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Investigations on the action of light on the germination polarity of fern spores

Badania nad wpływem światła na polarność kiełkowania zarodników paproci

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INTRODUCTION

Previous investigations (Pietrykowska 1962) have shown that the light conditions are among the most important factors influencing the course of germination of fern spores. The intensity and the wave length of light, the time of illumination and the direction of the light beam are factors playing a decisive part in this process. Too low light intensities or too short periods of illumination lead to a considerable drop of the percent of germinated spores. The ability of germinating in darkness depends on the species and the growth conditions, but is always much lower than in light.

Two ways of spore germination are known depending on the structural properties of the spores (thickness, colour, structure of the exosporium) and on light intensity. In some species the first cell to appear is a cell of the filament, in others the germinating spore forms first a rhizoid. In low light intensities, for instance, the spores of *Matteucia struthiopteris* begin to germinate by forming a cell of the filament, whereas, in higher light intensities the kind of germination changes and a rhizoid appears first (Pietrykowska 1962).

A similar phenomenon was observed in spores of mosses. According to Heitz (1942) brightly illuminated spores of *Funaria* germinate by developing first a rhizoid and subsequently a filamental cell. In lower light intensities the rhizoid, if any at all, appears after the cell of the filament has been formed.

Light influences decisively not only the growth sequence of filaments and rhizoids but also the polarity of spore germination. Mohr (1956 b) describes the polar germination of fern spores illuminated with light falling unilaterally and from above, i. e. in conditions unfavorable for the observation of polar growth. A protuberance, separated by a transversal wall from the rest of the spore, is formed on the light exposed the cell contains numerous chloroplasts. The major part of the side. In this way the first cell of the prothallium filament is formed;

cytoplasm and the cell nucleus concentrate on the apical pole of the filament. An intensive growth is connected with this process. The first rhizoid, almost free of chloroplasts, appears on the darkened side of the spore. Sometimes the cell of the rhizoid is situated sidewards in relation to the basis of the filament in dependance on the position of the seam along which the exosporium bursts.

The numerous investigations carried out on the action of light on spore germination allowed to establish the active spectrum (Mosbach 1943, Mohr 1956a and b, Haupt 1957), the intensity of light and the time of illumination necessary to induce polarity (Mosbach 1943, Mohr 1956b, Haupt 1957, 1958a, b). A detailed review of papers concerning the problems of polarity of germinating cells and light induction was published by Haupt in 1962. The influence of polarized light made also the object of numerous studies (Bünning, Etzold 1958, Haupt 1960, Bock, Haupt 1961, Haupt, Meyer zu Bentrup 1961, Jaffe 1956, 1958, 1960, Jaffe, Etzold, Kinley 1961, 1962).

Some differences in the germination rate and percentage of spores exposed to equal light intensities have been observed previously in various fern species presenting different spore structures (Pietrykowska 1962). For this reason the subsequent investigations on the polarity of germination have been carried out on two species with marked differences in the spore structure, viz. *Athyrium filix-femina* (L.) Roth and *Matteucia struthiopteris* (L.) Tod. Spores of *Athyrium filix-femina* are bean shaped, bright yellow with a thin exosporium without any protuberances, whereas, spores of *Matteucia struthiopteris* are big, oval, dark brown or almost black. They have a thick exosporium (Karpowicz 1927).

The present work was undertaken with the aim: 1) to investigate the germination of spores of the two above mentioned species exposed to unilateral light of varying intensity; 2) to establish the period of time necessary for the induction of polarity; 3) to elucidate the spore germination in plane polarized light.

MATERIAL AND METHOD

Spores of two various fern species: *Athyrium filix-femina* (L.) Roth and *Matteucia struthiopteris* (L.) Tod (Szafer, Kulczycki, Pawłowski 1953) provided the experimental material. Sporophylls of *Athyrium* were collected in October 1961 in Szczyrk from specimens growing in natural conditions whereas sporophylls of *Matteucia struthiopteris* were collected in September 1961 from specimens grown in the Botanical Garden in Cracow. Spores were obtained by shaking dried sporophylls over a white sheet of paper.

Differences in the structure of spores and in the pattern of the germination were decisive for this choice. In the growth conditions maintened in the course of this work spores of *Athyrium* formed first a rhizoid. The spores do not germinate in darkness, though in low light intensities a high germination percentage was observed. Spores of *Matteucia struthiopteris* germinated in light by forming the prothallium filament first. They are also able to germinate in darkness, though at a low percentage.

The spores were allowed to germinate on a agar medium in boxes made of transparent plexiglass (dimensions: 3 × 3, 1,2 cm). The boxes were covered with glass plates and tightened with vaseline to protect the cultures from excessive evaporattion.

In all experiments Hoagland's nutrient solution (Bonner and Galston 1952) solidified with 1,5% agar (1 ml per box) was used. A uniform suspension of spores in destilled water (1 ml water, 5 mg spores) was prepared for inoculation and 1,12 ml of this suspension was transferred into every box.

The cultures were kept in a light thermostat in which fluorescent tubes provided light of 914 lux intensity on the level of the culture. Light of 1360 lux was applied in experiments with polarized light. Temperature was maintained between 26—28° C.

In experiments on the action of unilateral unpolarized light the plexiglass boxes with the spores were placed in bigger boxes (Fig. 1a) made of black coated walls with one sidewall left free. Thus the

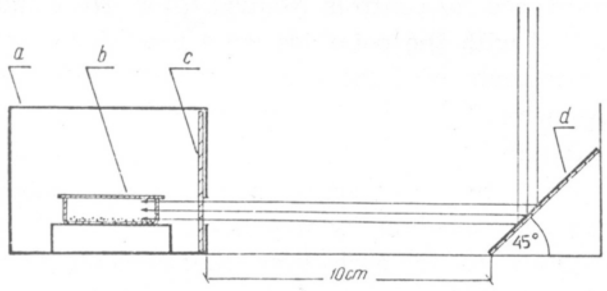


Fig. 1. Scheme of the arrangement for the unilateral illumination of spores *a* — box with dark coated walls; *b* — plexiglass box with germinating spores; *c* — neutral filter; *d* — mirror

access of light to the spores was made possible from one side only. Unilateral and horizontal light beams were reflected by mirrors (Fig. 1d) which were placed at an angle of 45° and received light from a light source placed above the mirrors. The distance separating the boxes from the mirrors was 10 cm. The intensity of the light entering the boxes was 353 lux.

Two modifications were introduced in the experiments performed with unilateral unpolarized light. In the first case the direction of the light beam was not changed during the time of the experiment. In the second case the direction of the light beam was changed every 24 hours by 180°. Changes of the direction of the light beams were made after 1, 2, 3 or 4 days following inoculation.

In experiments with unpolarized light, sitable neutral filters (series NG Schott, Jena) were applied to lower the basic light intensity.

Filter	Thickness of the filter in mm	Light transmission in %	Light intensity in lux
NG 11	2	58	194,4
NG 4	2	10,8	35,4
NG 3	2	1,2	4,2
NG 9	2	0,16	0,7
NG 1	1	0,016	0,1

In experiments with polarized light the spores were exposed to continuous light emitted by a source placed above the boxes. Plane polarized light was obtained by placing Bernotar-Zeiss polaroids (35% transmission) between the light source and the spores. The intensity of trasmitted light was 416 lux. Neutral filtres NG of a similar transmission were used for controls. Neutral filters NG 4 and 3 (mentioned formerly) mounted with the polaroids were used to lower the intensity of light. Measurements of light intensity were performed by means of a Zeiss luxometer. The results were recorded 5, 7, 9 and 13 days following inoculation.

Observations of the germinated spores were carried out directly on the nutrient agar medium by means of a PZO microscope (objective 10 ×, eyepiece 15 ×); each time the percentage of germinated spores was calculated. The burst of the exosporium and the formation of chlorophyll were the criteria of germination.

The direction of growth shown by the rhizoids and filaments was determined with reference to the direction of the incident light beam or — in experiments with polarized light — to the direction of the electric vector. The plane with the spores was divided into 8 equal segments (apical angle 45°) and the number of filaments and rhizoids situated in each sector was determined by direct observation. The results, expressed in percent of the total number of filaments or rhizoids were reported on the axes of the segments.

RESULTS

1. Unilateral illumination and light intensity

Figures 2 and 3 show the results of experiments on the action of unilateral light of varying intensity on the germination polarity of spores of *Matteucia struthiopteris* and *Athyrium filix-femina*. The data were obtained from 9 days old cultures (4 days following the first symptoms of germination). Analysis of earlier or somewhat later phases of the germination process reveals more or less similar results.

The polarity of germination manifests itself in the growth of filaments and rhizoids occurring in directions which are determined by the directional factor (light). If the action of this factor is maintained

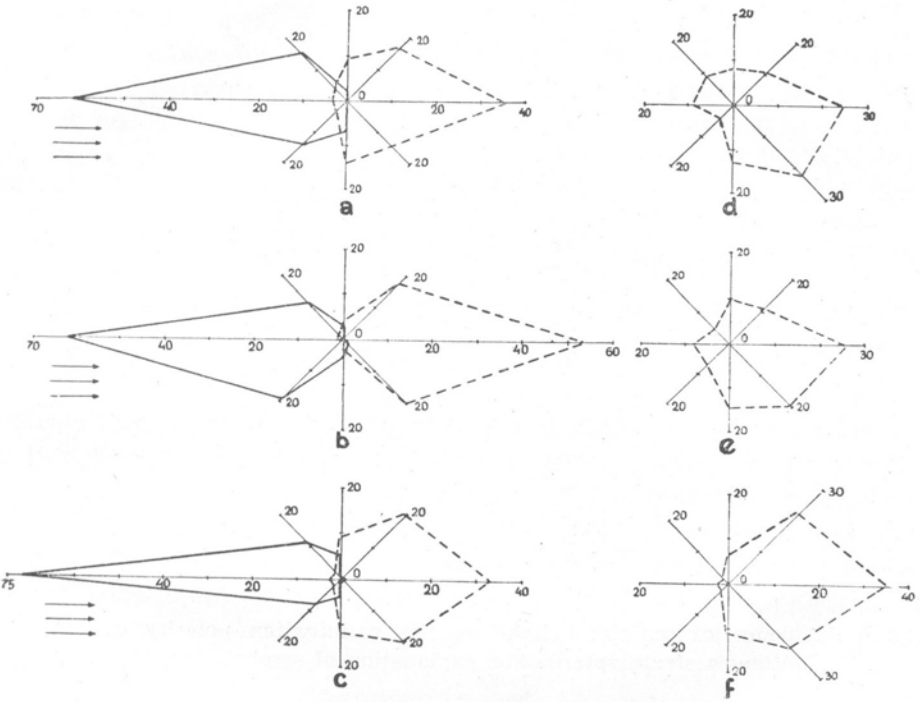


Fig. 2. Action of unilateral light on the germination polarity of spores of *Athyrium filix-femina*

a — full light intensity (100% — 350 lux); *b* — filter NG 11 (transmission 58%); *c* — filter NG 4 (10.8%); *d* — filter NG 3 (1.2%); *e* — filter NG 9 (0.16%); *f* — filter NG 1 (0.016%). Continuous lines refer to the prothallium filaments, broken lines — to rhizoids. Arrows indicate the direction of the light beam. Percentages are marked on every axis

a longer time the filaments and rhizoids continue to grow in the same directions. In this case it is more suitable to speak of phototropism instead of polar growth. Both terms i.e. polarity, for early stages of germination, and phototropism, for later stages of growth have been used in the present discussion.

Figures 2 and 3 very clearly show the effect exercised by the direction of the light beam on the direction of growth both of rhizoids and filaments in the two examined species. Filaments, however, show a greater sensibility and consequently display strictly unidirectional growth even in low light intensities.

Spores of both species show certain differences in germination, due to their different structure. Spores of *Athyrium* have a bright, thin exosporium and germinate easily even in low light intensities, but not in darkness. In the range of applied light intensities the

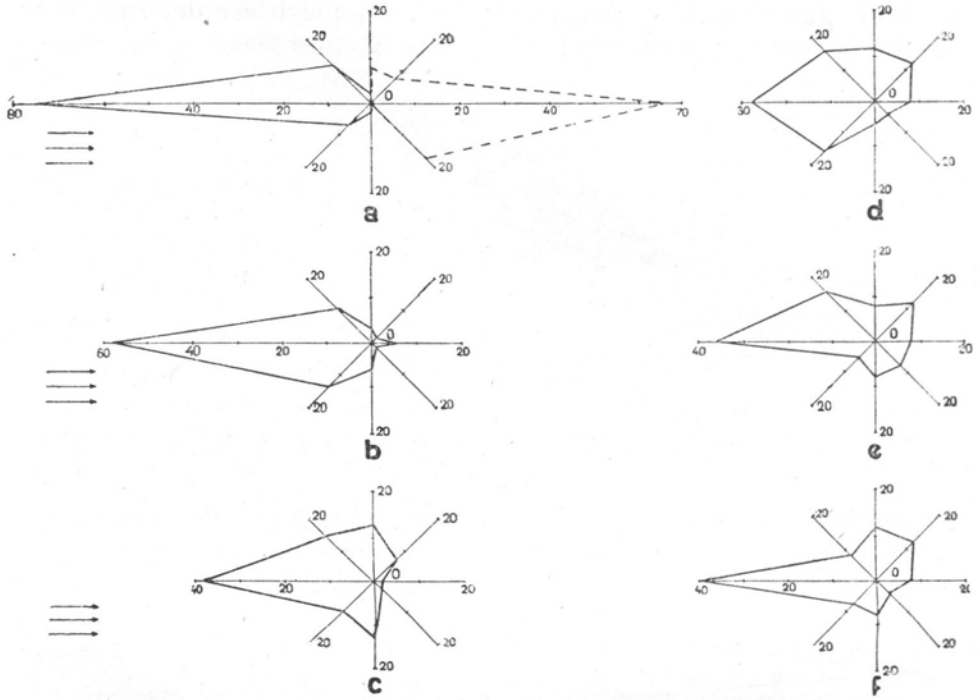


Fig. 3. Influence of unilateral light on the germination polarity of spores of *Matteucia struthiopteris*. For explanation of symbols see Fig. 2.

percentage of germination drops only from 87 to 66. Spores of *Athyrium* germinate by developing the rhizoid first and subsequently the filament. The reaction of a negative phototropism of rhizoids may be easily followed on this example.

It is interesting to note that the highest percentage of spores with rhizoids growing in direction opposite to the direction of the light beam was observed not in the highest, but in moderate light intensities — 194,4 lux (Fig. 2b).

According to Mosbach (1943) an intense illumination reduces the polar growth of rhizoids formed by germinating spores of *Equisetum*.

A similar reaction was observed with filaments of *Athyrium* which attain the maximum of sensibility to light in a still lower intensity (obtained by the use of a filter of 10,82% transmission of the basic light intensity, Fig. 2c). Concomitantly with decreasing light intensity the polar differentation of spores becomes less marked. A slight increase is, however, observed with spores germinating in very low light intensities.

Spores of *Matteucia struthiopteris* have a thick, rough dark pigmented exosporium characterised by slow light transmission. In darkness and low light intensities they germinate by forming a prothallium filament. The rhizoid appears after a certain delay. In high light intensities, however, the spores germinate by developing first a rhizoid.

A much higher sensibility to the unilateral action of light (in comparison with rhizoids) and consequently a very marked phototropic reaction is shown by germinating spores of *Matteucia struthiopteris*. The highest percentage of filaments presenting a positive phototropic reaction was recorded for spores exposed to the most intensive light. This percentage diminishes gradually with decreasing light intensity, but increases slightly again in spores developing in very low light intensities (Fig. 3). From his observations Mohr (1956b) concluded that in low light intensities about 10% of filaments have a negative phototropic reaction.

2. Unilateral illumination and changes of its direction

According to Haupt (1957) in germinating spores of *Equisetum* the first discernible result of the polarity induced by the action of light consists in a separate location of the chloroplasts and of the nucleus in the cells. The phase of sensibility to the action of light however, begins much earlier, namely at a time when there are no visible morphological symptoms of polarity yet, e. g. in spores of *Equisetum* already after 4 hours following inoculation (Mosbach 1943, Haupt 1957).

Experiments were undertaken in order to establish the duration of the light period necessary for the induction of irreversible polarity in fern spores. Spores of *Athyrium filix-femina* were exposed to the action of unilateral light for 4 days following inoculation, after this period the direction of the light beam being changed 180° every 24 hours. In controls the direction of the light beam was changed in the same way from the very beginning of the culture. The constant light intensity equalled 353 lux.

Figure 4d shows the results obtained in 9 days old cultures. Their analysis permits to state that the polarity of rhizoids of *Athyrium filix-femina* is definitely stabilised on the fourth day provided that during 4 days the direction of the light beam is not changed. The direction of growth of the rhizoids is opposite to the direction of the light beam. On the other hand the direction of growth shown by the filaments was perpendicular to the antagonistic directions of the light

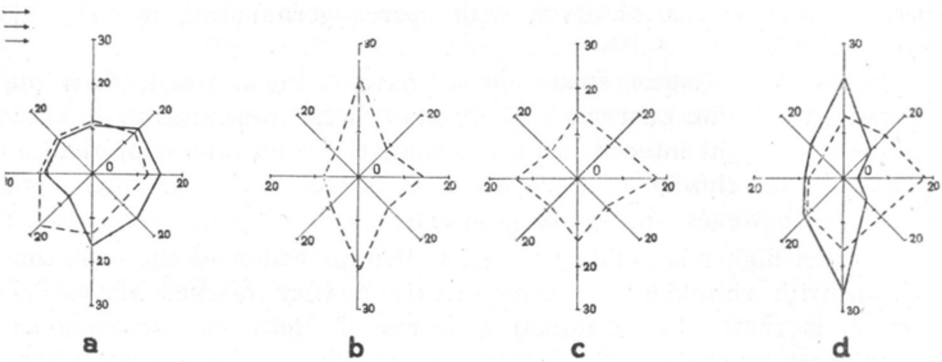


Fig. 4. Influence of unilateral light of periodically changing direction on the germination polarity of *Athyrium filix-femina* spores

a — changes of light direction introduced after 1 day of unilateral light; *b* — after 2 days; *c* — after 3 days; *d* — after 4 days. Arrows indicate the direction of light beam in the initial period. Other symbols as in Fig. 2

beams. Thus, in this case, the angle between the filaments and the rhizoids was 90°. This results shows that axial character of polarity is by no means a necessity (by axial polarity we mean the growth of filaments and rhizoids on the opposite poles of the spore). The polarity of rhizoids is induced earlier than the polarity of filaments. This phenomenon may be a consequence of the fact that in this species filaments grow later than rhizoids.

In subsequent experiments the direction of the light beam was changed 180° every 24 hours after a period of 2 and 3 days during which the direction of light was not modified. The results obtained in 9 days old cultures are presented in Fig. 4*b* and 4*c*. Exposure to unilateral light for 2 days following inoculation did not induce a durable polarity of spores, newertheless the rhizoids grew out as in the previous experiment the filaments perpendiculary to the directions of light. The controls (Fig. 4*a*) show a complete casuality in the polarity of garmination, the percentage of germinated spores being in this case, however, much lower.

In other experiments the spores were illuminated at the same time from opposite directions with light beams of equal intensity. The experiments however, did not lead to the expected results (i. e. lack of polarity), because, even small differences in the intensity of illumination were sufficient to cause a response similar to that obtained by applying unilateral light of constant direction.

The direction of growth perpendicular to the direction of the light beam shown in antagonistic illumination by the rhizoids (Fig. 4*b*) of *Athyrium filix-femina* was already observed by Mosbach (1943) in his study on the germination of *Equisetum* spores.

3. Plane polarized light

The action of plane polarized light of varying intensity on the germination of fern spores was also examined. In this case beside the direction of the light beam an additional directional factor is introduced viz. the constant plane of vibration (plane of polarization) of the light vector. In the experiments the spores were exposed to a light beam of plane polarized light falling from above.

Figures 5A and B show the results obtained with spores of *Athyrium filix-femina* and *Matteucia struthiopteris*. It may be easily noticed that the polarity of spore germination and the direction of subsequent growth of rhizoids and filaments is conditioned by position of the vibrational plane of the polarized light. In higher light intensities (Fig. 5A*a* and B*a*) this reaction is quite evident. The directions of growth shown by the rhizoids and the filaments are parallel, respectively perpendicular to the direction of the plane of polarization, and

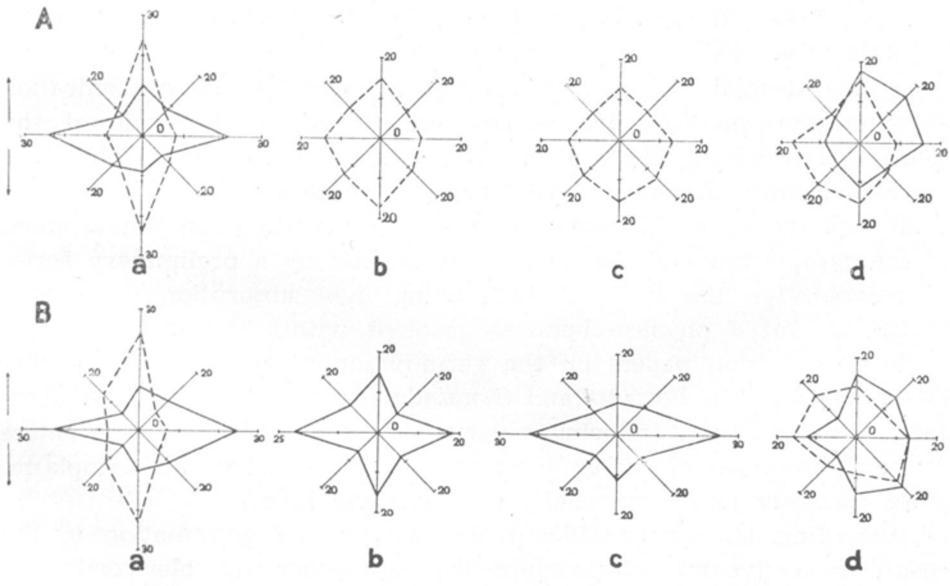


Fig. 5. Influence of polarized light on the germination of spores of: A — *Athyrium filix-femina*, B — *Matteucia struthiopteris*

a — full light intensity (100% — 416 lux); *b* — filter NG 4 10.8% transmission); c filter NG 3 (1.2%); *d* — control. Arrows indicate the vibration plane of the electric vector. Other symbols as in Fig. 2

form an angle of 90°. Thus the plane of polarization determines the orientation of the axis both of rhizoids and filaments but the actual senses of the growth directions are merely casual. The directions of growth of the first and second rhizoid are always opposite.

The action of low light intensities on the direction of germination of rhizoids is much weaker (Fig. 5 A*b, c*) in comparison with the response of filaments which do not show any decrease of sensibility when exposed to polarized light (Fig. 5 B*b, c*). The observation made in experiments with ordinary unpolarized unilateral light that filaments have a much higher phototropic sensibility than rhizoids has been herewith corroborated. A control culture placed in unpolarized light of the same intensity shows a casual distribution of the direction of germination (Fig. 5 A*d* and B*d*). A 17% higher germination rate in comparison to cultures exposed to polarized light has been, however, recorded. A further decrease of the percentage of germinated spores was associated with the decrease of the intensity of polarized light.

DISCUSSION

Many investigators have been interested in the problem of spore polarity. Among the factors influencing the polarity of germination or the subsequent growth of spores the following ones have been examined: temperature (Haupt 1957), narcotics (Wettstain 1953, Haupt 1957), growth substances (Olson and du Buy 1937, Heitz 1942, Wettstein 1953, Mohr 1956b, Haupt 1957, Nakazawa 1960).

A displacement of the cell content resulting in the concentration of cytoplasm, plastids and nucleus on the illuminated side of the spore (Nienburg 1922, 1924 after Mosbach 1943) is the first morphologically discernible symptom of polarity.

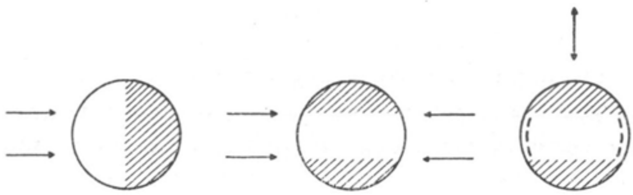
If light is the factor inducing spore polarity then the displacement of the cytoplasmic content must be preceeded by a preliminary series of reactions — the first of them being light absorption — leading to the rise of a physico-chemical gradient within the spore.

It results from papers on the germination of spores of *Equisetum* (Mosbach 1943), *Botrytis* and *Osmunda* (Jaffe, Etzold, Kinley 1962) that the light inducing polarity is absorbed by photoreceptors different from the chlorophyll pigments and located in the cytoplasm, more precisely in its external and peripheric layer.

According to Mohr (1956b) the polarity of germination is the result of a dynamic equilibrium leading, under suitable conditions, to an asymmetric distribution of growth substances within the cell and to the formation of an auxin gradient which in turn conditions the structural asymetry of the cell. In conditions favouring a high auxin production the gradient is very steep and manifests itself in a marked polarity and a rapid elongation of rhizoids and filaments. Factors tending to abolish the auxin gradient are the cause of perturbations of the polar growth of spores. Such factors are the action of blue light or an inflow of an excess of growth substances in the cell. For instance in these conditions apolar forms occur in moss spores (Heitz 1940 according to Wettstein 1953).

It might be supposed that yellow pigments are involved in the destructive action of light on the auxin gradient; the auxin concentration decreases on the illuminated side of the spore. The results obtained in the present experiments with spores exposed to unilateral light corroborate this supposition (Fig. 6a).

A low level of auxin on the illuminated pole stimulates the growth of filaments, whereas the formation of rhizoids is enhanced by a higher concentration of auxins. The results obtained by Olson and du Buy (1937) on the *Fucus* zygotes which develop rhizoids in the direction



a b c

Fig. 6. Scheme of the distribution of growth substances in spores
a — exposed to unilateral light; *b* — exposed to unilateral light of periodically changing direction; c — exposed to polarized light. Arrows indicate the direction of the light beam and the vibration plane of the electric vector (for polarized light). Hatched parts of the spores indicate a higher concentration of growth substances, broken line shows the distribution of the molecules of the photoreceptor

of a higher auxin concentration are in agreement with the present observations. In the experiments of Olson and du Buy the auxin gradient was obtained by placing the zygotes at the outlet of capillary tubes filled with growth substances, whereas in the experiments under discussion, the gradient was formed within the spores themselves.

The prothallia of the fern *Dryopteris varia* grown in a higher concentration of auxin form an additional rhizoid (Nakazawa 1960). Moss spores also form rhizoids in higher concentration of auxins (Heitz 1942).

Two equally illuminated poles with a dark zone between them were obtained when the spores of *Equisetum* were illuminated with two antagonistic light beams. Rhizoids grow out in an haphazard place of the dark zone which most probably, is the place of highest auxin concentration (Mosbach 1943).

The experiments on the action of unilateral light, described in this paper, have established that too low as well as too high light intensities lead to certain perturbations of the polarity of germination. The form of growth of spores exposed to white light is the resultant of the action exercised by the radiations of different wave length composing the white light. Obviously with the increase of the intensity of white light the participation of blue light increases as well. This leads to an inactivation of auxins followed by perturbations of polarity (Mohr 1956b). Mosbach (1943) reports that strong illumination diminishes the orientation of rhizoids in spores of *Equisetum*. High light intensities by decreasing the gradient of growth substances contribute also to the decrease of the polarity (Haupt 1957).

Three phases may be distinguished in germinating spores exposed to the action of a factor inducing polarity, viz. phases of: 1) insensibility, 2) sensibility and 3) stabilized polarity (Haupt 1957). Great differences, however, are observed with respect to these phases in spores of various species developing in indentical conditions. Experiments carried out on spores of *Athyrium filix-femina* showed that the phase of insensibility lasts for a relatively long time (more than 24 hours), whereas for *Equisetum* spores up to 3 hours (Mosbach 1943, Haupt 1957) and for zygotes of *Fucus* up to 10 hours (Haupt 1958b).

The stabilisation of rhizoid polarity in spores of *Athyrium filix-femina* is attained earlier (after 3 days) and is most probably connected with an early formation of rhizoids in this species.

A scheme of a spore illuminated with unilateral periodically changed light is presented in Fig. 6*b*. When the direction of the light beam is changed, already in the phase of sensibility, the rhizoids grow out on the pole of the darkened side of the spore, where the concentration of auxins is high. It is however, difficult to explain, in the light of the adopted hypothesis, why filaments grow out on the darkened poles when the light direction was changed 180° every 24 hours following a 4 days long application of unilateral light. It can not be ruled out that filaments are more sensible than rhizoids to that changes of light and auxin concentration and grow out in places where the intensity or concentration of these factors are comparatively low.

Numerous previous investigations as well as the present one have established that plane polarized light modifies the polarity of germinating spores and their further growth. Prothallium filaments of the fern spores of *Athyrium filix-femina* and *Matteucia struthiopteris* grow in polarized light in the direction which is perpendicular to the plane of light vibration and form a right angle with rhizoids which grow parallel to this plane. Spores of *Botrytis* and zygotes of *Fucus*

(J a f f e, E t z o l d, K i n l e y 1961) germinate parallel to the plane of light vibration. In polarized light the reaction of spores of *Funaria hygrometrica* is similar to that of fern spores (B ü n n i n g, E t z o l d 1958).

The influence of polarized light which causes the orientated germination, may be explained by assuming a determined arrangement of the photoreceptor molecules in the cell. According to J a f f e (1958—62) the molecules of the substance which absorbs light are localized in the surface layer of the cytoplasm and situated parallel to the surface of the cell (comp. H a u p t 1960). If the cell is spheric (as it is the case of spores) the plane of vibration of light and the direction of molecules are parallel in two areas of the peripheric plasma layer and perpendicular in two others. In the first two areas the absorption of light is intensse and low in the two others (Fig. 6c). These differences in absorption may lead, according the above formulated hypothesis, to the formation of a concentration gradient of growth substances inducing in turn polar germination.

This explanation of the polarity of germination resulting from the action of light is based on the assumption that only short wave light is engaged in this process; this is the case of *Equisetum* spores (M o s b a c h 1943, H a u p t 1957) and zygotes of *Fucus* (J a f f e 1958). M o h r (1956a), however, is of the opinion that germination is controlled by a phytochrome system sensible to the action of red light. Observations of B ü n n i n g and E t z o l d (1958) show that red polarized light has a marked effect on the germination of spores of *Dryopteris filix-mas*. In this connexion the question arises concerning the link between the phytochrome system and the auxin gradient. It must be supposed either that this system is able to decompose the auxins, or that the auxins are not involved in the considered process (what seems less probable). An answer to these questions can be expected from experiments on the action of chromatic light on the polar germination of spores.

SUMMARY

1. Spores of two fern species (*Athyrium filix-femina* and *Matteucia struthiopteris*) were exposed to the action of unilateral light beams of constant direction, of periodically changing directions (180°) and of plane polarized light. The polarity of spore germination induced by the light conditions and the initial stages of growth of the prothallia were the subject of a detailed study.

2. Spores of *Athyrium filix-femina* and *Matteucia struthiopteris* illuminated with an unilateral light beam of constant direction show a marked polarity of germination. Filaments grow in the direction

of the light beam, and rhizoids in the opposite one. Filaments show a greater phototropic sensibility than rhizoids and manifest a distinct response even in low light intensities.

3. In spores of *Athyrium filix-femina* exposed to unilateral light the polar growth of rhizoids is induced on the third day following inoculation of the spores on the nutrient medium and is more or less irreversible. Filaments require a longer action of undirectional light (more than 4 days) to acquire a stable polarity.

4. A characteristic growth response was obtained with spores exposed to the action of plane polarized light. Rhizoids grow parallel to the polarization plane, whereas filaments grow perpendicularly to this direction. Filaments manifest a marked phototropic reaction even in low intensities of polarized light and in this respect do not differ from filaments developed by spores germinating in ordinary light. In spores exposed to polarized light the percentage of germination is somewhat lower than in non polarized light.

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