Abnormalities in *Marchantia polymorpha* L.

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Various types of morphological abnormality on both vegetative and reproductive organs were observed in *Marchantia polymorpha* growing under natural and semi-natural conditions. These observations confirm the general argument that vegetative propagation occurs from various organs and, rather than sexual reproduction, plays the major role in reproduction in *Hepaticae*.

Introduction

Since Taylor's first report (1837) on androgynous gametophores in *Dumortiera irrigua* (Marchantiaceae), many authors have reported other types of abnormality in varying degrees in a number of genera of Marchantiales (Klein, 1881 ; Okamura, 1908 ; Kreh, 1909 ; Cutting, 1910 ; Bergdolt, 1926 ; Pandé & Srivastava, 1953 ; Pandé et al., 1953a, 1953b ; Bhattacharya & Pillai, 1959 ; Parihar & Jagdish Lal, 1972 ; Naidu, 1973 ; and others). In the present paper, the writer reports comparable abnormalities in *Marchantia polymorpha* growing under natural and semi-natural conditions.

Materials and Methods

The materials were collected from a population growing in a residential area of Morioka, where both male and female plants were intermingled. Some of them were collected for immediate observation, while others were cultured under semi-natural conditions using the following procedure.

A polyethylene box 39 cm × 32 cm × 14 cm, containing a slightly smaller inner box with a bottom of coarse mesh, was used as a culturing vessel. About 2 cm of nylon wool was placed in the bottom of the inner box, followed by an equal amount of well-washed sand. This box was then replaced in the larger box, which contained an appropriate amount of culture medium. The culture medium was absorbed by capillary action. The thalli collected in the field and/or the gemmae that had developed on the thalli were separated into male and female groups and transplanted onto the moistened sand in the culturing vessel. Voth's No. 5 inorganic nutrient solution (Voth, 1943) was employed as the culture medium. It was changed regularly. The culturing vessels were set on a table near a north-facing window to avoid direct sunlight. Neither light nor photoperiod was controlled ; the boxes received natural light through the window.

The materials used in this study were identified by Dr. Hiroshi Inoue of the National Science Museum, Tokyo. Voucher specimens have been deposited in the Herbarium, Department of Biology, Iwate University, Morioka (IUM).

Results

Almost all of the abnormalities observed were on archegoniophores except for one on an antheridiophore. The thalli bearing abnormal gametophores were always observed to show necrosis on the margin. The abnormalities of gametophores which were withered brown and/or bright green are classified into three main groups as follows.

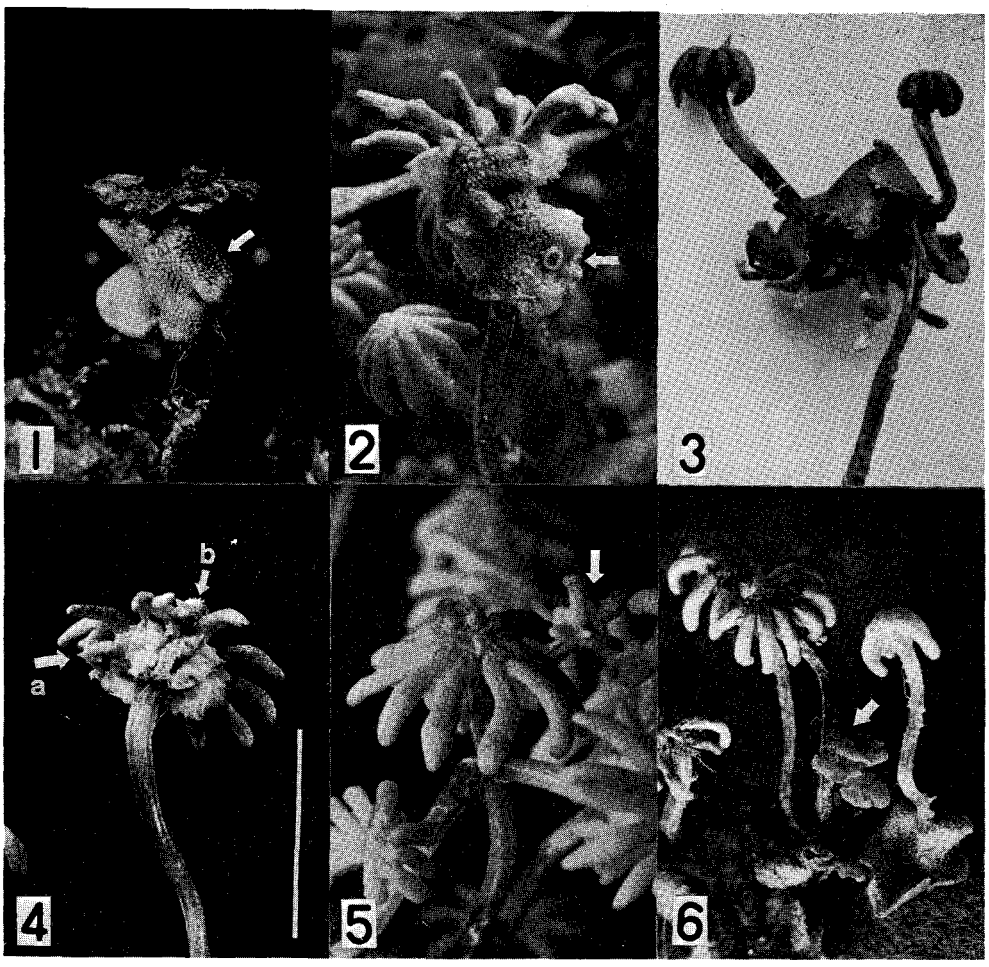
1. Abnormality on the disk

(1) The first case, the development of adventitious thalli from a female disk, was observed both on the plants collected in the field and in the culturing vessels. Viewed macroscopically the stalk was not injured. Usually the disk was green and did not seem to be very old. An involucre was clearly observed but neither spores nor elaters were found. The top of the disk was usually crumpled and frequently deformed into horn-like appendages (Inoue & Terui, unpublished). The maximum number of adventitious thalli observed from one disk was three.

(2) The second case, the development of an adventitious thallus from a male disk, seems very rare and only one example was found on a plant collected in the field (Fig. 1). An apparent injury caused by bending was observed on the stalk bearing the disk. Most of the disk had turned brown and was old enough to be withered. The disk had been partially broken and lost, but the antheridiophore seemed to have been as large as a normal one. The adventitious thallus had been developing from a convex part of the ventral side of the disk, approximately 2 mm away from the stalk. The adventitious thallus and its initiating base on the disk were light green in color, while most of the disk was withered and brown. The thallus bore rhizoids and developed downwards, enveloping the stalk.

(3) In the third case, an adventitious thallus bearing a gemma-cup developed from a female disk (Fig. 2). This was observed on a plant very similar to the first case except for a normal gemma-cup being borne on the dorsal surface.

(4) The fourth case, a female disk bearing an adventitious thallus on which a secondary archegoniophore was developing (Fig. 3), was observed on a plant in the field and also in the culturing vessel. Three examples of this case have been found so far. No macroscopic injury was found on any stalk. Two of the examples had an adventitious thallus which bore one rather small secondary archegoniophore, the third had two secondary archegoniophores. In all cases the secondary disk (ca. 4 mm) was less than half the diameter of the primary one (10 mm). In addition, the digitate ray number of the former (5-8) was less than that of a normal one (9).



Figs. 1 - 6. Abnormalities on gametophores (marked with arrows). Fig. 1 : A secondary thallus developing from the ventral side of a male disk ; Figs. 2 - 6 : Various abnormalities on archegoniophores. Fig. 2 : A secondary thallus bearing a gemma-cup. Fig. 3 : A secondary thallus bearing two secondary archegoniophores. Fig. 4 : A disk of a secondary archegoniophore (arrow a) and a secondary thallus with a gemma-cup developing from a broken part of a digitate ray (arrow b). Fig. 5 : A secondary archegoniophore developing directly from the ventral side of a disk. Fig. 6 : Two secondary thalli on a stalk. Scale (in Fig. 4) = 10 mm.

Fig. 7. Schematic drawings showing all the types of abnormality reported in this paper. Secondarily developed organs are black. The similar secondary organs are simplified by showing a representative one to avoid confusion in the drawings. Abbreviations : *c*, found in a culturing vessel ; *f*, found in the field ; *h app*, horn-like appendages ; *inj*, injury ; *inv*, involucre ; *lat sec th*, lateral secondary thallus ; *pr d*, primary disk ; *pr st*, primary stalk ; *pr th*, primary thallus ; *sec d*, secondary disk ; *sec g c*, secondary gemma-cup ; *sec st*, secondary stalk ; *sec th*, secondary thallus. For details see text.

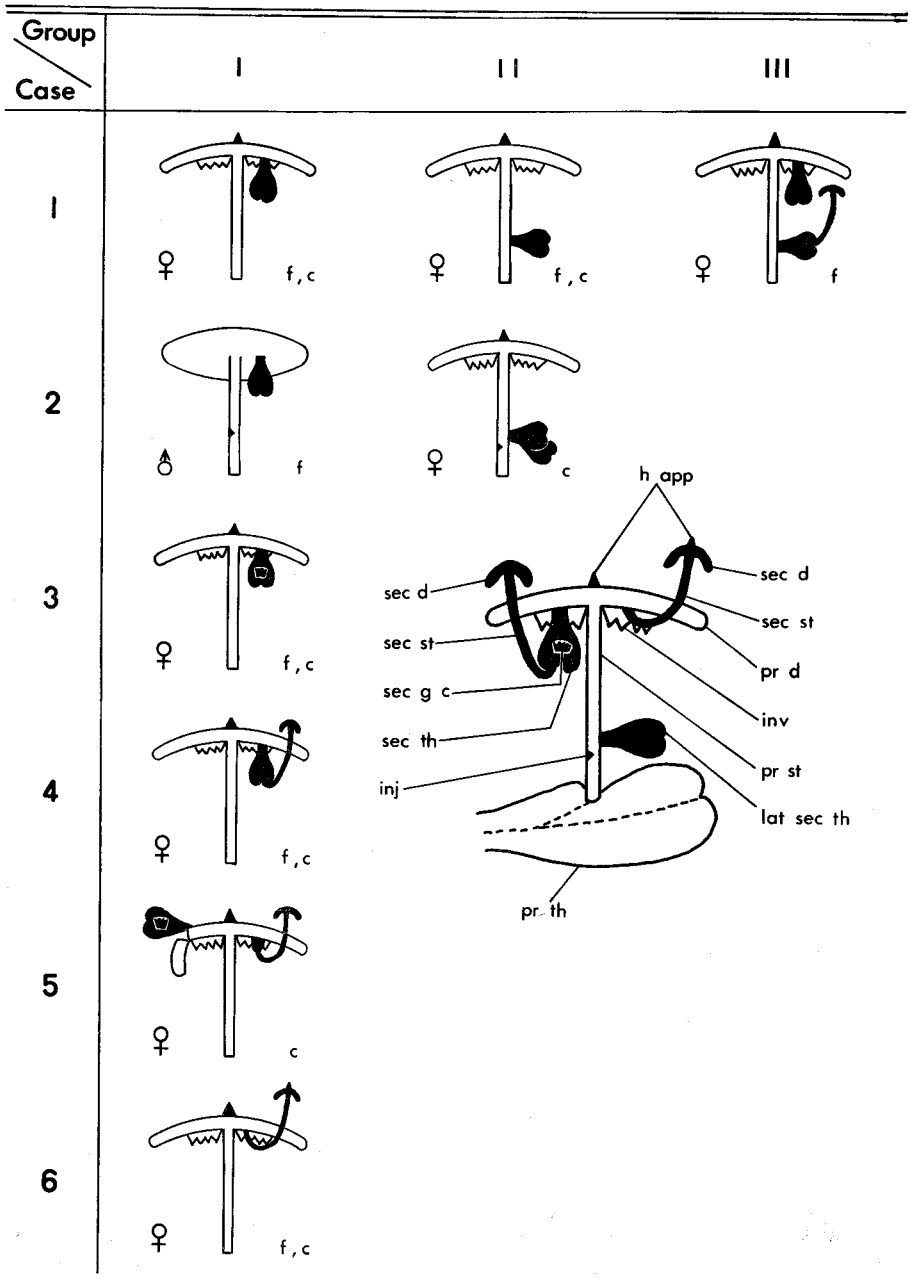

Group
Case
I
II
III
1
2
3
4
5
6
♀ f, c
♀ f, c
♀ f
♀ f
♂
♀ c
♀ f, c
♀ f, c
♀ c
♀ f, c
h app
sec d
sec st
sec g c
sec th
inj
sec d
sec st
pr d
inv
pr st
lat sec th
pr th

Fig. 7

The horn-like appendages were observed on the top of both or either the primary and/or secondary disk. Although involucres were observed on both types of disk, positive evidence of effective fertilization, that is, sporophyte development resulting in spore and elater formation, was not observed even on the plant collected in the field.

(5) Only one example of the fifth case, a female disk bearing both an adventitious thallus with a gemma-cup and a separate secondary archegoniophore, was observed on a plant in the culturing vessel (Fig. 4). The primary stalk was about 35 mm tall and normal in height. No macroscopic injury was found on it. The primary disk was as large as a normal one (10 mm in diameter) and had horn-like appendages on the top. One of the nine digitate rays was partially broken and hanging down from the remaining part. The adventitious thallus was regenerating from the upper section of the broken disk and was borne on its dorsal surface. It had a normal gemma-cup. The secondary archegoniophore appeared from the ventral side of the same disk. Its stalk was a little swollen and slightly conical at the base. The swollen stalk base may be inferred to be a deformed adventitious thallus. The secondary disk was also deformed in having a horn-like appendage on the top and only five digitate rays.

(6) The sixth case was the direct development of a secondary archegoniophore from a female disk (Fig. 5). This abnormality was found quite frequently on both plants in the field and those in the culturing vessels. No macroscopic injury was observed on the stalk of the primary archegoniophore. The top of the primary disk was usually crumpled and horn-like appendages were frequently observed. A maximum of three secondary archegoniophores developed from a primary disk. Usually the stalk of the secondary archegoniophore was developed into a J- or U-shape from the ventral side of the primary disk. The secondary disk also bore an involucre and horn-like appendages like those of the primary one. Five to eight digitate rays were counted on the secondary disk indicating a decrease in number.

2. Abnormality on the stalk

(1) The first case was an adventitious thallus developed laterally from a macroscopically intact stalk. Several examples were found on female plants both in the field and in culture.

(2) The second case was the development of two adventitious thalli from a stalk with a clear injury. Only one example was found on a plant in the culturing vessel (Fig. 6). One of the two adventitious thalli was divided into two near the base. It had developed the appearance of one thallus lying upon another. A clear macroscopic injury was observed about 2 mm below the base of this complicated lateral adventitious thallus. The development of rhizoids on these thalli seemed rather poor compared with that of other adventitious thalli.

3. Abnormality on the stalk and the disk

Only one example was observed in the field and this was the most complicated abnormality ever found. Three adventitious thalli developed from the disk and the stalk of an archegoniophore simultaneously. Of the two adventitious thalli which developed laterally from the macroscopically intact stalk, one bore a small secondary archegoniophore. The other two thalli, one developed from the stalk and another from the disk, were simple as in the first cases of group 1 and 2. The secondary archegoniophore on the lateral adventitious thallus was similar to that of the fourth case of group 1. The primary disk had horn-like appendages on the top like those described above.

Discussion

Based on the above observations, it appears that there is another type of vegetative propagation in *M. polymorpha* in addition to the common vegetative reproduction by gemmae and development of new thalli from older ones. This is the development of adventitious thalli from a disk and/or a stalk under certain conditions. The present observations endorse the general argument that vegetative propagation can occur from various organs and, in *Hepaticae*, plays the major reproductive role rather than sexual reproduction.

Vöchting (1885) reported detailed observations on experimental regeneration of various cut organs of *M. polymorpha*. The regeneration of an adventitious thallus from an injured female disk as described in the fifth case of group 1 may have been caused by the injury on the digitate ray. The writer thinks this is equivalent to the experimental cut in Vöchting's study.

Klein (1881) reported that development of adventitious thalli from a stalk were observed when the stalk was broken accidentally and came into contact with the ground or when the stalk fell over due to decay of the lower part. Vöchting (1. c.) also reported that adventitious thalli could regenerate from archegonial stalks that had been cut experimentally in various ways. These studies seem to suggest a possible correlation between injury on a stalk and the development of adventitious thalli from it. The writer, however, has failed in some cases to find clear macroscopic injury on stalks bearing lateral adventitious thalli (first case of group 2 above). The question of a possible correlation between injury and the development of lateral adventitious thalli will be the subject of a future detailed study.

Goebel (1898) commented on Vöchting's explanation and suggested that the cause of regeneration of adventitious thalli on a stalk would be found either in the direction of movement of 'plastic material' or in a wound-stimulus. The writer believes that not only the cause of regeneration of adventitious thalli from a stalk, but also the causes of all of the types of abnormality described here could be elucidated by studying the physiology of vegetative propagation.

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References

BERGDOLT, E. 1926. Untersuchungen über Marchantiaceen. Bot. Abhand. 10 : 1-86.

BHATTACHARYA, S. & C. K. C. S. PILLAI. 1959. On some abnormal female receptacles in *Marchantia* L. Bull. Bot. Soc., Univ. Saugar 11 : 11-16.

CUTTING, E. M. 1910. On androgynous receptacles in *Marchantia*. Ann. Bot. 24 : 349-357.

GOEBEL, K. 1898. Organography of Plants. Pt. I. Transl. by BALFOUR, I. B. Oxford Univ. Press, Oxford. 1900. pp. 48-49.

KLEIN, J. 1881. Ueber Sprossung an den Inflorescenz-Stielen von *Marchantia polymorpha*. Bot. Zentralbl. 5 : 26-28.

KREH, W. 1909. Über die Regeneration der Lebermoose. Nova Acta, Abh. d. Kaiserl. Leop.-Carol. Deuts. Ak. d. Naturf. 90 : 213-301.

NAIDU, T. R. B. 1973. Occurrence of androgynous receptacles in *Marchantia polymorpha*. Bryologist 76 : 428-430.

OKAMURA, S. 1908. Contributions to the study of Japanese Bryophyta. ii. On the regeneration of the antheridial receptacle of *Marchantia*. Bot. Mag. Tokyo 22 : 177-181.

PANDÉ, S. K. & K. P. SRIVASTAVA. 1953. Two more abnormal female receptacles of *Asterella blumeana* Nees. Jour. Indian Bot. Soc. 32 : 137-141.

———, ——— & S. A. KHAN. 1953a. On some anomalous female receptacles of *Ast(er)ella khasiana*. Bryologist 56 : 229-241.

———, ——— & ———. 1953b. On some abnormal female receptacles of *Asterella blumeana* Nees. Proc. Indian Acad. Sci. 38 : 21-26.

PARIHAR, N. S. & JAGDISH LAL. 1972. Anomalous carpocephala in *Marchantia* and their phyletic significance. Bryologist 75 : 73-77.

TAYLOR, TH. 1837. De Marchantieis. Trans. Linn. Soc. 17 : 375-395.

VÖCHTING, H. 1885. Ueber die Regeneration der Marchantieen. Jahrb. Wiss. Bot. 16 : 367-414.

VOTH, P. D. 1943. Effects of nutrient-solution concentration on the growth of *Marchantia polymorpha*. Bot. Gaz. 104 : 591-601.