an uneven boundary of the stomatal pores and a rugged surface of subsidiary cells were quite prominent in plants from site P (figures 1–4).

The adaxial leaf surface of *Lantana camera* and *Sonchus asper,* as well as the abaxial surface of *Cicer arietenum* from site NP and site P, were scanned to study the effect of air pollution on trichome characteristics (figures 5–8). Density and length of trichomes were relatively greater in plants from site P. There was more variation in trichome density and length on the adaxial surface than on the abaxial surface of site P plants. The electron microscope study supports the observations made with the light microscope (table 2).

Discussion. Air pollution apparently reduces the size of the stomatal pores on both the adaxial and the abaxial leaf surfaces. Sharma and Butler[1–3] have (on the basis of light microscope studies) reported a slight reduction in the sizes of stomatal pores in *Trifolium repens, Trifolium pratense* and *Acer saccharum* growing in polluted areas. According to these authors, a reduction in size of stomatal pores of plants from a polluted site could be considered as a favourable adaptation, as it might help in reducing the absorption of gaseous pollutants.

The subsidiary cells on the adaxial leaf surface of plants from the polluted site have numerous folds. Our observations do not match those of Godzik and Sassen[5], who reported a reduction in the number of folds on the outer epidermal cells in plants from a polluted area. However, they indicated that a variation in folds together with the changed ultrastructure of the outer cell wall of the epidermis may contribute to the loss of elasticity of leaves.

The length and density of trichomes on the adaxial leaf surface were greater in plants from the polluted site compared with those from the non-polluted site. At the abaxial surface, an increase in length only of trichomes was observed in plants from the polluted area. Sharma and Butler[2] suggested that these changes could have adaptive significance as the high density of trichomes may protect the leaf from direct exposure to the sun's rays, thus lowering the leaf temperature and hence reducing the rate of metabolism. In constrast, Eller[7] suggested that there would be an increase in surface temperature as dust on a leaf is responsible for high absorbance and low reflectance of IR-waves.

In short, air pollution reduces the length and breadth of stomatal pores, augments folding of the subsidiary cells and increases the length and the density of trichomes. These changes appear to have some adaptive significance, because ozone-resistant varieties of *Petunia* also have small stomatal pores and high trichome density compared with its sensitive varieties[8].

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Photoperiodism and morphogenesis of the protonema of *Ceratodon purpureus* (Hedw.) Brid

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Summary. Elongation of *Ceratodon* protonema is a long-day phenomenon. Branching is a short-day phenomenon. The two morphological systems are antagonists.

Light, which has very diverse effects on the protonema of bryales[2] controls morphogenesis by its influence on: 1. photosynthetic activity: a certain amount of trophic light is necessary for protonema to develop into a caulonema branched system. The spectrum of light activity on branching and growth of filaments can be shown to be virtually identical with the absorption spectrum of photosynthetic pigments in vivo[3]. 2. Phytochrome action, which intervenes the positioning of lateral buds branches from which originate. Its role depends on the existence of a substrate, previously synthesized during the course of photosynthesis[3]. 3. The effect of the cellular division factor, which is only present if cultures are submitted to a certain amount of light. This factor circulates in both the acropetal and basipetal directions from the same filament, and is responsible for the perpendicular mitosis generating the main axis[4].

During the course of these experiments, the notion of independence between the growth length of protonema and the branching of axes emerged on several accasions. Thus, the optimum amount of light, was required for lengthening the filament (mitosis rate)[5]. A unilateral and perpendicular light on the axes of protonema filaments is always less favorable for branching than multidirectional light of equal energy, although this has no effect on the mitotic rate[4]. In contrast to the cellular division factors, the branching factor (or factors) seems to be motionless in protonema.

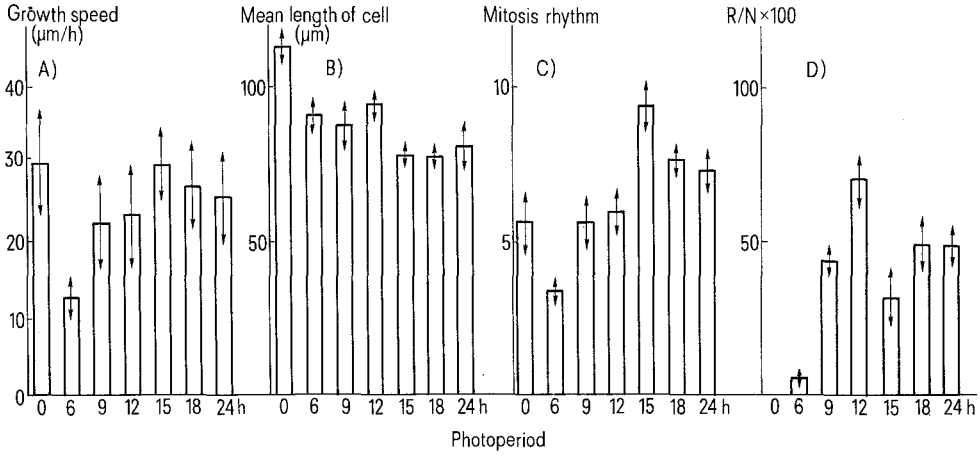
Little data is available concerning the photoperiodic responses of branched filamentous systems. Precise studies carried out on the rhodophyte, *Acrochaetium,* enabled us to reach the conclusion that this organism reacted like a higher plant of the long-day type[6]. For bryales at the protonematic stage only the sexualization phenomena have been studied until now[7–9]. In an endeavour to fill this gap, we decided to undertake this experiment.

Materials and methods. Protonema of *Ceratodon purpureus* (Hedw.) Brid. were grown under sterile conditions at 23 °C ± 1 °C on Kofler A medium[2] under multi-lateral light, of 2250, 4500 ergs cm^{-2} sec^{-1} and 11,000 ergs cm^{-2} sec^{-1} provided by fluorescent tubes (Mazda 'Blanc brillant de luxe' type).

The photo-periods chosen were 3, 6, 9, 12, 15, 18 and 24 h per 24 h. The parameters measured on 12 day-old cultures and characterizing development are the following: average cell length in µm, growth speed of the main axis per 24 h, branching density ($R/N \times 100$: R = number of lateral branches, N = number of cells composing the main axis).

Results. Photoperiodic effects on the elongation of the main axis: Cellular elongation does not appear to vary significantly according to the photo-period, no matter what energy is considered (figures 1, B and 2, B).

Growth speed (function of perpendicular mitoses), reached a maximum at a photo-period of 15 h light by 24 h at 4500 ergs cm^{-2} sec^{-1}, and in continuous darkness (etiolation). If



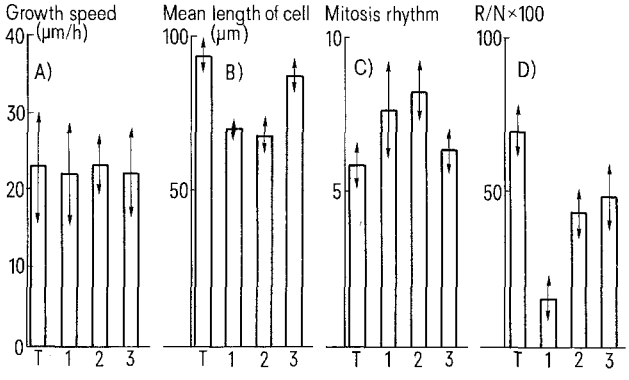


Fig. 1. Development of protonema of *Ceratodon purpureus* (Hedw.) Brid. as a function of various photoperiods. Light energy: 4500 ergs cm^{-2} s^{-1}; 0 h, continuous darkness, 24 h, continuous illumination. $R/N \times 100 = \frac{\text{number of ramifications}}{\text{number of cells}} \times 100$.

Fig. 2. Development of protonema of *Ceratodon purpureus* (Hedw.) Brid. with interruptions of the nycti-period. Light energy: 4500 ergs cm^{-2} s^{-1}. On the abscissa: T, blank: 12 h light/12 h darkness; 1, 12 h light, 1 h darkness, 2 h light, 9 h darkness/24 h; 2, 12 h light, 5 h darkness, 2 h light, 5 h darkness/24 h; 3, 12 h light, 9 h darkness, 2 h light, 1 h darkness/24 h. $R/N \times 100 = \frac{\text{number of ramifications}}{\text{number of cells}} \times 100$.

the light energy is doubled, the optimum is 12 h/24 h. This result is directly connected with the variations of mitosis rate along the length of the main axis as the optimum moves towards the longer photo-periods at lower energy. This fact leads us to presume that lengthening is under the control of long photo-periods.

In fact, interruptions of the dark period (9 h) by illumination for 2 h strongly stimulated the rate of mitosis (32% approximately) (figure 2). This phenomenon is even more pronounced when interruption by light is situated in the middle of the dark period. Physiological behaviour can therefore be compared to that of 'long-day plants'.

Moreover, thallus variations are a function of the trophic illumination provided. Indeed, light at 2250 ergs cm^{-2} sec^{-1} is practically sub-optimal for lengthening and mitosis rate. Higher energy (4500 ergs cm^{-2} sec^{-1}, 11,000 ergs cm^{-2} sec^{-1}) becomes an inhibitor for photo-periods of 12 h or 15 h per 24 h.

The effect of photo-period on the branching of protonema: Branching (R/N) reaches its optimum at photo-periods of 12 h/24 h (figures 1, D and 2, D). If the dark period (9 h/24 h) is divided by 2 h of light (figure 2, D), branching is inhibited. Inhibition is even more effective if the additional light is given at the beginning of the dark period, 77% as against 37% if it is given in the middle or at the end of the 'night'. It is thus possible to consider branching as a 'short-day plant' phenomenon. In addition, this parameter, contrary to the growth speed and mitosis rate, increases for a given photo-period as a function of light intensity.

Discussion. Thus, as in higher plants, the protonema morphogenesis of *Ceratodon purpureus* and perhaps other bryales is dependent on photo-period phenomena. Indeed, morphogenesis of the same protonema results from the complicated action of two phenomena, one stimulated by a long day (elongation) and one stimulated by a short day (branching).

Once again, we meet the antagonism between the two systems responsible for formation of this filamentous system. Mathematical analysis[10] has confirmed the opposition between these two phenomena.

These opposite reactions of two morphological phenomena to the same factors - light - are linked to cellular differentication. Indeed, the same cell, according to the position it occupies along the axis either apical or intercalary, has a division rate of either the long-day type (elongation) or the short-day type (branching). In certain higher plants (*Bryophyllum* for example), release of the phenomenon of flowering demands the growth of the plant first during long days and then during short days. If one or the other photoperiodic condition is missing, the plant continues its vegetative growth.

The type of photoreceptor implicated has yet to be defined, but there is evidence that the phytochrome factor is involved because we have shown its role in the positioning of lateral buds.

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