation of the frequent occurrence of so-called calcifuge mosses on rocks or soils tolerably rich in lime.

From the data given by Grimme (1903) for the time of "flowering" and the duration of the sporogonium of Central European mosses, and the habitats of these mosses as given in Rabenhorst's *Kryptogamenflora*, Kessler deduces some interesting generalisations as to the relation between habitat and time of fruiting. As a rule, mosses of dry sunny habitats ripen their sporogonia in spring, while those of moist habitats appear to follow no general law. Grimme divided the habitats of mosses into extremely dry (walls, roofs, dry sun-exposed rocks, etc.), fairly dry (well-lighted woods, exposed soil surfaces, tree-trunks, etc.), fairly moist (meadows, shaded woods, ravines, etc.), and extremely moist (flooded rocks, stream margins, etc.). For these four groups Kessler gives a curve showing the percentages of the species which ripen their sporogonia in winter, spring, summer, and autumn (Fig. 24). It will be noticed that in all four cases the minimum occurs in autumn; that the mosses of extremely moist habitats ripen fruit chiefly in summer, the curve for these being much more uniform than those for the other three habitat groups, all of which agree in showing a maximum in spring; and that the mosses of very dry habitats

show a much higher spring maximum and lower autumn minimum than the rest. That is,

Winter, Spring, Summer, Autumn, Winter.

Fig. 24. Curves showing the times of spore-ripening in mosses of different habitats. (From Kessler.)

— very moist. - - - - - fairly moist.
 fairly dry. ——— very dry.

moisture for germination is available. In the case of mosses of dry habitats, exposed to rapid evaporation, the period of maximum water-content (February to April) is somewhat earlier than that of maximum spore-ripening, but the latter occurs during the most favourable period for spore-dispersal, i.e. between the maxima of water-content and rainfall, a period during which water-content falls off very slowly owing to the compensating increase in rainfall; in autumn, when water-content reaches its minimum, none of these mosses show ripe fruits. In general, therefore, the time of spore-ripening of mosses of different habitats shows a close correlation with the moisture conditions obtaining in these habitats, the spores being shed at the time when the conditions for germination are most favourable.

An interesting point brought out by Kessler is that the spores of mosses which grow on dry rocks show relatively high specific gravity and immediately sink in water, while those of mosses inhabiting water-flushed rocks and other moist habitats float in water. He experimented with spores of mosses of the latter class, and found that their floating power was not due to an air-film on the surface nor to air contained in the spore-coat; when the spores were treated with cold alcohol or ether and then with water they still floated, so that oil-content is evidently not the cause, and since Kessler could find no difference in coat behaviour or in nature of contents between the sinking and the floating spores the explanation of the higher specific gravity of the former is left open for further investigation. In any case, the heaviness of the spores of dry-rock mosses is obviously an advantage to such species, since the spores when wetted during rains will tend to settle in chinks of the rock and germinate there, whereas those of other mosses would be carried away by flowing water. Another peculiarity of the spores of dry-rock mosses is that they germinate very slowly as compared with those of other mosses. Germination experiments with 30 species of widely differing habitats showed that those of dry habitats gave after

the moister the habitat the more uniform is the distribution of the fruiting-time over the year. The rainfall in Central Europe shows a summer maximum and a winter minimum; in general, in passing from the coast inland the spring and summer rainfall increases while the autumn and winter rainfall diminishes. According to Ramann (*Bodenkunde*, 1911) the water-content of the soil shows in spring and early summer a rapid decrease concomitant with the awakening of vegetation in general; this decrease continues, though moderated by the summer rains, until in autumn (in September and early October in Central Europe) the minimum is reached, then with the oncoming of winter the soil receives more moisture than is lost by evaporation and the transpiration of plants and becomes gradually saturated, the maximum water-content being attained between February and April. As compared with dry and exposed habitats, moist and shaded substrata show less variation in water-content and the mosses ripen their spores throughout the year, since at all times sufficient

a week a germ-tube only equal in length to the spore diameter, those of wet habitats a germ-tube 10 to 12 times longer than the spore, and those of intermediate habitats germ-tubes of intermediate lengths. An interesting exception to this rule was shown by *Polytrichum piliferum*, *Pogonatum aloides*, *Tetraphis pellucida* and *Sphagnum*, which though often growing in moist habitats showed very slow germination; but as already shown these are mosses which grow only on acid substrata, and this fact would protect them from competition with other mosses which germinate in neutral or alkaline media. Although in nature the differences in rate of germination between the spores of dry and moist habitats may not be so striking as those found in cultures, it is very probable that such differences do occur under natural conditions, and if so they would go far to account for the distribution of mosses—the spores of mosses of dry exposed habitats will on the whole have a better chance of wide distribution by wind, and the restriction of such mosses to dry habitats may be due to the much more rapid germination shown by mosses adapted for life in moist habitats, while on the other hand the spores of the latter may be prevented from colonising dry rocks owing to their floating spores being washed away from the rock surface.

Kessler's results are so interesting and suggestive that it is greatly to be hoped that further work will be done along the largely novel and very promising lines and methods which he has indicated. It need hardly be added that field observation and laboratory experimentation must go hand in hand if results of real ecological value are to be attained, and that the investigations must be undertaken on an extensive scale in both cases.

(IX) The author describes a wet heath association on Chard Common in Somersetshire, in which the dominant flowering plants are *Molinia caerulea*, *Erica tetralix* and *Myrica gale*. The portion chosen for detailed study is a gently sloping field along two sides of which runs a stream fed by many small tributaries which in turn are fed by water from a network of furrows between the *Molinia* tussocks. The tussocks vary in width and height from a few cms. to about a metre, and the furrows separating them are intermittent or continuous water channels of varying depth. The zonation of vegetation from the wet to the drier and more exposed positions is evident by the distribution of the vascular plants but is shown in greater detail by the bryophytes. Apart from the lowest zone which is dominated by *Potamogeton polygonifolius* six zones are distinguished each characterised by the dominance of a bryophytic species. The first (shallow-water or marginal) zone presents three facies with (1) *Aneura pinguis* and *Pellia epiphylla*, (2) *Hypnum scorpioides* and (3) *Sphagnum cymbifolium* respectively; the alternation of these three facies seems to depend on the supply of fresh water, the first facies occurring where the water is continually being replaced, the pockets of the *Sphagnum* being formed in depressions which are nearly always wet, while the *Hypnum* occurs in smaller patches in shallow peaty pools whose surfaces are above those of the interlinking channels. The second zone, at the sides of the furrows just at the water level, consists of almost pure *Aneura multifida*, occurring immediately above the *A. pinguis* and *Pellia* zone and sometimes extending down into it; where the facies of *Hypnum scorpioides* or of *Sphagnum cymbifolium* occurs, *A. multifida* may form the next zone in a wet to dry succession but is not so definite as when it abuts directly on the *A. pinguis* and *Pellia* facies. The third zone shows two alternative facies, the dominant bryophyte by the margins of the smaller channels being *Sphagnum subnitens*, which is almost entirely replaced by *Hypnum intermedium* by the sides of the more definite tributaries where there is a slow but constant current; the *Hypnum* seems to require a more constant water supply because it cannot take up so much water as the *Sphagnum*. The *S. subnitens* is accompanied by other *Sphagnum* spp., *Cephalozia connivens* and *Calypogeia fissa*; the *H. intermedium* by other *Hypnum* spp. The fourth zone, characterised by

Hypnum cuspidatum, is seldom sharply distinguished from the third, though sometimes this moss forms a fairly definite border, and it is accompanied by either *H. intermedium*, *H. giganteum*, or *H. stellatum*, while occasionally *Sphagnum subsecundum* becomes dominant and is mixed with *Calypogeia trichomanis*. The fifth zone is dominated by *Brachythecium purum*, accompanied by *Cephalozia connivens*, a tufted form of *Aneura multifida*, *Sphagnum papillosum*, etc. In the driest part of the tussocks bryophytes are scarce, the only frequent one, forming a sixth zone, being *Hypnum cupressiforme* v. *ericetorum*.

The heath is regarded as the remnant of a formerly much more extensive one and as representing a stage, showing a number of successional phases, between a wet undrained peat-moss (Sphagnetum) and a dry heath, this view being supported by the marginal associations and the local history. The two main factors determining the succession are increased drainage, leading to diminished soil mixture, and increased accumulation of humus on the hummocks isolated by the drainage channels. Five stages of succession are distinguished in the present vegetation. (1) Sphagnetum recurvii, the wetter pockets of *S. recurvum* representing a more primitive condition of the heath than those of *S. cymbifolium*. (2) Sphagnetum subnitentis, *S. subnitens* becoming dominant as the heath became drier while the *Hypnum* and *Sphagnum* spp. now prevalent in the lower swampy portion and in the pockets gradually retreated to the wetter areas, erosion of humus from these and its retention and increase on the drained areas then enabling the establishment of the next stage. (3) Molinietum which does not here, as appears general in cases of progressive desiccation of a Sphagnetum, follow an intermediate Eriophoretum stage. (4) The central portions of the *Molinia* tussocks are invaded by *Ulex gallii*, *Potentilla erecta*, *Holcus lanatus*, etc., though *Calluna* has not yet obtained a footing in these areas. (5) On the drier edges of the wet heath and on the adjoining dry heath there occurs an extension of the fourth succession phase, or what may be considered as a fifth, with a rich vegetation of characteristic dry-heath plants.

This paper is illustrated by exceptionally clear and instructive diagrams showing the distribution and relationships of the vegetation zones described, besides figures of the various growth-forms of some of the characteristic bryophytes.

SOME RECENT WORK ON TRANSPIRATION

- (I) **Darwin, F.** "On a method of studying transpiration." *Proc. Roy. Soc. Lond.*, B, **87**, 1914, pp. 269-280.
- (II) **Darwin, F.** "The effect of light on the transpiration of leaves." *Ibid.*, pp. 281-299.
- (III) **Blackman, V. H.**, and **Paine, S. G.** "A recording transpirometer." *Ann. of Bot.*, **28**, 1914, pp. 109-113.
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- (V) **Dixon, H. H.** "Transpiration and the ascent of sap in trees." London (Macmillan), 1914, 216 pages; price 5s. net.
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