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INFLUENCE OF NUTRIENT DEFICIENCY ON HAIR FORMATION IN *STIGEOCLONIUM*

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Eleven strains of *Stigeoclonium tenue* Kütz. and one of *Chaetophora incrassata* (Hudson) Hazen were subjected to deficiencies of Mg, Ca, Fe, N, P and S. The responses between strains differed, but in general the greatest amount of hair formation was brought about by P deficiency, with N deficiency having almost as great an effect. In most, but not all, strains Fe deficiencies led to moderate hair formation. In *Chaetophora incrassata* both S and Ca deficiencies led to moderate hair formation, but in *Stigeoclonium tenue*, the effect was much less or not detectable at all. Mg deficiency had almost no effect on hair formation in any strain.

Colourless hairs (Huber, 1892) occur in many algal genera, but are especially widely distributed in the Chaetophorales. It has been reported in a number of cases (for references, see Sinclair & Whitton, 1977) that hair formation in this order may be favoured by a deficiency of nitrate in the medium. This was shown, for instance, in Stigeoclonium amoenum Kütz. by Abbas & Godward (1963); other observations indicating that nitrate deficiency may favour hair formation in Stigeoclonium are those of Uspenskaya (1936: S. tenue) and Reynolds (1951: S. farctum). This behaviour contrasts with that found in the blue-green algal family Rivulariaceae (Sinclair & Whitton, 1977) where the level and type of nitrogen source had relatively little effect on hair formation. Deficiency of phosphate was the only factor found to lead to hair formation in all strains of Rivulariaceae capable of forming them; Fe deficiency also led to hair formation in eight out of 13 strains, and Mg deficiency in one strain. Ca, Mo and SO_4 deficiencies however had no such effect, and subsequent research (unpublished data) has shown that K deficiency similarly has no effect on hair formation. As a result of this apparent contrast in the behaviour of Chaetophorales and Rivulariaceae, it was decided to establish more clearly what are the factors leading to the formation of hairs in Stigeoclonium.

METHODS

CULTURE MEDIUM

The complete medium was that used by Harding & Whitton (1976) for the growth of *Stigeoclonium*. Deficiencies of Mg, Ca, Fe, N, P and S were obtained, respectively, as follows: substitution of MgSO₄ by Na₂SO₄, Ca(NO₃)₂ by NaNO₃, Fe omitted from chelating agent stock, Ca(NO₃)₂ by CaCl₂, KH₂PO₄ by KCl, MgSO₄ by MgCl₂.

ALGAE

Eleven strains of *Stigeoclonium tenue* Kütz. and one of *Chaetophora incrassata* (Hudson) Hazen were tested. Populations of *Stigeoclonium tenue* were obtained from streams and rivers as described by Harding & Whitton (1976) and maintained as unialgal cultures in the laboratory.

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Chaetophora incrassata was isolated from a small water tub at Durham University by Dr C. Sinclair. The various strains of Stigeoclonium tenue are referred to by stream/reach/population isolate (Table I). Details of streams and reaches are held on computer disc at Durham University and can be sent to anyone needing this information. Further data on the populations may be obtained from the account of Harding & Whitton (1976), the site numbers in that paper corresponding to stream/reach codes given here: 0001/01 = site 13, 0025/50 = site 18, 0096/01 = site 2, 0102/15 = site 25, 1002/35 = site 33 and 4014/01 = site 32.

ASSAY PROCEDURE

Several different procedures were used to assay the influence of deficiencies on hair formation; all gave similar results for any one strain. The following is the procedure used for the results summarized below: the alga was first grown under standard conditions $(20^{\circ}C, 4,000 \text{ km})$ cool white light, moderate shaking, with 10 ml medium in boiling tubes) in full medium in order to obtain a standard inoculum. Hairs were absent in the inocula used for all strains of *S. tenue*, but a few (on 1% branches) were present in *Chaetophora incrassata*. A few small pieces of alga were washed in each test medium and then incubated in the test medium under the standard conditions described above. Four replicates of each strain were used, material being harvested for microscopy on days 7, 11 and 14; one of the replicates was subcultured into a further tube of deficient medium on day 11 and observed on day 14.

Since a large number of strains were examined under several experimental treatments, it was not practicable to make detailed measurements on the filaments. Observations were therefore made on a subjective, semi-quantitative basis. The following observations were made for each strain every time the cultures were inspected.

(i) Ranking of each deficiency condition with respect to the extent of growth before symptoms of marked deficiency developed. Growth was assessed visually by comparison with the control tube in each case.

(ii) Estimate of percentage of filaments with hairs, given to the nearest 10% for values greater than 5%. For the purposes of the present study, a hair was defined as a terminal portion of a filament composed of one or more narrow and elongated cells lacking any visible chloroplast. Filaments or parts of filaments composed of cells with visible chloroplasts were classed as "non-hair growth".

(iii) Ranking of each deficiency condition with respect to the ratio of total length of hairs to amount of non-hair growth. This ratio is referred to as "hairiness". Although these observations were subjective, the differences in hair production were often very great and it seems unlikely that absolute measurements would often have changed the ranking.

Tests were also included on the effect of adding the missing element to Fe, N and P deficient cultures of *Stigeoclonium tenue* 0050/25/01 and of *Chaetophora incrassata*.

RESULTS

The results are summarized in Table I by comparing, for each strain under each deficiency, the morphology of the alga as seen on the last occasion before it appeared obviously unhealthy. Each strain of *Stigeoclonium tenue* grew to a similar extent in the complete medium during the experiment. With the exception of a few short hairs that had developed by day 14 in material not subcultured into fresh complete medium on day 11, no hairs developed in any of the *S. tenue* controls.

The addition of the missing element to Fe, N and P deficient cultures of *Stigeoclonium tenue* 0025/50/01 and *Chaetophora incrassata* in each case led to a rather similar result. Cells in the lower part of the hair developed into normal vegetative cells, with the chloroplast being prominent. No obvious change took place in the hair cells above this zone. The transition between each cell type was usually abrupt, and the remaining hair cells eventually fell off. This usually occurred at the junction with a healthy cell, but a hair sometimes broke up into pieces, leaving a small fragment next to the healthy cell. This latter pattern was especially common in previously phosphate deficient *Stigeoclonium tenue*.

	Control			– Mg				Ca			Fe			- N			P			S		
	Growth	% hairs	Hairiness	Growth	% hairs	Hairiness	Growth	% hairs	Hairiness	Growth	% hairs	Hairiness	Growth	% hairs	Hairiness	Growth	% hairs	Hairiness	Growth	% hairs	Hairiness	
Stigeoclonium tenue																						
0001/01/04	7	0	0	2	1	2	3	0	3	5	5	4	1	50	7	4	40	6	6	5	5	
0025/50/01	7	0	0	3	0	0	6	0	0	4	90	6	1	100	5	2	100	7	5	1	4	
0071/60/01	7	0	0	1	1	2	3	5	3	6	5	5	2	10	6	4	30	7	5	1	4	
0071/70/01	7	0	0	5	0	0	3	5	3	6	5	4	1	20	6	5	40	7	4	5	5	
0071/90/02	7	0	0	5	5	2	3	5	3	4	20	6	1	5	4	2	40	7	6	5	5	
0071/99/01	7	0	0	5	5	3	2	0	0	6	5	5	1	50	7	3	30	6	4	1	4	
0096/01/04	7	0	0	2	0	0	6	1	3	5	1	5	1	20	7	3	10	6	4	5	4	
0102/15/03	7	0	0	4	0	0	2	1	3	6	30	6	1	30	5	3	60	7	5	1	4	
0124/99/01	7	0	0	4	0	2	3	1	3	5	20	5	1	- 30	6	2	60	7	6	1	4	
1002/25/01	7	0	0	3	0	0	4	1	3	5	5	5	1	20	6	2	30	7	6	5	4	
4014/01/01	7	0	0	5	5	5	2	0	0	6	1	4	1	5	6	3	30	7	4	1	3	
Chaetophora incrassata	7	0	0	4	5	2	5	20	4	3	90	6	1	90	5	2	90	7	6	10	3	

 TABLE I. Hair formation by 11 strains of Stigeoclonium tenue and one of Chaetophora incrassata.

 Data for "growth" and "hairiness" are summarized by ranking the observations made for each of the six deficiencies and the control in each case, with seven indicating the highest value. For explanations of growth and hairiness, see Methods section of text

DISCUSSION

All the strains were capable of forming long colourless multicellular hairs; Cox & Bold (1966) reported that four out of 100 Stigeoclonium strains studied by them could not produce hairs. Although there are clearly differences between strains, the results in Table I indicate that under the conditions of batch culture used, phosphate deficiency generally brought about the most marked and universal effect on hair formation. Nitrate and iron deficiencies also produced marked effects in most strains. Calcium and sulphate deficiencies led to obvious hair formation in Chaetophora incrassata, but little if any with the Stigeoclonium strains. Magnesium had a negligible effect on every strain. Direct comparison of results is difficult because nitrate deficiency, in particular, brought about a rapid cessation of growth. Where hairs were present in phosphate deficient cultures, they were usually very long and often extended for 500 μ m or more: similar very long hairs were also often found in iron deficient cultures and sometimes in nitrate deficient cultures. Since the development of such hairs markedly increased the length of the branched filaments in comparison with the controls, which had branches rarely exceeding 200 μ m, it seemed very unlikely that the hair cells arose simply as a result of degeneration of existing cells.

It is uncertain whether the results for nitrate deficiency would have more closely resembled those for phosphate deficiency if continuous culture techniques had been available; this technique would have permitted indefinite culture under conditions of moderate nitrate deficiency. It is clear that, although magnesium and calcium deficiencies did not bring about such an abrupt cessation of growth in batch culture, such deficiencies did not lead to marked hair formation. The present results with Stigeoclonium tenue show some similarities to those obtained for the prokaryotic Rivulariaceae by Sinclair & Whitton (1977), but they are not as clear-cut. As with the Rivulariaceae, phosphate deficiency brought about marked hair formation in every strain, and iron deficiency did so in many but not all strains; in contrast, nitrogen deficiency also had a marked effect with S. tenue. In the Rivulariaceae, apart from the one example of hair formation under magnesium deficiency, there was no evidence of hair formation under any deficiency other than those of phosphate and iron. In contrast a low percentage of S. tenue filaments formed hairs under sulphate deficiency, and in some cases also a few filaments did so under calcium and magnesium deficiencies.

It is evident from the above results that hair formation in *Stigeoclonium tenue* is not a general response to every factor reducing the growth rate. Further, levels of zinc which partially inhibit growth do not lead to the formation of hairs (Harding & Whitton, 1976, 1977). It therefore seems possible that the development of hairs under phosphate, nitrate and sometimes iron deficiencies is not merely a symptom of degeneration, but may be a specific morphogenetic response to these conditions. Since the development of hairs markedly increases the surface area: volume ratio of the plants, it is tempting to speculate that hairs may have a role in the uptake of certain nutrients under limiting conditions.

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