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THE EFFECT OF LIGHT INTENSITY AND LIGHT PERIOD ON THE DEVELOPMENT OF THALLUS FORM IN THE MARINE RED ALGA *PLEONOSPORIUM SQUARRULOSUM* (HARVEY) ABBOTT (RHODOPHYTA: CERAMIALES).

I. APICAL CELL DIVISION - MAIN AXES

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Abstract: An analysis and discussion of two mechanisms of apical cell division in filaments of *Pleonosporium squarrulosum* (Harvey) Abbott (Ceramiales) is given. It is suggested that the alternate, oblique orientation of cross-wall formation during sequential divisions of apical cells of filaments of unlimited growth is characteristic of actively growing axes and is involved in determining the alternate branching pattern of the thallus. A second method of apical cell division, namely, that resulting in the formation of horizontal crosswalls, is frequently characteristic of filaments that have become limited in growth.

The rates of division of apical cells of main axes of regenerates were determined under light intensities ranging from 269–1614 lx and light periods of 16L–8D and 8L–16D. Rates of division were found to be highly affected by both light intensity and light period, and a significant interaction between the two was demonstrated. The effects of light period are interpreted as acting by increasing or decreasing the duration of exposure to illumination rather than as a 'trigger' effect. A method of presenting a summary of the effects of light period and light intensity is to express the data in terms of Mean Daily Illuminance (MDI = illumination (lux) × day – length (h)/24 h). Analysis of the data as MDI show that the rate of division of apical cells increased with increasing MDI up to a value of 538 MDI.

INTRODUCTION

The external form of the thallus is a major criterion for taxonomic discrimination among the Florideophyceae. It has been demonstrated through field studies (*e.g.*, Dixon, 1958, 1960, 1963b, 1966; Knaggs 1966a, b, c; Powell, 1964; Stewart, 1968) that the morphological variation in florideophycean taxa may, however, be considerable and be correlated with diverse ecological, seasonal, and geographical conditions of growth. In order to understand the morphological variation of a given taxon which may be attributed to habitat diversity, the basic principles of florideophycean morphogenesis must be established. The general principles of thallus development in Florideophyceae have been dealt with by Dixon (1958, 1960, 1963a, b, 1966, 1970, 1971) who established that variation in external thallus form can be expressed in terms of three basic parameters, namely, 1) the disposition of axes;

2) the shape of axes; 3) the longevity of axes.

Temporal and spatial patterns of cell division and cell enlargement directly govern the disposition, shape and longevity of axes, and hence, to understand the range of external form of a given taxon the influence of environmental factors on the processes of cell division and cell enlargement must be known.

Florideophycean red algae are ideal subjects for investigations of this nature because of certain characteristic features of their thalli. First, all florideophycean thalli are constructed of filaments or aggregations of filaments. Secondly, with a few special exceptions, these filaments are composed of cells produced solely by the division of apical cells. Even in those florideophycean genera where there is, however, an increase in filament cell number by the division of other than apical cells (= intercalary cell division), divisions take place in a highly specific and regular manner. This is unlike the indiscriminate intercalary cell divisions of many other algal groups, such as the Chlorophyceae.

As a consequence of this pattern of development, once a cell is formed by the division of an apical cell, it will not divide again in the same plane for Florideophyceae exhibit strictly apical growth, and, in the absence of intercalary cell division, the number of cells of a given filament is a direct indication of the number of apical cell divisions in that filament. The relative ages of individual filament cells are dependent upon their positions with respect to their apical cell origin although this relationship between cells cannot be assumed to be linear with respect to time. Furthermore, in Florideophyceae, the cells produced from apical cells enlarge as they mature. This increase in size is considerable and much greater than that reported for most other groups of plants, *e.g.*, in *Ceramium rubrum*, there may be an increase in volume of 35,000 times (Dixon, 1966, 1970, 1971) and in *Antithamnion plumula* 48,000 times as a cell enlarges from its formation to maturity. The magnitude and pattern of the enlargement of cells derived from the divisions of apical cells will, therefore, exert a very strong influence on thallus form.

In an earlier paper based upon field data (Dixon, 1971), the enlargement of cells in relation to the form of certain florideophycean thalli has been discussed in detail, and provides the basis for laboratory studies in which the effects of light intensity and light period on the processes of cell division and cell enlargement, and hence thallus form, have been investigated in the florideophycean red alga, *Pleonosporium squarrulosum* (Harvey) Abbott (Ceramiaceae). The present contribution is concerned with the methods and rates of division of apical cells of main axes as affected by light intensity and light periodicity. The process of cell enlargement will be dealt with in a subsequent paper.

Materials and Methods

Pleonosporium squarrulosum epiphytic on drift material of the red alga *Ptilota densa* C. Ag. (Ceramiaceae) was collected at Montana de Oro State Park, San Luis Obispo

County, California, on November 10, 1968. Vegetative axes were removed from regions of new growth on freshly collected material, washed in filtered (0.45 μm) sea water, passed through 0.5 % sea-water agar in an effort to remove epiphytes (after Fries, 1963) and washed again in filtered (0.45 μm) sea water prior to inoculation. Portions of *P. densa* plants held in culture gave rise to additional *Pleonosporium squarrulosum* material.

Cultures were grown in 100 × 80 mm glass storage dishes (Pyrex No. 3250) in a modified (von Stosch, 1964; Murray, Dixon & Scott, 1972) enriched natural sea-water medium. Sea water (salinity 30–33 $^{0}/_{00}$, pH 7.6–7.9) was stored in 10-gallon polyethylene carboys for at least 30 days prior to use. Sterilization of all sea water was effected by microfiltration (0.45 μm) or by steam (30 min).

Light regimes of 16 h light–8 h dark (16L–8D) and 8 h light–16 h dark (8L–16D) and light intensities of 269 lx, 538 lx, 1076 lx and 1614 lx were employed during the course of the investigation. Illumination was provided by G. E. 30w 'Cool White' fluorescent lamps and light intensity was measured with a Weston Model 750 Illumination meter. All cultures were grown at 16 ± 1 °C.

Cultures providing inocula for purposes of experimentation were derived from female plants and maintained under illumination conditions of 16L–8D, 538 lx and 1076 lx and 8L–16D, 1076 lx. No appreciable differences in results between inocula grown under any of these conditions were found. Twelve- to thirty-celled filaments, each containing an actively growing apical cell, were removed from axes of unlimited growth as inocula. It was decided that a minimal amount of stress would be likely in working with inocula consisting of fragments of this size rather than with one- or two-celled fragments. Filaments selected for inoculation were carefully examined microscopically and the number of cells comprising each axis was determined. One to four inocula were then distributed in glass storage dishes and grown in 250 ml of medium under selected conditions of illumination. Inoculated filaments readily attached to the bottom of glass storage dishes by producing short rhizoid-like growths from freshly cut basipetal portions. Occasionally inocula failed to attach or attached at portions other than basipetal regions and so changed their natural polarity. Samples failing to attach at the basipetal region or showing obvious indications of alteration in polarity were excluded from analyses.

The majority of experiments lasted 21 days or less, in which case it was not necessary to replenish the nutrient medium. At the conclusion of each experiment, samples were carefully detached from glass dishes and fixed in 3–4 % formaldehyde-sea water. Permanent preparations were made for further detailed analyses: glycerine-jelly preparations were found to be satisfactory. Although there was a small amount of shrinkage using this mounting medium, the reduction in size of cells was consistent when compared with that of living material. The number of apical cell divisions in a given axis was then determined for each sample by subtracting the number of cells that composed an axis at the time of inoculation from the number of cells at the end of an experiment.

Results and Discussion

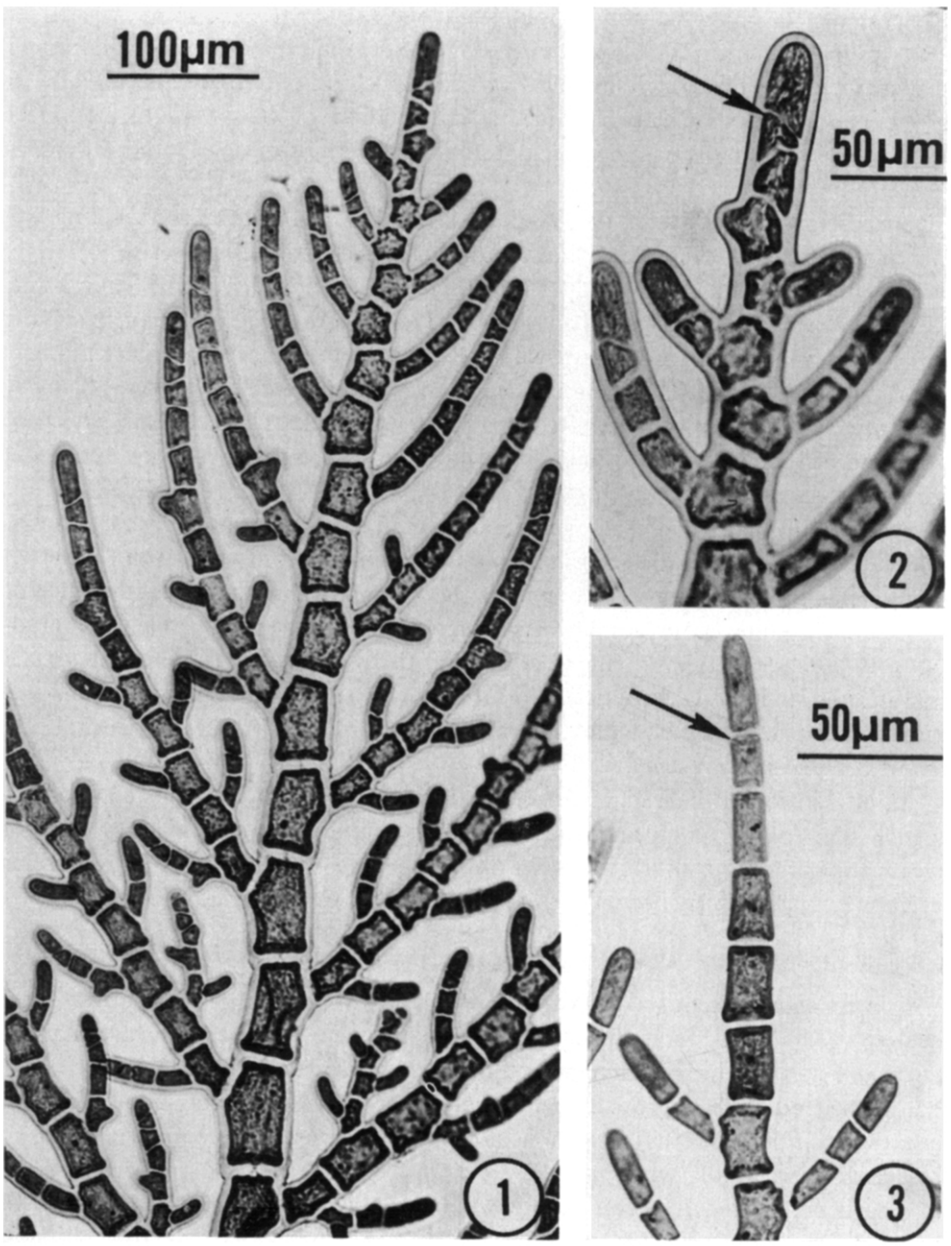
Analysis of the mechanisms of apical cell division

The thallus *P. squarrulosum* (Fig. 1) is composed of alternately branched uniaxial filaments exhibiting strictly apical growth. Mature axes become corticated by the downward growth of filaments produced by the basal cells of lateral axes. In an actively growing filament, the apical cell generally produces a segment cell by means of a cross wall (Fig. 2) which is formed at an angle oblique to the plane of the axis. The orientation of this plane of division alternates during repeated apical cell divisions thereby producing a series of wedge-shaped segment cells that are alternately greater in length on one side than on the other. In *P. squarrulosum* the single lateral initial produced by each segment cell is always formed from that region of the segment cell which was greatest in length at its inception. This mechanism of apical cell division, and hence filament growth, is the first discrete gross morphological indication of the highly regular alternate branching pattern characteristic of this taxon.

Filaments of *P. squarrulosum* which have become limited in growth generally exhibit, however, a different method of apical cell division. In these filaments, cross-walls are often formed (Fig. 3) at an angle perpendicular to the plane of the axis, and as a consequence the segment cells adjacent to the apical cell of such a filament are more-or-less rectangular rather than wedge shaped. Filaments which have become limited in growth generally terminate in several unbranched cells.

The alternate, oblique orientation of cross-wall formation during sequential apical cell division reported here for *P. squarrulosum* has been reported previously (*e.g.*, Berthold, 1882; Cramer, 1864; Falkenberg, 1901; Kny, 1873; Konrad-Hawkins, 1964a, b, 1968, 1972; Kylin and Skottsberg, 1919; Rosenvinge, 1888, 1902; and Tseng, 1944) for members of the Ceramiales. As pointed out by Konrad-Hawkins (1968), it was believed by some workers (*i.e.*, Schwendener, 1880) that oblique cross-walls of segment cells were a secondary phenomenon becoming unilaterally raised after, and as a result of, the development of lateral branches. Others (*e.g.*, Berthold, 1882; Rosenvinge, 1902) reported that the formation of oblique cross-walls occurred prior to the development from axial cells of lateral initials. The latter view, that oblique cross-wall formation during apical cell division is a primary phenomenon was supported by the studies of Konrad-Hawkins (1964a, b, 1968, 1972) on *Callithamnion roseum* as it is by the present evidence for *Pleonosporium squarrulosum*.

Rosenvinge (1902) reported that unbranched segment cells of *Polysiphonia urceolata* were delimited by horizontal rather than oblique cross-walls. Konrad-Hawkins (1964a, b; 1968) indicated that in regenerates of *Callithamnion roseum* branchless axial cells were generally formed by the production of parallel or horizontal cross-walls but, oblique cross-walls were formed as the regenerates re-gained a normal, alternately branched pattern of growth. Konrad-Hawkins (1972) has recently reported that the stages in the morphological development of sporelings and



Figs 1–3. *Pleonosporium squarrulosum* (Harvey) Abbott.

Fig. 1. A major axis of a plant grown in laboratory culture; glycerine-jelly preparation.
Fig. 2. Filament showing the method of apical cell division characteristic of an actively growing axis; glycerine-jelly preparation.
Fig. 3. Filament showing the method of apical cell division characteristic of an axis that has become limited in growth; glycerine-jelly preparation.

regenerates of *C. roseum* are morphologically equivalent.

It is probable that in *Pleonosporium squarrulosum*, the type of cross-wall formed during apical cell division is involved in the branching pattern of the thallus: in agreement with Konrad-Hawkins (1972) the method of cross-wall formation is probably the gross morphological manifestation of a series of developmental events during cell division.

Konrad-Hawkins (1964a, b, 1968) indicated that in *Callithamnion roseum*, segment cells of normally growing plants formed by oblique cross-walls gave rise to lateral initials after they had reached a position three cells removed from the apical cell, *i.e.*, after two additional apical cell divisions. In *Pleonosporium squarrulosum*, in $\approx 80\%$ of the cases examined it was the fourth cell beneath the apical cell where the first lateral initial was observed and an indication that the apical cell of a lateral filament has switched from active, unlimited growth to give the characteristic alternate branching of segment cells, to limited growth is often the production of horizontal cross-walls during division.

In the case of many of the simple uniaxial Ceramiaceae, and possibly the Rhodomelaceae (*cf.*, Rosenvinge, 1902), it seems that the method of cross-wall formation during apical cell division may be used as the first gross morphological evidence of the future branching pattern and growth characteristics of a given filament. Konrad-Hawkins (1964a, 1972) has pointed out that the distribution of organelles with special regard to the characteristics of newly formed daughter nuclei during unequal, oblique apical cell divisions may be highly important in determining the developmental pattern in *Callithamnion roseum*.

The ultrastructural characteristics of unequal cell division and the relationships of such to patterns of hormone distribution are interesting problems in need of investigation if one is to gain further understanding into the control of thallus development in *Pleonosporium squarrulosum* and other Ceramiaceae.

RATES OF APICAL CELL DIVISION UNDER EXPERIMENTAL CONDITIONS OF ILLUMINATION

Environmental effects on growth and development of multicellular algae have been reported but few studies have attempted to include detailed quantitative analyses of cell division and cell enlargement. For florideophycean red algae, many investigators have described growth and development under different laboratory and natural conditions, but almost without exception in terms of biomass or changes in gross external features; rates and patterns of cell division and cell enlargement have been considered in detail only by Konrad-Hawkins (1964a, b, 1968, 1972), Dixon & Richardson (1970), Dixon (1970, 1971), Duffield, Waaland & Cleland (1972), and Waaland & Cleland (1972).

The number of apical cell divisions in major axes of plants of *Pleonosporium squarrulosum* grown under 8L–16D and 269, 538, 1076, 1614 lx and 16L–8D at 269, 538, 1076, 1614 lx after a 21-day period of growth, are given in Table I and Fig. 4 as mean number of cell divisions/day. The differences in growth of *P. squarru-*

TABLE I

Rates of apical cell division under experimental conditions of illumination

Photoperiod	Light intensity (lux)	No. observations	Mean no. apical cell divisions/day	±S.D.
8hL–16hD	269	6	1.17	0.30
	538	12	1.71	0.18
	1076	11	1.87	0.17
	1614	11	2.06	0.17
16hL–8hD	269	6	1.52	0.12
	538	11	1.95	0.22
	1076	11	1.96	0.17
	1614	10	1.91	0.18

losum under these conditions of illumination were attributable to effects of illumination rather than to 'lag periods' occurring at the beginning of experiments. An analysis of 'lag period' responses shows that there was a 'lag period' equivalent to 0–3 apical cell divisions/21 days, but the magnitude of observed 'lag period' was not related to the illumination.

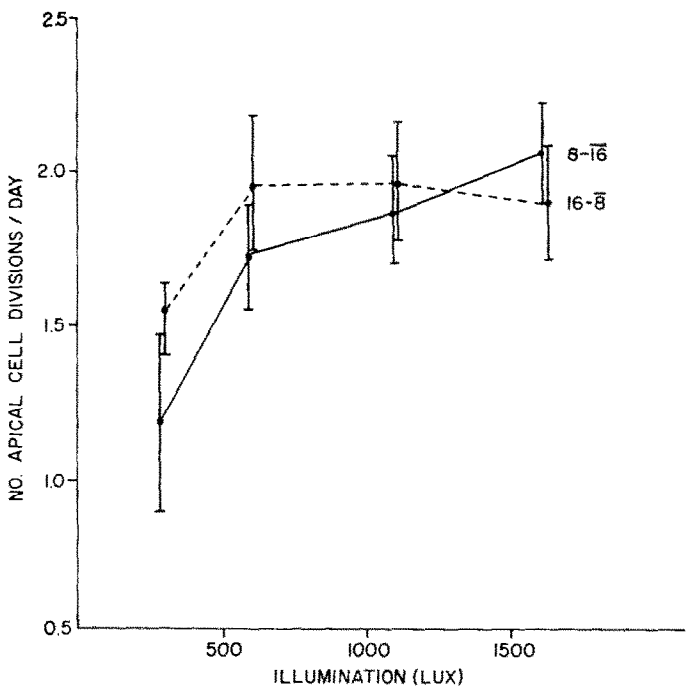


Fig. 4. Mean number of apical cell divisions per day in plants of *Pleonosporium squarrulosum* grown under 8L–16D and 16L–8D light-dark cycles at light intensities ranging from 269 to 1614 lx.

The rates of apical cell division ranged from of 1.17–2.06 divisions/day. This range is somewhat similar to that for *Callithamnion tetricum* (Dixon & Richardson, 1970), *C. roseum* (Konrad-Hawkins, 1964a, b) and *Griffithsia pacifica* (Duffield, Waaland & Cleland, 1972; Waaland & Cleland, 1972). Dixon & Richardson (1970) found the principal apical cell of *Callithamnion tetricum* to divide at an average of 1.1 times/day under a 8L–16D regime and 2.1 times per day under a 16L–8D regime. For *C. roseum*, Konrad-Hawkins (1964a, b) reported the apical cell of the principal axis to divide 15 times over a period of 5 days. Duffield, Waaland & Cleland (1972) found that apical cells of regenerates of *Griffithsia pacifica* added new cells at the rate of 2/day for the first 1–2 days but subsequently at 1/day. In further experimentation on *G. pacifica*, Waaland & Cleland (1972) found means after a period of 7 days of 6.6–9.0 cells/day for primary filaments in cultures which originated from single-cell inocula.

Because of unequal sample sizes, the data were analysed statistically using the method of weighted means squares (Yates, 1934; *cf.*, Steel & Torrie, 1960) to give unbiased estimates and tests of main effects (*e.g.*, light intensity and light period) and to provide information on interaction when one of the criteria of classification contains only two categories. The results of the analysis are given in Table II and show that

TABLE II

Analysis of rates of apical cell division under experimental conditions of illumination (lux): weighted mean squares (unequal and disproportionate sample size); *** $P < 0.001$, ** $0.01 > P > 0.001$.

Source of variation	D.f.	Sum of squares	Mean square	F
Light intensity	3	3.479	1.160	32.033 ***
Light period	1	0.319	0.319	8.815 **
Interactions	3	0.626	0.209	5.765 **
Error	70	2.531	0.036	
Total	77	6.955	1.724	

both main effects, light intensity ($P < 0.001$) and light period ($0.01 > P > 0.001$) significantly affected the rate of apical cell division and that there is interaction ($0.01 > P > 0.001$) between light intensity and light period. In breaking down the interaction effects, it was found that interactions between light intensity and light period were most pronounced at the minimum (269 lx) and maximum (1614 lx) light intensities employed. Rates of apical cell division were least additively depressed under 8L–16D, 269 lx and 16L–8D 1614 lx, *i.e.*, the lowest and highest illumination in terms of the total amount of light energy received/24 h-period, respectively. This is interpreted as indicating minimal and maximal illumination conditions for the rate of division of apical cells of main axes of this particular clone of *Pleonosporium squarrulosum*. The most significant, non-additive, enhancement was under 8L–16D at 1614 lx and 16L–8D at 269 lx, which is interpreted as indicating an increased significance of light intensity under the shorter 8 h-day and of light period under conditions of minimal light intensity.

In an effort to evaluate in more detail the effects of light intensity, each photoperiod and its series of four light intensities was considered separately and analyzed separately by a single classification analysis of variance with unequal sample size. *A priori* tests among means were used to determine the effects of increasing light intensity under each of the two photoperiods. The results show that under the 8 h light period the number of apical cell divisions/day increased significantly from 269 to 538 lx ($P < 0.001$), and from 1076–1614 lx ($0.05 > P > 0.01$). The number of apical cell divisions/day not did significantly increase ($0.10 > P > 0.05$) with the increase in light intensity from 538–1076 lx. In the case of plants grown under the 16 h light period, the number of apical cell divisions/day increased significantly with increased light intensity only from 269–538 lx ($P < 0.001$). At light intensities > 538 lx (1076, 1614 lx) there were no significant differences ($P > 0.05$) between rates of apical cell division.

TABLE III

Analysis of variance (single classification) of rates of apical cell division, variable light intensity, 8L–16D photoperiod; *** $P < 0.001$; *$0.05 > P > 0.01$.

Source of variation	D.f.	Sum of squares	Mean square	*F*
Among groups (among light intensities)	3	3.228	1.076	27.951 ***
269 lx *vs* 538 lx	1	1.163	1.163	30.203 ***
538 lx *vs* 1076 lx	1	0.145	0.145	3.761 n.s.
1076 lx *vs* 1614 lx	1	0.200	0.200	5.205 *
Within groups (error)	36	1.385	0.039	
Total	39	4.613	1.115	

TABLE IV

Analysis of variance (single classification) of rates of apical cell division, variable light intensity, 16L–8D photoperiod: *** $P < 0.001$.

Source of variation	D.f.	Sum of squares	Mean square	*F*
Among groups (among light intensities)	3	0.919	0.306	9.089 ***
269 lx *vs* 538 lx	1	0.714	0.714	21.181 ***
538 lx *vs* 1076 lx	1	0.002	0.002	0.048 n.s.
1076 lx *vs* 1614 lx	1	0.017	0.017	0.502 n.s.
Within groups (error)	34	1.146	0.034	
Total	37	2.065	0.340	

As a method of expressing light period and light intensity treatments as the total amount of illumination received/24 h day, Chapman & Burrows (1970) introduced Mean Daily Illuminance (M.D.I., illumination (lux) × length of light period (h)/24 h). Although useful to simplify the presentation of complex light intensity and light

period data M.D.I. is applicable only with certain reservations. First, 'trigger-like' photoperiodic effects must be absent. Secondly, care must be taken in the treatment of data obtained below light intensities or periods eliciting minimal responses and above illumination conditions eliciting maximal responses. Thirdly, care must be taken not to overlook statistically significant interactions between light period and light intensity. If the experimental data are quantifiable, statistical procedures should be employed for testing the compatibility of data obtained under similar M.D.I. generating illumination conditions. In that the primary effect of light period on rates of apical cell division in *P. squarrulosum* was to affect the duration of exposure to light rather than to act as a 'trigger' effect, M.D.I. is considered to be a reasonable method of summarizing our results.

Analysis of the data in terms of M.D.I. shons (Table V) that the number of apical cell divisions/day increased with total illumination/24 h up to a value of 538 M.D.I. (8L–16D, 1614 lx). Illumination giving M.D.I. values greater than 538 were not

TABLE V

Analysis of variance (single classification) of rates of apical cell division for M.D.I.: *** $P < 0.001$, * $0.05 > P > 0.01$.

Source of variation	D.f.	Sum of squares	Mean square	F
Among groups (among M.D.I. values)	5	4.186	0.837	22.026 ***
89.7 M.D.I. *vs* 179.3 M.D.I.	1	1.018	1.018	26.789 ***
179.3 M.D.I. *vs* 358.7 M.D.I.	1	0.680	0.680	17.895 ***
358.7 M.D.I. *vs* 538.0 M.D.I.	1	0.168	0.168	4.421 *
538.0 M.D.I. *vs* 717.3 M.D.I.	1	0.049	0.049	1.289 n.s.
717.3 M.D.I. *vs* 1076.0 M.D.I.	1	0.016	0.016	0.421 n.s.
Within groups (error)	72	2.711	0.038	
Total	77	6.897	0.875	

effective ($P > 0.05$) in increasing the rate of apical cell division, so that under our conditions growth as determined by the number of apical cell divisions/day, is saturated at less than 717 M.D.I. (Fig. 5). The regression equation is $\hat{Y} = 1.1754 + 0.002566X - 0.00000179X^2$, with $\hat{Y}$ the rate of division of apical cells of main axes of *P. squarrulosum* and X, as the M.D.I.

There is little published information with which to compare the effects of light intensity and light period on these rates of apical cell division. Dixon & Richardson (1970) found the rate of division of the principal apical cell of *Callithamnion tetricum* to increase from a mean of 1.1 divisions/day under 8L–16D to 2.1 divisions/day under 16L–8D. Waaland & Cleland (1972) found that four times as many 'shoot' cells were produced after a period of 7 days under a light intensity of 300 ft-c (= 3229 lx) as under 40 ft-c (= 431 lx) in *Griffithsia pacifica*, and as the light period was shortened, the number of 'shoot' cells was found to decrease. This resulted from

increased branching of 'shoots' under the higher light intensity and longer light periods, rather than from differences in rates of apical cell division of primary axes. Although they found apical cell division to be reduced under 8L–16D, division rates at 40 and 300 ft-c were considered to be equivalent, and they concluded without

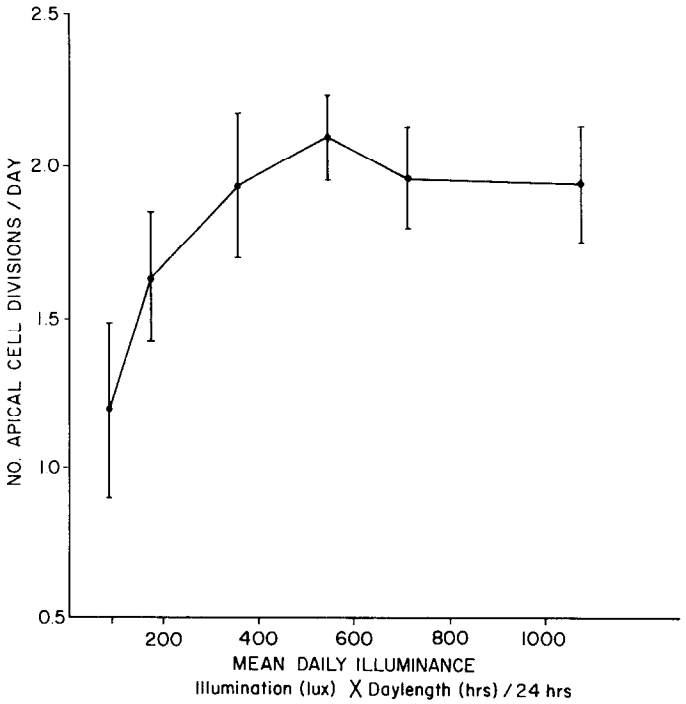


Fig. 5. Mean number of apical cell divisions per day in plants of *Pleonosporium squarrulosum* grown under conditions of Mean Daily Illuminance ranging from 89.7 to 1076 M.D.I.

statistical analysis of their data that apical cell divisions were relatively insensitive to either light intensity or light period. The production of lateral initials by cells of primary axes is a highly characteristic feature of the development of the alternately branched thallus of *Pleonosporium squarrulosum*, but in *Griffithsia pacifica* branching of primary axes is most irregular: it is difficult, therefore, to make direct comparisons of the effects of illumination on the developmental processes of these two species.

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