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Data on the Ecology of Bryophytes III

The Significance of Hydrogen-Ion Concentration on Germination of Spores and Development of some Mosses

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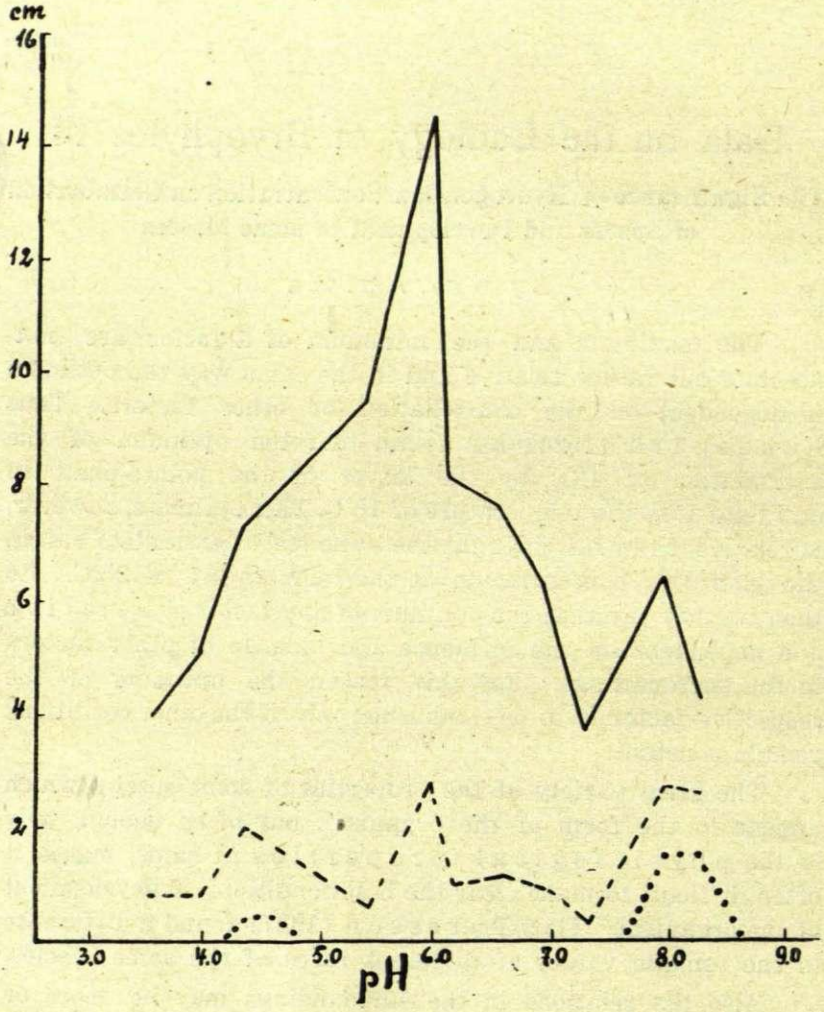
The maximum and the minimum of a factor are not absolute but rather relative and in the same way the optimum is dependent on the constellation of other factors. Thus Lundegård (1924) has found that the optimum of the assimilation of CO_2 by the leaves of the potato-plant in dull light is at the temperature of 10°C. This optimum, however, is relative, as in full daylight the same leaves assimilate best in the same CO_2 concentration at the temperature of 20°C. So then we may say that the optimum of any factor is relative and dependent on the influence and balance of other factors in the surroundings. For this reason the optimum of the respective factor is to be established only if the other conditions remain constant.

The great variety of the properties of some species which appear in the form of the organism, but often enough only in the physiological properties of same, makes it often difficult to make clear the best conditions of development of the organism. Thus Turesson (1927) found a difference in the osmotic values of different races of the same species.

Also the relations in the surroundings may be more or less specifically different for the stages of development of a plant. Growing *Trapa* seedlings in solutions with differrent pH (pH 3.5—8.3) it was established in repeated tests that fruits germinate quickest in alkaline solutions (pH 7 . 9—8 . 3), less quickly in acid (pH 4 . 2—5 . 2) and most slowly in neutral and moderately acid solutions (pH 5.2—7.8).

After remaining two weeks in strongly alkaline solution where the seedlings were most quickly germinating from the very start, the seedlings died. The same occurred with those which germinated in strongly acid solutions. Those germinating in moderately acid and neutral solutions later developed best. The same is recorded of fruits which were kept in cultures with the same pH at a lower temperature for a considerable time but afterwards transferred to higher temperature for



Length of *Trapa* seedlings in the following developmental stages.
. . . . . After two weeks . . . . . . — 4th March 1938.
— — — — After two weeks and 5 days — 9th March 1938.
———— After two weeks and 13 days — 18th March 1938.

germination. For this reason it can be said that for the first stage of development the alkaline solution is most favourable, but later while the seedlings differentiate the functions of them cannot adapt themselves to those solutions and the young plant dies. Of course, if the seedling is then transplanted to a neutral solution or given the possibility to regulate the alkalinity of the solution, its development is not hindered. I believe that this example will illuminate also the part of different developmental stages in the optimum. Proving the peculiarities of the different developmental stages, the example quoted shows that as to the cH factor there are two optima of germination, but later, in the growth, there is only one optimum. These facts are observed also in the case of the germination of the spores.

W e b b (1921) found two maxima for the germination of spores of several fungi *(Aspergillus niger, Botrytis cinerea, Fusarium)*. Also H o p k i n s (1922) established in the growth of *Gibberella* 2 maxima and the minimum of pH 5 . 5—6 . 0. B e r g (1929) in germinating pollens, found even 3 maxima. It can be concluded from these facts that the optimum of germination of spores is by no means monolythic, but is usually divided in two or three parts. This critical or minimal point, observable in the optimum of germination and growth, which exists for different species at a different pH, but often at about pH 5 . 0, has in the conception of the American scientist R o b b i n s (1928) met with a well reasoned explanation. He explains this minimum in the optimum by the dependence of the state of the protoplasma on the pH of the solution, provided the constituents of the protoplasma, the so-called ampholites in the cell, behave like the protein-hydrosoles in the electric field. Therefore R o b b i n s and other authors suppose that these minima in the optimum of the germination and growth of plants are to be identified with the isoelectric state of the ampholites of the protoplasma (I. P. E.).

The researches of L o e b (1922) also give evidence that many properties of proteins like gelatine in the isoelectric state, as conductance, viscosity, osmotic pressure, etc. are most minute, while some other properties, as e. g. coagulation by high temperature, are greatest. The protoplasma in the living cell behaves likewise, as obvious from special researches in this direction by several scientists.

Among the green plants, mosses are known to have a specific pH amplitude on natural substrata. Wide observation of materials and literature have allowed of the definition of the absolute and optimal limits of growth conditions for the cH factor in the substrata (A p i n i s and L ā c i s 1936) of each species. According to the respective pH amplitudes the species of mosses are divided into 13 groups and these in their turn into 3 classes:

A. Mosses of acid substrata.
B. Mosses of moderately acid and weakly alkaline substrata.
C. Mosses of alkaline and neutral substrata.

As to mosses, being a large plant group, a powerful mode of distribution by one-cell spores is established. Taking into consideration the above-mentioned reaction of mosses towards the substrata in natural conditions it was necessary to ascertain the dependence of the cH on the germination of moss-spores.

This problem has already its own history. Treboux (1905) growing the protoneme of mosses, observed that two acid substratum mosses *(Sphagnum* and *Dicranella cerviculata)* germinated better in an acid culture solution.

Kessler (1914) found that the germination of moss spores is greatly dependent on the reaction of the solution. It was possible to state that mosses of limestone substratum germinate well in alkaline solutions or in water clouded by this substratum. Spores of mosses growing in bogs and other acid substrata germinate better in acid synthetic solution or in extractions of the respective acid substrata. Likewise mosses of weakly acid and neutral mineral substrata germinate best in neutral and moderately acid solutions. It must be stated that at that time the authors mentioned possessed no precise cH indicating methods, for which reason their conceptions only approximately correspond to the real facts.

Pringsheim (1921) sees no significance in the reaction of the solution for the germination of moss-spores and the development of protoneme. He reaffirms this in his work which appeared in 1935.

Ikenberry (1936) in enquiring into the dependence of germination of moss spores of various substrata on pH of the solutions, found that usually there is no sufficient connection with pH values of the substratum. There is, however, a connection between the optimum of germination of spores and growth of protoneme on one hand and pH of the substratum in nature on the other hand.

It is apparent from the above that there is a certain uncertainty about this matter. Therefore continuous observations of ecologically different species have been arranged in experiments on germination of spores, development of protomeme and moss plants in pure cultures under different cH conditions.

Materials and Methods

For these experiments *Sphagnum plumulosum* Röll was collected by myself in the spring of 1934 at Ķemeri with immature spore capsules. For about a month I grew the tufts in the laboratory until the spores in the capsules matured. These were then stored with the capsules in small test-tubes with stoppers of cotton. The plant grows in natural conditions in boggy pine forests and wet leafy woods. Nordhagen (1928) found the pH values of the substratum 5.2 and 5.3. Therefore this species is to be counted among the mesoacidophilous mosses.

Matured capsules of *Funaria hygrometrica* (L.) Sibth. have been collected in small test-tubes at Ķemeri at the edge of a boggy forest on the site of an old fire on 14th August 1932. Several races of this species are distributed in our territory on limestone covered with soil, on dolomite, sandstone (Old Red), old walls, gravel soil, but especially on places where there have been fires, where they develop very well. The acidity of the natural substrata varies, between pH 5.3 to 8.3, usually 6.1—8.0 (Apinis and Lacis 1936). This moss thus belongs to the meioeuryionic plants.

The *Polytrichum juniperium* Willd. spore material was collected at Vecāķi in a dry pine forest on dune sand substratum on 17th July 1932. The plant usually grows on acid humous sand substratum in pine forests, on dry turf and other similar places. The pH interval of substrata in natural conditions has been established for 22 samples, being 4.0—5.9 (Apinis and Lacis 1936). The plant belongs to the acidophilous mosses.

The indispensable condition of experiments and observation of spore germination and development is a pure culture. Therefore the solutions or other synthetic substrata and culture-dishes were sterilized in autoclaves at 120° C for half-an-hour. Also the spore material for the respective series of cultures was obtained aseptically from several capsules, carefully blended, and then by means of a sterile platinum needle the spores were introduced into the solutions (cultures).

The pH series of culture solutions are primary ($m/15\ KH_2PO_4$, or 9.078 gr in 1 lit. redistilled water) and secondary ($m/15\ Na_2HPO_4 \cdot 2H_2O$ or 11.878 gr in 1 lit. redistilled water) K-Na phosphates according to Sörensen (1909). A greater alkalinity or acidity respectively in the phosphate pH series is obtained in individual cases by n/10 NaOH and n/10 H_3PO_4. The content of phosphates in all culture solution series was as follows:

No. 1	20 ccm m/15 $Na_2HPO_4 . 2H_2O$			pH 8.3
No. 2	19.4 „ „ „	„	0.6 ccm m 15 KH_2PO_4	pH 8.0
No. 3	19.0 „ „	„	1.0 „ „	pH 7.9
No. 4	16.0 „ „	„	4.0 „ „	pH 7.3
No. 5	14.0 „ „	„	6.0 „ „	pH 7.2
No. 6	12.0 „ „	„	8.0 „ „	pH 7.0
No. 7	8.0 „ „	„	12.0 „ „	pH 6.6
No. 8	6.0 „ „	„	14.0 „ „	pH 6.5
No. 9	4.0 „ „	„	16.0 „ „	pH 6.2
No. 10	2.0 „ „	„	18.0 „ „	pH 5.9
No. 11	0.2 „ „	„	19.8 „ „	pH 5.8
No. 12			20.0 „ „	ph 4.5
No. 13			20.0 „ „	0.2 ccm n/10 H_3PO_4 pH 3.8
No. 14			20.0 „ „	1.0 ccm n/10 H_3PO_4 pH 3.3
No. 15			20.0 „ „	3.0 ccm n/10 H_3PO_4 pH 2.8

These phosphate solutions were diluted with 9 parts of redistilled water, i. e. the concentration of salts in the culture solution was about 0.1%. For the culture solutions glass test-tubes of 20 mm diam. have been applied, closed by means of cottonwool and afterwards covered with greaseproof paper to reduce evaporation of the water. The quantity of liquid in the tubes 15 ccm. pH in solutions was indicated electrometrically by means of a quinhydrone electrode or in cases of strongly alkaline solutions and agars by means of Michaelis (1930) indicators at beginning and close of every experiment. In all experiments the vitality of the spores was carefully tested by means of plasmolysis in KNO_3 or sugar solutions.

First Experiment

This series of cultures was commenced with the abovementioned phosphates, which were diluted in 9 parts of redistilled water on the 26th August 1934. There were 15 ccm solution in each test-tube. After placing the spores in them the tubes were closed by means of cottonwool and covered with greaseproof paper to reduce water evaporation. The cultures were placed at a window facing N at the temperature of about 15°C. In this experiment spores of *Sphagnum plumulosum* Röll, *Funaria hygrometrica* (L.) Sibth. and *Polytrichum juniperinum* Willd. were used. The results of tests on the 30th March 1935 are arranged in Table 1.

Table 1

Sphagnum plumulosum Röll

Culture No.	pH 26. VIII. 34.	Tests on 30th March 1935	
1	8.3	Spores brown, swollen, do not plasmolyse	pH 8.3
2	8.0	As previous	pH 8.1
3	7.9	As previous	pH 8.0
4	7.3	As previous	pH 7.8
5	7.2	About the half of spores swollen, plasmolyse, several spores germinating	pH 7.4
6	7.0	Spores swollen, greenish, about ⅓—½ with 15—80 μ long protoneme	pH 7.2
7	6.6	At least three-quartes of spores (plasmolysis) with 15—80 μ long protoneme in the latter little chlorophyll	pH 6.7
8	6.5	Spores little germinating, green and swollen	pH 6.6
9	6.2	As in culture No. 7	pH 6.4
10	5.9	As previous	pH 6.1
11	5.0	All spores swollen, faintly green, half of spores with 15—80 μ long, pale protoneme	pH 5.4
12	4.5	Spores a little swollen, with light brown contents did not germinate	pH 5.1
13	3.8	As in 12, spores a little greenish, no plasmolysis observed	pH 4.3
14	3.3	As. No. 13	pH 3.4
15	2.8	As. No. 13	pH 3.0

Funaria hygrometrica (L.) Sibth.

Culture No.	pH 26.VIII. 34.	Tests on 30th March 1935	
1	8.3	About three-quarters of spores swollen, green, plasmolyse. One third had a pale 30—1100 μ long protoneme	pH 8.1
2	8.0	As previous	pH 7.8
3	7.9	One-third to a half of spores had pale protoneme 30—240 μ long	pH 8.0
4	7.3	As previous	pH 7.5
5	7.2	As No. 4, 16—240 μ long protoneme	pH 7.3
6	7.0	As No. 5, pale protoneme of germinating spores 80—1300 μ long	pH 7.1
7	6.6	As No. 5	pH 6.6
8	6.5	As No. 6. Part (one-third) of spores had light brown contents, others green. Part of brown spores plasmolyse	pH 6.5
9	6.2	Spores as previous. Half of them green contents. Others brown. Half of spores had pale protoneme 30—240 μ long.	pH 6.2

Culture No.	pH 26. VIII. 34	Tests on 30th March 1935	
10	5.9	About three-quarters of spores swollen. Some had to 80 μ long protoneme .	pH 5.9
11	5.0	As previous	pH 5.3
12	4.5	As previous	pH 4.9
13	3.8	Some spores swollen. All had brown contents. Spores did not germinate .	pH 4.0
14	3.3	Spores did not germinate. Contents brown.	pH 3.5
15	2.8	As previous	pH 2.9

Polytrichum juniperinum Willd.

Culture No.	pH 26. VIII. 34	Tests on 30th March 1935	
1	8.3	Spores did not germinate, nor swell, light contents, did not plasmolyse . .	pH 8.0
2	8.0	As previous	pH 8.0
3	7.9	As previous	pH 7.9
4	7.3	As previous	pH 7.6
5	7.2	About three-quarters of spores swollen (plasmolysis), some light green (plasmolysis) some light brown (plasmolysis) some had protoneme of about 80 μ .	pH 7.3
6	7.0	A half to three-quarters of spores swollen, with light contents. A half plasmolyse, some with short protoneme	pH 6.5
7	6.6	About three-quarters to all spore swollen. A third to a half of them green or light green. About a twentieth of them had partly short, more seldom long protoneme	pH 6.5
8	6.5	As previous	pH 6.4
9	6.2	As previous	pH 6.3
10	5.9	As previous	pH 6.0
11	5.0	As previous, but some spores had a 320 μ long protoneme	pH 5.3
12	4.5	Three-quarters of spores swollen light green. A third to a half quite pale (plasmolysis)	pH 5.0
13	3.8	As previous	pH 4.0
14	3.3	As previous	pH 3.4
15	2.8	No germinating spores. A half of spores with light contents	pH 3.0

Sphagnum plumulosum Röll spores germinate in the solutions of the pH interval 5.0—7.2. Weaker germination in culture 8 with pH 6.5. Best germination in cultures with pH 5.0, 6.6, and 7.0. The alkaline solutions pH 7.3—8.3 as well as the acid cultures with pH 2.8—4.5 are detrimental to spores in the prolonged time (no plasmolysis).

To the spores of *Funaria hygrometrica* (L.) Sibth. acid solutions with 2.8—3.8 are detrimental, but this is not the case with the alkaline solutions. The spores of this species germinate at pH 5.0—8.3, but very well at pH 6.0—8.0.

Polytrichum juniperinum Willd. spores do not germinate at all in solutions of pH 7.5—8.3 and pH 2.8. They germinate in solutions of pH 3.3—7.2, very well in pH 5.9—6.6.

Second Experiment

Of the above-mentioned series of phosphates diluted in redistilled water 1:9 a series of 2% agar are prepared. After sterilization and cooling on sloping agar *Sphagnum plumulosum* Röll and *polytrichum juniperinum* Willd. spores were placed by means of a platinum needle in 2 series of cultures on the 26th August 1934. The cultures were placed at a window in the laboratory facing S in usual indoor temperature in indirect sunshine. The results tested on 1st July 1935 are as follows.

Table 2

Sphagnum plumulosum Röll

Culture No.	Tests on 1st July 1935	
1	Spores did not germinate	pH 7.6
2	As previous	pH 7.5
3	As previous	pH 7.5
4	As previous	pH 7.4
5	Spores germinated. Developed a green protoneme	pH 7.1
6	Spores green, strongly swollen, some had short germinating tubes. Protoneme and some moss plants up to 1 mm long on the edge of the agar, attached to the glass of the tube	pH 6.6
7	Spores green, swollen. Some had short protoneme as in previous culture, some 1 mm long moss plants, developed at the edge of the agar attached to the glass of the tube	pH 6.4
8	On the agar a green protoneme and several 1 mm long moss plants	pH 6.3
9	As No. 8	pH 6.0
10	Green protoneme on the agar well developed. Several plants (green) 1 mm long	pH 5.8
11	Green protoneme and several green plants, well developed 2 cm long	pH 5.8
12	Green protoneme, specially well developed green plants 1—2 cm long	pH 5.7
13	As No. 12. Mosses in compact tuft	pH 5.6
14	No plants developed. The culture had dried up.	pH 5.5
15	All as previous	pH 4.3

Polytrichum juniperinum Willd.

Culture No.	Tests on 27th April 1935	
1	Spores germinated, developing green protoneme . .	pH 7.6
2	As previous	pH 7.4
3	As previous	pH 7.3
4	Developed 10 about 2 mm long moss-plants . . .	pH 7.1
5	As previous	pH 6.9
6	No mosses developed	pH 6.5
7	5 mosses about 1 mm long	pH 6.1
8	As previous	pH 5.8
9	8 mosses about 5 mm long	pH 5.8
10	8 mosses about 10 mm long	pH 6.0
11	No moss developed	pH 5.7
12	About 20 mosses developed 2—5 mm long . . .	pH 5.5
13	About 20 plants developed 3—20 mm long . . .	pH 5.3
14	5 plants developed 1—2 mm long	pH 5.1

After 11 months *Sphagnum plumulosum* Röll spores did not germinate in cultures 1—4 as well as in cultures 14, 15. Germination of spores was observed in cultures 5—13, but mosses on agar developed in cultures 8—13. Optimum development of mosses is observed in cultures 12—13 with pH 5.5—5.7 (the agar was mixed with distilled water into a half liquid mass where pH was measured by means of quinhydrone electrodes).

Polytrichum juniperinum Willd. spores germinated in all the pH series but mosses did not develop in cultures 1, 2, 3, 6, 11, 15. Development of mosses was observed in cultures 4, 5, 7, 8, 9, 10, 11, 12. They developed best in cultures 12 and 13 with pH 5.3 and 5.5.

Third Experiment

The phosphates mentioned on page 6 diluted 1:9 being taken, 10 ccm were poured in each test-tube on 15 gr. washed sand. After sterilization, *Funaria hygrometrica* (L.) Sibth. spores were transferred to 2 series of cultures and *Polytrichum juniperinum* Willd. spores as well, on the 28th August 33. Testing the cultures after 5 months, it was found that *Funaria* spores had germinated in all the series at about 50% (pH in all the series at the end was 5.9—7.5). *Polytrichum* spores did not germinate in culture No. 1 with pH 7.5. In culture No. 2 with pH 7.3 a few spores had germinated. In the remaining cultures with pH 4.9—7.2 most spores germinated, making up to 150 μ long protoneme. The cultures with sand dried fairly soon, which fact is considered responsible for the lack of development of mosses.

Fourth Experiment

In this experiment *Funaria hygrometrica* (L.) Sibth. and *Polytrichum juniperinum* Willd. spores in pure cultures were grown on agar with a diluted Knop's solution and $CaCO_3$ or $MgCO_3$ of different quantities not exceeding 5% and in combination of the latter two substances. Also on substrata of washed sand with similar quantity of $CaCO_3$ and diluted Knop's solution. After 10 months these culture series in glass test tubes were tested. pH in the cultures ranged between 7.1 and 9.0, tested by means of indicators. *Funaria* developed on calcium carbonate agar substratum with pH 7.2—8.1 well developing 1—2 cm long mosses.

A similar development was achieved on agar with a minute quantity of $MgCO_3$ (pH 8.5), but with a greater quantity of $MgCO_3$ *Funaria* did not develop moss, but only protoneme. *Polytrichum* spores germinated and even developed 1—2 cm long moss-plants on agar and different substrata with less $CaCO_3$ and pH 6.4—7.2 to the close. Development of protoneme was observed on agar containing less $MgCO_3$ (pH about 8.8), but on agar containing more $MgCO_3$ spores did not germinate. *Funaria* spores on sand and $CaCO_3$ or $MgCO_3$ containing substrata (pH 7.1—9.0) developed only protoneme. Yet *Polytrichum* protoneme were observed on agar with lesser quantity of $CaCO_3$ and $MgCO_3$ (pH 7.4—8.5). On substrata containing more carbonate (especially $MgCO_3$) the latter species did not develop protoneme.

Discussion

The sensitivity of *Sphagnum* species towards lime was already known. Paul (1908) found that the calcium-ion is not detrimental to Sphagna but it is so with calcium carbonate or bicarbonate solutions. Mevius (1921/24) and Olsen (1923) could give evidence by experiments that Sphagna cannot stand lime substrata because of the sensitiveness of these plants towards OH-ions. As proved by previous experiments *Sphagnum plumulosum* Röll spores are also sensitive towards alkaline media. However, development of protoneme is detected also on neutral substrata, but a good tuft of moss of this species develops on substrata with pH 5.5—5.7, which fact corresponds with observations in natural conditions.

Funaria hygrometrica (L.) Sibth. usually grows on lime substrata (subcalciphilous), in pH interval 5.8—8.4, usually in natural conditions pH 6.0—8.0. Ikenberry (1936) has detected germination of spores in solutions of pH 5.0—9.0 with an optimum pH about 6.0. In the experiments mentioned, in solutions and on solid substrata it was found that spores germinate and form protoneme within pH limits of 4.5—9.0, but moss development is detected only on neutral and alkaline substrata pH 7.1—8.8. However, germination of spores may be achieved (Apinis and Bluķis M. S.) in this case even with pH 3.7, yet a further development of moss is not established. Pringsheim (1921) found that *Leptobryum pyriforme* (L.) Wils. is indifferent as to spore germination and protoneme-development to the pH of the solution, but development of the leaf-bearing moss begins in alkaline solution. As is known, the pH interval of this species in natural conditions is 5.3—9.0, usually 6.1—7.5 (Apinis and Lācis 1936). This fact proves that the formation of the moss plant out of protoneme is considerably influenced by the pH of the solution. In order that this may occur in experiment it is necessary that the pH of the solution correspond to the pH interval observed in natural conditions.

Polytrichum juniperinum Willd. grows in natural conditions on acid substrata with pH interval of 4.0—5.9. As established by Schoenau (1913) and Boas (1914) *Polytrichum* species like Sphagna are sensitive towards alkaline solutions. Alkaline solutions dye the mosses deep violet. Ikenberry (1936) has found pH for the germination of spores of this species 5—6 with the optimum 6.0, although in natural conditions they are established also on more acid substrata. Ikenberry tries to explain this fact by saying: "These observations indicate that the various mosses studied are specific in their reactions towards hydrogen-ion concentration during the period of germination and early protonemal development, and it seems reasonable to conclude that at least some mosses may in similar manner show differential reactions towards a certain hydrogen-ion concentration in their later growth." By the first experiment it was established that *Polytrichum juniperinum* Willd. spores can germinate even at pH 3.3 but on solid substratum (agar with carbonates and nourishing solutions) also at pH 8.5—8.9, — yet moss plants develop best on substrata with pH 5.3 and 5.7. A weak development of moss plants is established also on neutral and even weakly alkaline substratum.

As the test-tables and other observations indicate, the germination optimum is not constant, i. e. in the culture series with different pH between the various optima of spore germination and protonemal development one, two or even three optima in development are observable. On these it is intended to render some indications in one of the further works.

Summary

1) The spores of tested mosses can germinate and develop protoneme in a far wider interval of pH of the solution than found in natural conditions of these species.

2) The spores of acidophilous mosses *(Sphagnum* and *Polytrichum)* germinate and develop protoneme better in acid than in neutral and alkaline solutions, but *Funaria* spores (this being a lime substrata moss) germinate and develop protoneme best on weakly acid, neutral and alkaline substrata.

3) Spores of *Polytrichum* can germinate and develop protoneme in alkaline, but *Funaria* spores also in acid solutions, i. e. in a pH interval not found in natural conditions.

4) The vitality of acidophilous spores of mosses is preserved longer in acid solutions, but *Funaria* spores are preserved longer in neutral and alkaline solutions.

5) On a prolonged culture on agar the protoneme of acidophilous mosses *(Sphagnum* and *Polytrichum)* forms moss plants which develop well only in a narrower pH interval. The latter corresponds with the pH of substratum in natural conditions.

6) Protoneme of *Funaria* develop leaf-bearing mosses well on agar with carbonates in neutral and alkaline substrata, i. e. pH interval similar to the natural conditions.

7) The pH interval or optimum of the germination of spores and development of protoneme indicates or indicates only approximately the pH interval of the respective moss in natural conditions.

8) In the species mentioned it was experimentally found that the pH interval of the leaf-bearing moss development or its optimum corresponds to the acidity of the substratum of the respective mosses in natural conditions.

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Materiali sūnu oikoloģijai III

Vides pH ietekme sūnu sporu dīgšanā un sūnaugu attīstībā[1])

Arv. Apinis

Zinams, ka daudzi dzīvā organisma stāvokļi un norises atkarīgi no kāda vides faktora koncentracijas vai intensitates. Pati dzīvība eksistē kāda faktora iedarbības divās robežās, piem., noteiktā temperaturas intervalā. Šajās robežās, ko dēvējam par šī faktora minimu un maksimu, atrodas arī vislabākais organisma stāvoklis, resp. tā attiecīgās dzīvības norises, ko tad apzīmē par optimu. Organisma maksims un minims vidē nav absoluti, bet relativi, tāpat arī optims atkarīgs no citu faktoru konstellacijas. Tā Lundegård's (1924.) atrada kartupeļu lapu CO_2 asimilacijas optimu vājā gaismā 10°C temperaturā. Tomēr šis optims ir relativs, jo pilnā dienas gaismā lapa vislabāk asimilē tai pat CO_2 koncentracijā, ja temperatura 20°C. Tāpēc var teikt, ka kāda faktora optims ir relativs un atkarīgs no citu vides faktoru ietekmes vai līdzsvara. Šī iemesla dēļ arī attiecīgā faktora vides optims precizi novērtējams eksperimentā tad, ja pārējie vides apstākļi paliek konstanti.

Organismu attīstībai vislabāko vides apstākļu noskaidrošanu bieži dara sarežģītu sugu īpašību lielā daudzveidība, kas izpaužas organ. ārējā formā, bet bieži arī vienīgi fizioloģiskās īpašībās. Tā Turesson's (1927.) atrada vienas sugas dažādām rasēm atšķirību to osmotiskās īpašībās.

Arī atsevišķa auga attīstības stadijām attiecības vidē var būt lielākā vai mazākā mērā īpatnēji dažādas. Diedzējot *Trapa* augļus vidēs ar dažādu cH (pH 3.5—8.3), atkārtotos mēģinājumos pierādijās, ka visātrāk augļi izdīgst alkaliskā vidē (pH 7.9—8.3), pēc tam drīzi skābā vidē (pH 4.2—5.2), bet vislēnāk neutralā un mēreni skābā vidē (pH 5.3—7.8). Pēc 2 nedēļām stipri alkaliskā vidē, kur dīgsti visātrāk sākumā izdīga, tie aizgāja bojā. Tas pats notika ar stipri skābā vidē izdīgušiem. Vislēnāk dīgušie mēreni skābā un neutralā vidē attīstijās vēlāk vislabāk (skat. līknes 2. l. p.). Arī zemākā temperaturā pH rindā glabāti augi pēc ilgāka laika apliecina to pašu. Šī iemesla dēļ var teikt, ka pirmām at-

[1]) Nolasīts Latvijas bioloģijas b-bā 1938. g. 6. maija sēdē.

tīstības stadijām vislabāka alkaliska vide, bet vēlāk, dīgstam diferencējoties, tā funkcijas vairs nevar pieměroties šai videi un jaunais augs aiziet bojā. Protams, ja dīgstus pārnes neutralā vidē vai ļauj tiem regulēt vides alkalinitati, to attīstība netiek traucēta. Domāju, ka šis piemērs apgaismos arī dažādu attīstības fažu lomu optimā. Atzīmētais piemērs apliecinādams dažādo attīstības fažu īpatnības rāda, ka attiecībā uz faktoru ch dīgšanas optimi ir divi, bet vēlāk dīgstu augšanā optims viens. Tāda parādība novērojama arī vienšūnu dīgļiem — sporām.

Webb's (1921.) dažām sēnēm (*Aspergillus niger, Botrytis cinerea, Fusarium*) atrada divus sporu dīgšanas maksimus. Arī Hopkins's (1922.) *Gibberella* augšanā konstatēja 2 maksimus ar minimu pH 5.5—6.0. Berga (1929.), diedzējot ziedputekšņus, atrada pat 3 augšanas maksimus. No tā spriežams, ka sporu dīgšanas optims, atkarībā no vides ch, nav viengabalains, bet dalīts parasti divās vai trīs daļās. Šis dīgšanas un augšanas optimā novērojamais kritiskais vai minimstāvoklis, kas atsevišķām sugām ir dažādā pH, bet bieži ap pH 5.0, atradis amerikāņu pētnieka Robbins'a (1923.) uztverē ticamu izskaidrojumu. Šo minimu optimā viņš izskaidro ar protoplazmas stāvokļa atkarību no vides ch, pieņemot, ka protoplazmas sastāvdaļas, t. s. amfoliti, šūnā izturas līdzīgi proteinu hidrosoliem elektriskā laukā. Tāpēc Robbins's un citi autori domā, ka šos sēklu un sporu dīgšanas vai auga daļu augšanas minimus optimā var identificēt ar protoplazmas amfolitu izoelektrisko stāvokli (I. P. E.).

Loebs'a (1922.) pētijumi arī liecina, ka proteiniem, līdzīgi želatinai, izoelektriskā stāvoklī daudzas īpašības, kā vadītspēja, viskozitate, osmotiskais spiediens u. c., ir vismazākās, kamēr dažas citas īpašības, kā piem. siltumkoagulacija, vislielākās. Arī dzīvā šūnā protoplazma izturas analoģiski, kā to liecina vairāku zinatnieku specialie pētijumi šai virzienā.

No zaļajiem augiem arī sūnas pazīstamas ar īpatnēju pH oikoloģisko amplitudi dabiskos substratos. Plašs novērojumu materials, kā arī dati literaturā atļāvuši definēt ikkatrai sugai, to absolutās un optimalās augšanas apstākļu robežas faktoram pH augtenēs (Apinis un Lācis 1936.). Pēc to augteņu pH amplitudes sūnu sugas iedalītas 13 grupās un tās savkārt 3 klasēs:

A. Skābu substratu sūnas.
B. Mēreni skābu neutralu un vāji alkal. augsnu sūnas.
C. Alkalisku un neutralu substratu sūnas.

Sūnām, kā samērā lielai zaļo sporaugu grupai, sastopams spēcīgs izplatīšanās veids ar vienšūnu sporām. Ievērojot iepriekš sacīto par sūnaugu attiecībām pret substratiem dabiskos apstākļos, bija nepieciešams pārbaudīt sūnu sporu dīgšanas atkarību no vides cH eksperimentali.

Šim jautājumam ir jau zinama vēsture. Tā Trebú (1905.), audzēdams sūnu protonemas, ievēro, ka divas skābu substratu sūnas (*Sphagnum* un *Dicranella cerviculata*) labāk dīgst skābā vidē kulturās.

Kessler's (1914.) atrod, ka sūnu sporu dīgšana lielā mērā atkarīga no vides reakcijas. Varēja konstatēt, ka kaļķa substratu sūnas labi dīgst alkaliskos šķīdumos, vai šo substratu uzduļķojumos. Purvu un citu skābu substratu sūnu sporas labāk dīgst skābā sintetiskā vidē vai attiecīgos skābu substratu filtratos. Tāpat neutralu un vāji skābu mineralsubstratu sūnas — neutralā un mēreni skābā vidē.

Jāpiezīmē, ka toreiz min. autoru rīcībā nebija precizas cH noteikšanas metodes, kādēļ šīs atziņas tuvināti atbilst īstenībai.

Pringsheim's (1921.) vides reakcijai neatrod nozīmes sūnu sporu dīgšanā un protonemas attīstībā. To pašu autors apliecina arī 1935. g. iznākušajā darbā.

Ikenberry (1936.), pētijot dažādu augteņu sūnu sporu dīgšanas atkarību no vides cH, atrod, ka vispār te nepastāv apmierinoša sakarība ar substrata pH vērtībām. Sakars ir gan starp sporu dīgšanas un protonemas augšanas optimu un augteņu pH dabā.

Sacītais liecina, ka jautājumā pastāv zinama neskaidrība. Šī iemesla dēļ ar 3 oikoloģiski dažādām sugām tika izdarīti ilgstoši novērojumi eksperimentos sporu dīgšanā, protonemas attīstībā un sūnaugu veidošanā tīrkulturu pH rindās.

Materials un technika

Eksperimentiem *Sphagnum plumulosum* Röll ievācu Ķemeros 1934. g. pavasarī ar negatavām sporu kapselēm. Kādu mēnesi sūnu velēnu audzēju laboratorijā, līdz nogatavojās sporas kapselēs. Tās uzglabātas kopā ar kapseli mazos stobriņos ar vates aizbāžņiem. Augs dabiskos apstākļos aug purvainos priežu mežos un dumbrājos. Nordhagen's (1928.) atradis substratā pH 5.2 un 5.3, kādēļ šo sugu var pieskaitīt mesoacidofilām sūnām.

Funaria hygrometrica (L.) Sibth. nogatavojušās kapseles ievāktas mazos stobriņos Ķemeros, purvaina meža malā, veca ugunskura vietā 14. VIII. 32. Šī suga vairākās rasēs izplatīta mūsu teritorijā uz kaļķakmeņa (plaisās vai nedaudz apbērtās vietās), smilšakmeņa (Old Red), mūru gruvešiem, grantainas zemes, bet sevišķi labprāt attīstas vecās ugunskuru vietās. Dabisko substratu aciditate svārstas pH 5.3—8.3, parasti 6.1—8.0 (A p i n i s un L ā c i s 1936.), tamdēļ šī sūna pieskaitama m e i o e u r y i o n ā m.

Polytrichum juniperium Willd. sporu materials ievākts Vecāķos, sausā priežu mežā, uz kāpu smilts substrata 17. VII. 32. Augs parasti aug uz skābas humozas smilts substrata priežu mežos, uz sausas kūdras un citās tamlīdzīgās vietās. Substrata pH intervals mūsu dabiskās augsnēs 22 paraugos atrasts 4.0—5.9 (A p i n i s un L ā c i s 1936.). Augs pieskaitams acidofilām sūnām.

Nepieciešams priekšnoteikums eksperimentiem sporu dīgšanā un attīstības novērošanā ir tīrkulturas. Tamdēļ šķīdumi vai citi sintetiski substrati un kulturu trauki sterilizēti autoklavā ½ stundu apm. 120°C. Arī sporu materials atsevišķām kulturu serijām iegūts aseptiski no vairākām kapselēm, rūpīgi sajaukts un ar sterilu platinas adatu lielāks skaits sporu ienests kulturās.

Kulturu pH rindu pamatsastāvdaļa primarais (m/15 KH_2PO_4, resp. 9.078 g 1 litrā redest. ūdens) un sekundarais (m/15 $Na_2HPO_4 . 2H_2O$, resp. 11.876 g 1 litrā redest. ūdens). K-Na fosfati pēc S ö r e n s e n'a (1909.). Lielāka alkalinitate vai aciditate fosfatu pH rindā iegūta atsevišķos gadijumos ar n/10 NaOH un n/10 H_3PO_4. Fosfatu rindas sastāvs visās kulturu serijās kā 6. l. p. atzīmēts.

Šie fosfati kulturām atšķaidīti ar 9 daļām redestilēta ūdens, t. i. sāļu koncentracija kulturās bija ap 0,1%. Kulturām lietoti 20 mm diam. stikla stobriņi, noslēgti ar vates korķiem un nosieti ar pergamenta papīru lai samazinātu ūdens izgarošanu. Šķīduma daudzums ik stobriņā 15 ccm. pH šķīdumos noteikts elektrometriski ar hinhidrona elektrodi, vai stipri alkaliskos šķīdumos un agarā ar M i c h a e l i s'a (1930.) indikatoriem sākumā un eksperimenta beigās. Visos eksperimentos sporu vitalitate pārbaudīta ar plazmolizi KNO_3 vai cukura šķīdumā.

I. e k s p e r i m e n t s

Šī kulturu serija sākta ar augšā pieminētiem fosfatiem, kas atšķaidīti 9 daļām redest. ūdens 26. VIII. 34. Stobriņos 15 ccm šķīduma. Pēc sporu ievietošanas virs vates korķa, stobriņi nosieti ar pergamenta papīru, lai samazinātu ūdens izgarošanu. Kulturas novietotas uz N loga, temperaturā 12—15°C. Šai eksperimentā lietots *Sph. plumulosum* Röll, *Funaria hygrometrica* (L.) Sibth. un *Polytrichum juniperinum* Willd. sporas. Kontrolu rezultati 30. III. 35. sakopoti tabulā nr. 1 (7. un 8. l. p.).

Sphagnum plumulosum Röll sporas fosfatu šķīdumos dīgst pH intervalā 5.0—7.2. Vājāka sporu dīgšana kulturā nr. 8 ar pH 6.5. Vislabāk dīgst k-rās ar pH 5.0, 6.6 un 7.0. Alkaliskie šķīdumi pH 7.3—8.3, līdzīgi kā skābie ar pH 2.8—4.5, ilgākā laikā sporām kaitīgi (plazmolize neiestājas).

Funaria hygrometrica (L.) Sibth. sporām kaitīgi skābie šķīdumi ar pH 2.8—3.8, bet ne alkaliskie šķīdumi. Sporas śai sugai dīgst pH 5.0—8.3, bet vislabāk pH 6.0—8.0.

Polytrichum juniperinum Willd. sporas nedīgst vidē ar pH 7.5—8.3 un pH 2.8 kulturā. Sporas dīgst vidē ar pH 3.3—7.2, bet vislabāk pH 5.9—6.6.

II. eksperiments

No iepriekš pieminētās (6. l. p.) fosfatu rindas atšķaidijumā ar redest. ūdeni 1:9 pagatavots 2% agara serija. Pēc sterilizacijas un atdzišanas uz slīpagara ar platinas adatu ievietotas 2 serijās *Sphagnum plumulosum* Röll un *Polytrichum juniperinum* Willd. sporas 26. VIII. 34. Kulturas novietotas laboratorijā uz S loga istabas temperaturā netiešā saules gaismā. Kontroles rezultati 1. VII. 35. sakopot tabulā 2 9. un 10. l. p.

Pēc 11 mēnešiem *Sphagnum plumulosum* Röll sporas nav dīgušas k-rās 1—4, kā arī kulturās 14 un 15. Sporu dīgšana novērota kulturās 5—13, bet sūnaugi uz agara attīstas kulturās 8—13, bet optimalā sūnaugu attīstība novērojama k-rās nr. 12 un 13 ar pH (agars sajaukts ar dest. ūdeni pusšķidrā masā, kur elektrometriski ar hinhydrona elektrodi mērots pH) 5.5 un 5.7.

Polytrichum juniperinum Willd. sporas dīgušas visā pH rindā, bet sūnaugi nav attīstijušies kulturās nr. 1, 2, 3, 6, 11 un 15. Sūnaugu attīstība novērojama kulturās nr. 4, 5, 7, 8, 9, 10, 11 un 12. Tie vislabāk attīstijušies kulturās nr. 12 un 13 ar pH 5.3 un 5.5.

III. eksperiments

6. l. p. pieminetā fosfatu rinda tai pat atšķaidijumā 1:9; ik kulturā ar 10 ccm. šķīduma aplietas 15 g. izskalotas smiltıs. Pēc sterilizacijas 2 kulturu serijās iepotētas *Funaria hyrometrica* (L.) Sibth. un *Polytrichum juniperinum* Willd. sporas 28. VIII. 33. Kontrolējot kulturas pēc 5 mēnešiem, atrasts, ka *Funaria* sporas dīgušas visā serijā apm. 50% (pH visā rindā beigās bija 5.9—7.5). *Polytrichum* sporas nedīga kulturā nr. 1 ar pH 7.5. Kulturā nr. 2 ar pH 7.3 maz sporu dīgušas. Citās kulturās ar pH no 4.9—7.2 lielākā daļa sporas dīgušas,

izveidojot līdz 150 μ garu protonemu. Kulturas ar smiltīm diezgan ātri iežuva, ar ko var izskaidrot tālāko attīstības stadiju iztrūkšanu sūnaugiem.

IV. eksperiments

Šais eksperimentos *Funaria hygrometrica* (L.) Sibth. un *Polytrichum juniperinum* Willd. sporas tīrkulturās audzētas uz agara ar atšķaidītu Knopa šķīdumu un $CaCO_3$ vai $MgCO_3$ dažādām devām līdz 5% un pēdējo divu savienojumu kombinacijā. Arī izskalotas smiltis substratiem kombinētas ar līdzīgām $CaCO_3$ devām un atšķaidītu Knopa šķīdumu. Pēc 10 mēnešiem šīs kulturu serijas stobriņos kontrolētas. pH kulturās svārstijās 7.1—9.0, kas tika noteikts ar indikatoriem. *Funaria* uz kalcija karbonata agara substratiem ar pH 7.2—8.1 labi attīsta 1—2 cm garus sūnaugus ar lapām.

Līdzīga attīstība uz agara ar mazu $MgCO_3$ devu (pH 8.5), bet lielākās $MgCO_3$ devās uz agara neattīstas *Funaria* sūnaugi, bet gan tikai protonema. *Polytrichum* sporas dīgušas un pat attīstijušas 1—2 cm garus sūnaugus uz agara un dažāda mazāk $CaCO_3$ saturoša substrata ar pH beigās 6.4—7.2. Protonemas attīstība novērota uz maz $MgCO_3$ saturoša agara virsmas (pH ap 8.8), bet uz vairāk $MgCO_3$ saturoša agara sporas nedīgst. *Funaria* sporas uz smilts un $CaCO_3$ vai $MgCO_3$ saturoša substrata (pH 7.1—9.0) attīsta tikai protenemu, bet *Polytrichum* protonema novērota uz agara, kas mazāk satur $CaCO_3$ un $MgCO_3$ (pH 7.4—8.5). Vairāk karbonatus (sevišķi $MgCO_3$) saturošos substratos pēdējā suga neattīsta protonemu.

Diskusija

Sphagnum sugu kaļķa jūtība jau agrāk pazīstama. Paul's (1908.) atrada, ka kalcija ions sfagniem nav kaitīgs, bet gan kalcija karbonats, resp. bikarbonata šķīdums. Mevius's (1924.) un Olsen's (1923.) eksperimentali varēja apliecināt, ka sfagni nepanes kaļķa substratu šo augu jūtīguma dēļ pret OH ioniem. Kā iepriekšējos eksperimentos atrasts, arī *Sphagnum plumulosum* Röll sporas jūtīgas pret alkalisku vidi. Protonemas attīstība gan novērojama arī neutralā vidē, bet laba sūnaugu velēna šai sugai attīstas uz substrata ar pH 5.5 un 5.7, kas atbilst novērojumiem dabiskos apstākļos.

Funaria hygrometrica (L.) Sibth. parasti aug uz kaļķa substratiem (subkalcifila) pH intervalā 5.3—8.4, parasti 6.0—8.0 dabiskos apstākļos. Ikenberry's (1936.) atradis sporu dīgšanu vidē pH 5.0—9.0, ar optimu pH ap 6.0. Pieminētos eksperimentos, šķīdumos un uz cieta substrata, atrasts, ka sporas dīgst un izveido protonemu pH robežās no 4.5—9.0, bet sūnaugu attīstība novērojama tikai uz neutrala un alkaliska substrata ar pH 7.1—8.8. Sporu dīgšanu šai sugai (Apinis u. Bluķis 1933.) iespējams panākt vidē pat ar pH 3.7, bet tālākā sūnaugu attīstība te nav novērojama. Pringsheim's (1921.) atradis, ka *Leptobrym pyriforme* (L.) Wills. sporu dīgšanā un protonemas attīstībā nav novērojama vides cH ietekme, bet lapotā sūnauga attīstība iestājās alkaliskā vidē. Kā zinams, šīs sugas pH intervals dabiskos substratos 5.3—9.0, parasti 6.1—7.5 (Apinis un Lācis 1936.). Tas norāda, ka sūnaugu izveidošanos no protonemas ievērojami ietekmē vides cH; lai tā iestātos, vidē nepieciešams tāds pH, kādu novēro sūnu dabiskos substratos.

Polytrichum junipernium Willd. dabiskos apstākļos aug uz skāba substrata pH intervalā no 4.0—5.9. Schoenau's (1913.) un Boas's (1914.) atraduši *Polytrichum* sugām, līdzīgi *Sphagnum,* jūtību pret alkalisku vidi. Alkaliski šķīdumi iekrāso sūnaugus tumši-violētus. Ikenberry's (1936.) atradis šai sugai sporu dīgšanu pH 5—6, ar optimu 6.0, lai gan dabiskos apstākļos tās parasti atrastas arī uz skābāka substrata. Šo parādību Ikenberry's (1936. p. 277.) mēģina izskaidrot ar citādāku sūnaugu izturēšanos pret vides cH vēlākās attīstības fazēs (skat. cit. 12. l. p.). I. eksperimentā atrasts, ka *Polytrichum juniperinum* Willd. sporas var dīgt pat pH 3.3, bet uz cieta substrata (agrs ar karbonatiem un sāļu šķīdinājumu) arī pH 8.5—8.9, bet sūnaugi vislabāk attīstas uz substrata ar pH 5.3 un 5.7. Vāja sūnaugu attīstība novērojama arī uz neutrala un pat vāji alkaliska substrata.

Kā kontrolu tabulas un citi novērojumi liecina, sporu dīgšanas optims nav viengabalains, t. i. pH rindā starp atsevišķiem sporu dīgšanas un protonemas attīstības optimiem novērojams arī viens, divi vai pat trīs minimi attīstībā. Par tiem nodomāts sniegt tuvākus norādijumus kādā no nākošiem darbiem.

Kopsavilkums

1) Pētīto sūnu sporas var dīgt un izveidot protonemu daudz plašākā vides pH intervalā, kā attiecīgās sugas augiem atrasts dabiskos substratos.

2) Skābā vidē acidofilo sūnu (*Sphagnum* un *Polytrichum*) sporas labāk dīgst un attīsta protonemu, kā neutralā un alkaliskā vidē, bet *Funaria,* kā kaļķu substratu sūnai, sporas vis-

labāk dīgst un izveidojas protonema vāji skābā, neutralā un alkaliskā vidē.

3) *Polytrichum* sporas var dīgt un attīstīt protonemu alkaliskā vidē, bet *Funaria* sporas arī skābā vidē, t. i. tādā cH, kāda nav dabiskiem substratiem.

4) Sporu vitalitate acidofilo sūnu sporām ilgāk uzglabājas skābā vidē, bet *Funaria* sporām tā ilgāk uzglabājas neutralā un alkaliskā vidē.

5) Ilgākā kulturā uz agara acidofilo (*Sphagnum* un *Polytrichum*) protonema rada sūnaugus, kas labi izveidojas tikai šaurākā pH intervalā. Pēdējais atbilst sūnu substratu pH dabiskos apstākļos.

6) *Funaria* protonema labi attīsta lapotus sūnaugus uz agara ar karbonatiem neutralā un alkaliskā vidē, t. i. līdzīgā pH intervalā kā dabiskos apstākļos.

7) Sporu dīgšanas un protonemas attīstības pH intervals vai optims nenorāda, vai tikai tuvināti norāda attiecīgai sugai attīstības pH intervalu dabiskos apstākļos.

8) Pieminētām sugām eksperimentā atrastā lapotā sūnauga izveidošanās pH intervals vai optims atbilst substratu aciditatei attiecīgo sugu dabiskās augtenēs.

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