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Reproduction Induced by Blue Light in Female Gametophytes of *Laminaria saccharina*

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Summary. In red light at 15° C, female gametophytes of *Laminaria saccharina* continue to grow indefinitely without becoming fertile, but 6–12 hours' irradiation with blue light induces the production of eggs. At lower temperatures, some gametophytes become fertile in red light, but blue irradiation increases the percentage of fertile gametophytes.

Culture studies of many species of Laminariales have shown that the size at which female gametophytes become fertile varies widely. Eggs may be produced by gametophytes which consist of only one or a few vegetative cells. Alternatively, the gametophytes may continue to grow vegetatively until they are profusely-branched, filamentous plants, and they may even become macroscopic without reaching maturity. The change from vegetative to reproductive development has been attributed to various environmental factors, including temperature, nutrient concentration and the intensity of the incident light (Kain, 1964; Hsiao and Druehl, 1971). Although the effects of temperature and light intensity on the growth and reproduction of gametophytes have often been investigated, the specific effects of light quality on reproduction have not been investigated in detail since the report by Harries (1932) that sporophytes of three species of *Laminaria* were produced in blue light but not in red light. The present authors have re-examined this observation, using the facilities of the Photobiological Laboratory of the Biologische Anstalt Helgoland.

Zoospores of *Laminaria saccharina* specimens growing near Helgoland were released into enriched sea water (Provasoli), and allowed to settle on cover glasses in petri dishes. They were cultured at 15° C in red fluorescent light [Philips red fluorescent lamps TL 40 W/15, combined with 3 mm red Röhm & Haass Plexiglas Nr. 501; emitted waveband of lamp-filter combination 610–700 nm, with peak emission at 660 nm, according to Mohr and Ohlenroth (1962); incident quantum flux density = 1.4 nE/cm^2·sec = 2500 erg/cm^2·sec]. Every three days one cover glass, with several hundred gametophytes attached, was transferred to blue light (interference filter with peak transmission at 447 nm; 2.40 nE/cm^2·sec = 6400 erg/cm^2·sec) at the same temperature. Irradiation was continued for 48 hours, and the cover glass was then returned to the red light for a further 8 days, when the percentage fertility of the female gametophytes was estimated. A fertile gametophyte was defined as one that had released one or more eggs, and the number of such gametophytes in a total of 500 females was counted.

In red light at 15° C, no eggs were produced. Both female and male gametophytes became profusely branched, and were visible to the unaided eye after 3–4 weeks. 48 hours' irradiation with blue light, however, induced egg production in some (5%) of the female gametophytes only 6 days after settlement of the zoospores, and, thereafter, the reponse to blue light increased with age, reaching 99% in 28-day-old gametophytes (Fig. 1, broken curve). Gametophytes grown in red light for longer periods became too large to work with using our present techniques. However, fragments of old gametophytes, which had been grown in red light for 6 months or more, could be settled onto cover glasses, and treated in the same way as gametophytes derived directly from zoospores. Such gametophyte fragments respond to blue light more rapidly, over 90% of females being induced by 48 hours of blue light given only 6 days after fragmentation (Fig. 1, solid curve).

The effects of different lengths of blue irradiation were investigated at 15° C for both types of female gametophyte. All gametophytes were pre-treated with red fluorescent light (1.4 nE/cm^2·sec) for 8 days. Irradiation treatments with 485 nm light (2.4 nE/cm^2·sec) were all started simultaneously, and individual cover glasses were returned to red light at different times. Percentage fertility of the females was estimated 10 days after the start of the blue irradiation. The response of the fragmented, old gametophytes increased linearly up to 12 hours, and became saturated after 72 hours (Fig. 2, solid curve). Gametophytes derived directly from zoospores showed a lower response (Fig. 2, broken curve), probably because the 8-day-old gametophytes were not old enough to respond optimally (compare Fig. 1).

Since other workers have demonstrated the importance of temperature as an environmental factor for the gametophytes of Laminariales (Kain, 1964), the interaction between temperature and light quality was also investigated, using fluorescent sources for both red and blue light [red source: as detailed above; blue source: Philips blue fluorescent lamps TL 40 W/18, combined with 3 mm blue Röhm & Haass Plexiglas

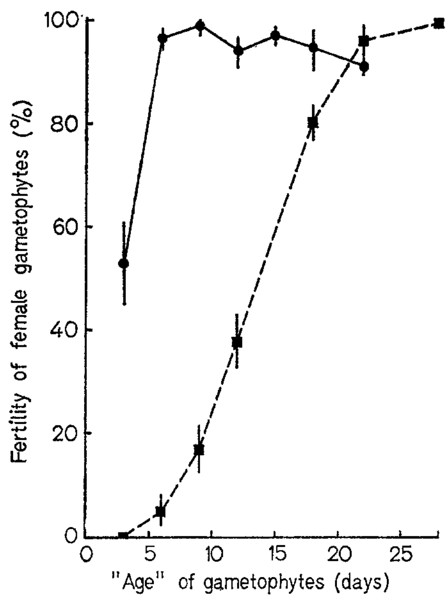

Fig. 1. Effects of 48 hours of blue irradiation (447 nm, 2.4 nE/cm^2·sec) on female gametophytes of *Laminaria saccharina* of different ages at 15° C. Solid curve: gametophytes derived from fragments of red-grown filamentous gametophytes ("age" is time since fragmentation). Broken curve: gametophytes derived directly from zoospores ("age" is time from settlement). Percentage fertility was estimated 10 days after beginning of blue irradiation. Each value plotted is based on a count of 500 gametophytes, and vertical bars are 95% confidence limits derived from tables for percentages (Rohlf and Sokal, 1969)

Nr. 627; emitted waveband 400–520 nm, with peak emission at 445 nm, according to Mohr and Ohlenroth (1962)]. Eggs were produced in red light at low temperatures (Table 1), although the percentage fertility was far lower than in blue light of the same quantum flux density. The optimal temperature for egg production was 10° C in blue light, but 5° C in red light, and the differential effects of temperature were accentuated at low irradiances. Eggs were not produced in either blue or red light at 20° C, but this temperature lies close to the upper limit tolerated by *L. saccharina* gametophytes (Kain, 1969).

Reproductive activity in female gametophytes of *L. saccharina* is induced by 6 hours or less of irradiation with blue light, even though the formation of the eggs does not become apparent until at least 5–6 days after the blue light treatment. This observation suggests that the blue light is specifically affecting the reproductive development of the gametophyte, rather than acting through its effect on the photosynthetic

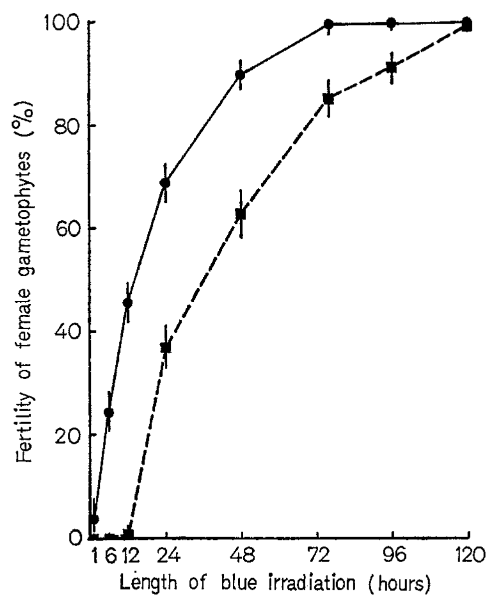

Fig. 2. Effects of different periods of blue irradiation (485 nm, 2.4 nE/cm²·sec) on 8-day-old female gametophytes of *Laminaria saccharina* at 15° C. Details as Fig. 1

Table 1. Percentage fertility of female gametophytes of *Laminaria saccharina* after 10 days' irradiation with blue or red fluorescent light at different irradiances and temperatures

Gametophytes derived from fragments of red-grown filamentous gametophytes, pre-treated for 8 days in red fluorescent light (1.4 nE/cm²·sec) at 15° C. Each value is based on a count of 500 gametophytes.

Wave-band	Irradiance		Temperature			
	nE/cm²·sec	erg/cm²·sec	5° C	10° C	15° C	20° C
Blue	0.16	400	15.9	39.7	0.02	0.00
	0.38	1000	52.0	70.4	35.5	0.00
	0.96	2600	93.1	98.8	98.5	0.02
Red	0.60	1100	16.5	0.00	0.00	0.00
	1.56	2800	21.8	14.7	0.00	0.00
	3.84	7000	48.0	34.9	1.1	0.00

system. This response can, therefore, be regarded as another example of a photomorphogenic response in a simple, filamentous alga (Dring, 1971).

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