Control by Light Quality of Chlorophyll Synthesis in the Brown Alga *Desmarestia aculeata*

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The chlorophyll synthesis in the brown algae *Desmarestia aculeata* is affected by light quality and by the nutrient state in the medium before the illumination. Pulses of 5 min of red, green and blue light together with 200 μM nitrate in plants growing under natural conditions determined similar induction of chlorophyll synthesis. However, when the plants were incubated previously under starvation conditions the light effect was different. The induction of chlorophyll synthesis was greater after blue and green light than after red light pulses. Red-light photoreceptor was only involved in the chlorophyll synthesis under no nutrient limitations and under starvation conditions after previous illumination with blue light followed by far-red light. The induction of chlorophyll synthesis by green and blue light pulses applied together with nitrate was greater when the algae were incubated in starvation conditions than in natural conditions (normal nutrient state).

Because all light effects were partially reversed by far-red light the involvement of a phytochrome-like photoreceptor is proposed. In addition, a coaction between blue- and a green-light photoreceptors and phytochrome is suggested.

Introduction

The photoregulation of photosynthetic pigment synthesis by light quality has been reported in various green and red algae [1–3] but any report about wavelength regulation in brown algae has still not been published. Chlorophyll synthesis in green microalgae is controlled by a specific blue-light photoreceptor [4]. López Figueroa and Niell [5] proved in the green macroalga *Ulva rigida* that in addition to blue light regulation, chlorophyll synthesis was induced by red light through a phytochrome system when the pulses were applied together with nitrate. In the red alga *Porphyra umbilicalis* only involvement of phytochrome was determined [5]. Biliprotein synthesis in cyanobacteria is regulated by a red-green photoreversible system [6, 7]. Chromatic adaptation has also been reported in various red algae incubated previously under nitrate starvation [5]. Ley and Butler [8] observed that cells of the red alga *Porphyridium cruentum* growing in high intensity red or blue light presented twice the Phycoerythrin : Chlorophyll ratio than cells growing in high intensity green light. *Porphyra* exposed to blue light contained more phycoerythrin and less chlorophyll that plants exposed to green light [9]. In addition to red-green light regulation, the involvement of phytochrome in the control of biliprotein synthesis in *Corallina elongata* was proposed [10].

The algae can also modulate the pigment composition in response to light quantity ("light intensity") [11–14]. In the brown algae, *Fucus* and *Ascophyllum,* changes of fucoxanthin / Chl *a* ratio attributed to light intensity [15]. In *Dyctiota dichotoma* changes in the rate Chl *c*/Chl *a* and fucoxanthin/Chl *a* ratios decreased at the surface and in deep-waters increased [16].

In this work the effect of light pulses of different quality (red, blue and green) on chlorophyll synthesis in the brown alga *Desmarestia aculeata* is studied. After these pulses far-red light was applied in order to test a possible involvement of phytochrome. The role of nitrate in coaction with light on chlorophyll accumulation is also analyzed. In addition to light quality a possible exposure (*i.e.* lenght × irradiance) effect was tested.

Abbreviations: Chl *a,* chlorophyll *a;* B, blue light; FR, far-red light; G, green light; P_{fr}, far-red absorbing form of phytochrome; R, red light; WL, white light.

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Materials and Methods

The brown alga *Desmarestia aculeata* was collected in summer 1990 at 5 m deep in the coastal waters of Helgoland (North Sea). Then two different pretreatments were conducted: firstly, the plants were maintained in incubation chambers of a capacity of 100 l with circulating sea water. The sea water came directly from the sea. The plants were incubated three days under green light (about 15 μmol m^{-2} s^{-1}) with no nutrients deficiency. The green light dominates in the natural environment in which these algae grow [17]. Secondly, the plants (about 200 g FW) were incubated during seven days in continuous white light (Osram-L 65 W/25 S, Universal white, 60 μmol m^{-2} s^{-1}) followed by 12 h in darkness in chambers containing 2 l of sea water. The medium was aerated with an air pump but it was not changed in this preincubation period. In these conditions it has previously demonstrated that the maximal amount of nitrate is consumed and the algae are under starvation conditions [3, 18].

Light sources and radiation measurement

Red light (R) was obtained from three red fluorescent lamp (Philips TL 40 W/Red) with a red plastic filter (Röhm, plexiglas filter PG 501). Green (G) and blue light (B) was obtained from a Prado Universal projector (Leitz, Wetzlar, F.R.G.), fitted with a quartz-iodine lamp (24 v, 250 W) with a Schott green (SFK 11) and blue (SFK 20) glass filters respectively. Far-red light (FR) was obtained from three Linestra lamps (Osram NU 4 60 W) with a red (Rhöm, plexiglas PG 501) and a two blue (Rhöm, plexiglas, PG 627) plastic filters. The spectral characteristics of the filter are represented in Fig. 1. The spectral photon fluence rate (SPFR) of the light was determined with a spectroradiometer (Licor, Li-1800 UW). In the Table I and Fig. 2 are indicated the different photon fluence rate (PFR) used in each light.

Experimental design and light treatments

After the two pretreatments indicated above the plants (1.5 g FW) were transferred to 400 ml sea water containing 200 μM KNO_3. Two different experiments were conducted: (1) Immediately after the nitrate addition 5 min light pulses of R, B and G light of 12 μmol m^{-2} s^{-1} were applied (Table I). In addition after these treatments 5 min FR of 10 μmol m^{-2} s^{-1} was applied to test for a possible phytochrome involvement. The plants were kept 3 h in darkness and then 8 samples were taken in each treatment for chlorophyll determination. The experiment was repeated 3 times and (2) a possible light dosis effect was studied. The plants were irradiated 5 min B with various irradiances: 12, 7.5, 6.0, 5.0, 3.0 and 1.0 μmol m^{-2} s^{-1}, 5 min G: 15, 12, 7.5, 4.0, 1.5 μmol m^{-2} s^{-1} and 5 min R with the same light quantities used in G light treatments. Chlorophyll concentration was determined after these treatments and 3 h in darkness. The exposures (length × irradiance = mmol m^{-2}) used are indicated in Fig. 2 and Table II. In each treatment 8 replicates were taken. In addition to the light treatments in both (1) and (2) experiments a dark control was conducted. The standard deviation for each point is represented in Fig. 2 and Table III. All data were tested with a Model 1 one-way ANOVA.

Chlorophyll determination

Chlorophyll *a* (Chl *a*) and chlorophyll *c* (Chl *c*) were determined spectrophotometrically in a Kontron Uvikon 810 spectrophotometer according to Jeffrey & Humphrey [19] equations. This assay does not discriminate between chlorophyll and chlorophyllide. The extraction was made in a mortar from fresh algae with quartz in acetone (90%) neutralized with Na_2CO_3.

Results

Experiment 1: Effect of light pulses with the same photon fluence rate

The synthesis of Chl *a* was significantly ($p < 0.05$) greater after light pulses than in the dark control in both pretreatments except for R light pulses after starvation conditions (Table I). The effect of R, B and G light pulses and nitrate on chlorophyll synthesis was similar when the plants were incubated previously under natural conditions (Table I). However, under previous starvation conditions, B and G light pulses determined greater Chl *a* accumulation after 3 h in darkness than after R light pulses (Table I). R light pulses did not affect the Chl *a* content under this condition. After both pretreatments 200 μM Nitrate was applied, thus, the previous nutrient state seemed

Table I. Concentration of chlorophyll *a* expressed in mg Chl *a* per g FW in the brown alga *Desmarestia aculeata* after 5 min pulses of different light qualities: blue (B), green (G), red (R) and far-red (FR) followed by 3 h in darkness (3 h D). Together with the pulses 200 μM KNO_3 was added into the seawater. Two pretreatments were conducted: (A) Preincubation 7 days in continuous white light (WL) followed by 12 h in darkness under starvation conditions (STARVATIONc) (B) preincubation under natural conditions with no nutrients limitations (NATURALc).

Light treatments	STARVATIONc	NATURALc
Dark control (3 h D)	0.60 ± 0.03	0.80 ± 0.02
5 min B + 3 h D	0.96 ± 0.04	0.89 ± 0.03
5 min B + 5 min FR + 3 h D	0.79 ± 0.04	0.83 ± 0.02
5 min B + 5 min FR + 5 min R + 3 h D	0.88 ± 0.02	NT
5 min R + 3 h D	0.63 ± 0.02	0.93 ± 0.03
5 min R + 5 min FR + 3 h D	0.51 ± 0.04	0.84 ± 0.03
5 min R + 5 min B + 3 h D	0.92 ± 0.03	0.90 ± 0.05
5 min G + 3 h D	0.92 ± 0.02	0.96 ± 0.05
5 min G + 5 min FR + 3 h D	0.59 ± 0.03	0.86 ± 0.02

Photon fluence rate of R, B and G was 12 μmol m^{-2} s^{-1}, FR 10 μmol m^{-2} s^{-1} and white light 60 μmol m^{-2} s^{-1}. NT = no tested.

to be very important for determining the light quality and nitrate effects on Chl *a* synthesis. On the other hand red and blue light applied successively produced a similar effect to B applied alone (Table I). However red light applied after B and FR reversed partially the effect of FR light. The amount of chlorophyll after B + FR + R was greater that after B + FR and R applied alone (Table I). Thus, R light induced chlorophyll synthesis under starvation conditions only when the inductive effect is started by B light and this was partially reversed by FR. In both experiments (pretreatments A and B) far-red light reversed partially the inductive effect of R, G and B light (Table I). The reversion by FR was greater when the plants were incubated previously under starvation conditions than after natural conditions (Table I).

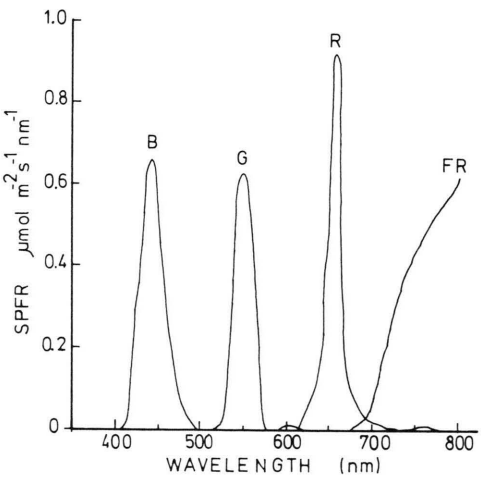

Fig. 1. Spectral photon fluence rate (μmol m^{-2} s^{-1} nm^{-1}) of the different light sources used: B, blue light; G, green light; R, red light and FR, far-red light.

The changes of Chl *c* concentration were lower than that of Chl *a* (Table II). Under previous incubation in starvation conditions some significant ($P < 0.1$) differences between B and B + FR light treatments and G and G + FR light treatments were observed. Under previous natural incubation, Chl *c* was also significant greater ($p < 0.1$) after R than after R + FR light treatments. The ratio Chl *c*:Chl *a* was significantly ($P < 0.1$) greater after R, B and G light pulses than in the dark control. Under natural conditions, the ratio Chl *c*: Chl *a* decreased when FR was applied immediately after R, B or G light pulses (Table II). The ratio Chl *c*:Chl *a* was greater after previous incubation in natural conditions than after previous incubation in starvation conditions (Table II). The increment of Chl *a*, expressed as the difference between Chl *a* concentration after pulses and 3 h in darkness and Chl *a* concentration after the same time in the dark control, was significantly ($p < 0.1$) greater after previously being stressed in starvation conditions than after previous incubation in a natural nutrient state (Table III).

Table II. Concentration of Chl *c* expressed as mg Chl *c* per g FW and ratio Chl *c*:Chl *a* after 5 min pulses of different light quality and different preincubations as Table I.

Light treatments	STARVATIONc		NATURALc	
	Chl *c*	Chl *c*:Chl *a*	Chl *c*	Chl *c*:Chl *a*
Dark Control (3 h D)	0.10 ± 0.005	0.16	0.10 ± 0.006	0.12
5 min B + 3 h D	0.16 ± 0.008	0.16	0.17 ± 0.009	0.19
5 min B + 5 min FR + 3 h D	0.12 ± 0.006	0.15	0.13 ± 0.008	0.15
5 min B + 5 min FR + 5 min R + 3 h D	0.15 ± 0.008	0.17	NT	NT
5 min R + 3 h D	0.10 ± 0.004	0.16	0.17 ± 0.009	0.18
5 min R + 5 min FR + 3 h D	0.10 ± 0.005	0.19	0.10 ± 0.005	0.12
5 min R + 5 min B + 3 h D	0.16 ± 0.008	0.17	0.16 ± 0.009	0.17
5 min G + 3 h D	0.17 ± 0.009	0.18	0.18 ± 0.01	0.19
5 min G + 5 min FR + 3 h D	0.12 ± 0.008	0.20	0.10 ± 0.005	0.11

Photon fluence rate R, B and G was 12 μmol m^{-2} s^{-1}, FR 10 μmol m^{-2} s^{-1} and white light 60 μmol m^{-2} s^{-1}.

Table III. Increment of chlorophyll accumulation expressed as the difference between concentration of Chl *a* after a determined light pulses (5 min) followed by 3 h in darkness and the concentration of chlorophyll in the dark control (3 h in darkness). Together with the light pulses and in the dark control 200 μM KNO_3 was added. The plants were incubated previously under starvation conditions (STARVATIONc) and under natural conditions (NATURALc) with no nutrient deficiency. Photon fluence rate (PFR) and exposure (length × irradiance) are indicated.

Light treatments	PFR	EXPOSURE	Δ mg Chl *a* $(gFW)^{-1}$	
	μmol m^{-2} s^{-1}	mmol m^{-2}	STARVATIONc	NATURALc
5 min B	12	3.60	0.33	0.09
	7.5	2.25	0.05	–
	6.0	1.80	0.06	–
	5.0	1.50	0.10	–
	3.0	0.90	0.10	–
	1.0	0.30	0.23	–
5 min B + 5 min FR	12 + 10	6.60	0.20	0.03
5 min R + 5 min FR + 5 min R	12 + 10 + 12	10.20	0.27	–
5 min R	15	4.50	0.03	–
	12	3.60	0.04	0.13
	7.5	2.25	−0.11	–
	4.0	1.20	−0.10	–
	1.5	0.45	−0.12	–
5 min R + 5 min FR	12 + 10	6.60	−0.08	0.04
5 min R + 5 min B	12 + 12	7.20	0.31	0.10
5 min B + 5 min R	12 + 12	7.20	0.33	0.09
5 min G	15	4.50	0.18	–
	12	3.60	0.30	0.16
	7.5	2.25	0.27	–
	4.0	1.20	0.28	–
	1.5	0.45	0.11	–
5 min G + 5 min FR	12 + 10	6.60	0.00	0.06

The standard deviation was between 5–12%.

Experiment 2: Exposure (length × irradiance) effect on Chl a synthesis

In order to determine the dosis effect with different light qualities on chlorophyll accumulation, the plants were exposed to various light intensity and the same time (5 min). No linear relationship between the exposure of coloured light treatment and chlorophyll concentration was found (Fig. 2). Three patterns in the relation between B, G and R exposures and chlorophyll accumulation were observed. The differences between R, B and G treatments were significant ($p < 0.1$). After B light pulses, a hyperbolic-like curve was determined. Similar chlorophyll induction was produced after exposure with 0.9 mmol m^{-2} that after 3.6 mmol m^{-2}. However after G exposure a para-

bolic-like curve was found (Fig. 2). Exposures from 1.2 to 3.6 mmol m^{-2} determined the same chlorophyll induction. Up 3.6 mmol m^{-2} the induction of Chl *a* synthesis declined (Fig. 2). After red light exposure a clear saturation curve without a clear decline phase was observed (Fig. 2). Exposure from 0.45 to 2.25 mmol m^{-2} determined less chlorophyll than that in the dark control. Up 3.5 mmol m^{-2} the induction of Chl *a* synthesis was significantly ($p < 0.1$) greater after R light than that in the dark control (Fig. 2).

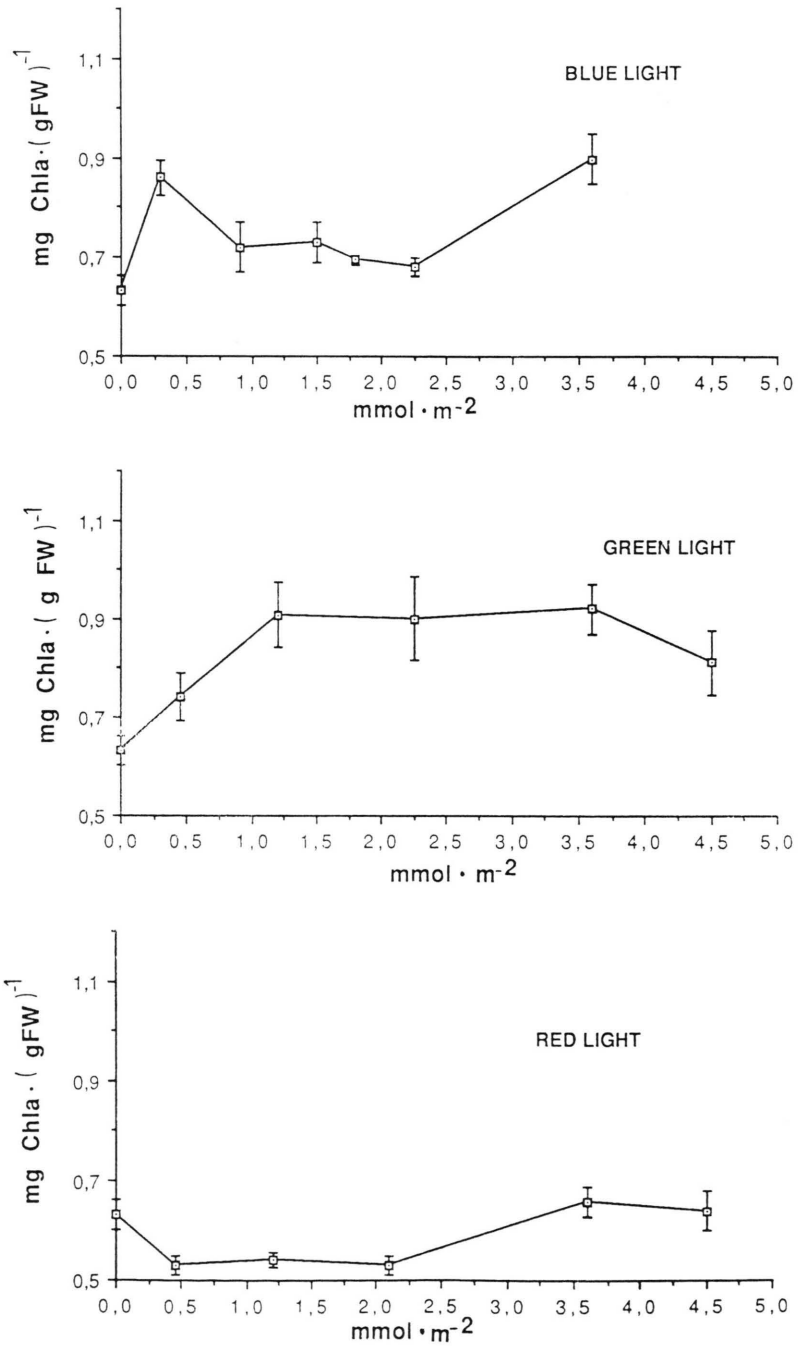

Fig. 2. Effect of exposure (length × irradiance) expressed in mmol m^{-2} on chlorophyll *a* synthesis in *Desmarestia aculeata*. The exposure was 5 min length and under different irradiances of various light qualities (Blue, Green and Red). The concentration of chlorophyll is expressed in mg per g fresh weight (FW).

Discussion

Chlorophyll *a* and *c* synthesis are clearly affected by light quality in the brown algae *Desmarestia aculeata*. Short-term light expositions of 5 min followed 3 h in darkness were enough for producing a significant ($p < 0.05-0.1$) increase of chlorophyll concentration in respect to the dark control. The effect of light qualities depended on the previous nutrient state of the plants. The light induction together with nitrate was greater when the plants are maintained previously under starvation conditions than under natural conditions with no deficiency of nitrate. The induction of Chl *a* synthesis by R light was similar to that by blue and green only under previous incubation in natural conditions and when previously blue light followed far-red light were applied. A red light photoreceptor seems to be active only when the plants are maintained previous to light pulses under natural conditions. Because all light effects, B, G and R, are partially reversed by far-red light, the involvement of phytochrome system is proposed. The reversion by far-red light depended also on the nutrient state previous to the illumination. The reversion effect was greater when the plants were maintained under starvation conditions. These results seem to indicate that the action of photoreception system depended of the nutrient state of the plants. Previously, light effect on chlorophyll, biliprotein and protein synthesis in various green and red algae mediated by nitrate has been reported [5, 18]. Some experiments on chromatic adaptation in cyanobacteria have been performed also with light pulses and immediately before a dark period with increased concentrations of nitrate or other nitrogen sources [20, 21] Phycoerythrin synthesis in the cyanobacteria *Fremyella diplosiphon* is achieved under these conditions with one wavelength maximum ($\lambda = 540$ nm) but its photoreversal with two maxima, at $\lambda = 650$ and 360 nm [22]. In the brown algae *Desmothricum undulatum* release of spores from plurilocular sporangia requires blue light but light quality also affects hair formation only when ammonium is present in the culture medium [23]. The mechanisms whereby light and nitrogen together control chlorophyll and protein synthesis is not clear. López-Figueroa & Rüdiger (1991) [24] found in *Ulva rigida* that nitrate uptake and reduction is controlled by phytochrome in addition to a blue light photoreceptor. The nitrate uptake and reduction correlates with light-regulated accumulation of protein [18]. In green algae some steps of nitrogen metabolism is regulated by blue light and by the nitrogen content in the cells [25]. Two factors have an antagonistic effect on nitrate reductase activity, NH_4^+ inactivating the enzyme and blue-light re-activing it [26]. In addition nitrate uptake in the green alga *Chlamydomonas reinhardii* can be stimulated by light leading to indirect activation of nitrate reductase activity [27]. Quiñones & Aparicio [28] reported recently that red light was sufficient for promoting the biosynthesis of nitrate reductase in the green alga *Monoraphydium braunii* which lacked this enzyme by previously being grown in NH_4^+ medium.

This is the first report about phytochrome-like photoreceptor involvement on chlorophyll synthesis in a brown alga. Previously, mainly blue-UV light effects in some photomorphogenic responses in brown algae have been reported [29–31]. The involvement of phytochrome in brown algae has also reported for stipe elongation in *Nereocystis* [32] and *Saccorhiza polyschides* [33]. Phytochrome was detected recently with immunological methods in the brown algae *Cystoseira abies-marina* and *Cystoseira tamariscifolia* and in some species of red and green macroalgae [34].

The action of B, G and R light in *Desmarestia* cannot be attributed only to phytochrome-like photoreceptor system. Although phytochrome absorbs also blue and green light, the photoconversion to P_{fr}, the active form of phytochrome, is more effective in red light [35]. Since R, G and B illumination after previous cultivation under natural conditions produced a similar effect, the involvement of specific blue and green reception systems in addition to phytochrome is proposed. After starvation conditions phytochrome seems to induce Chl *a* synthesis only when a blue photoreceptor is previously involved and its effect is partially reversed by FR light. Coaction between phytochrome and blue-light photoreceptor has previously been reported in *Ulva rigida* for Chl *a* synthesis [5] and for total protein synthesis [18].

In addition to the action of a phytochrome-like photoreceptor and a B-light photoreceptor, the action of a specific G-light photoreceptor is proposed. Green light has been reported to affect pigment composition in a cryptomonad [36] and in a dinoflagellate [37] and the differentiation somatic

and reproductive cell in synchronized *Volvox* cultures [38]. Rhodopsin has been proposed as G-light photoreceptor [38]. In *Ulva rigida,* a G-light photoreceptor was proposed to control the total protein synthesis [18] and phycoerythrin synthesis in some red algae [3]. However, more investigations are certainly necessary to demonstrate the involvement of this new candidate in green photoreception in algae.

The non-linear response to exposure after pulses of different light qualities could be of ecological significance. The photoreception system can be activated in two different ways depending on irradiance. In coastal waters the plants would adapt to the high changes in light quality and quantity in twilight and with depth (López-Figueroa, submitted).

In this work, a clear light control on chlorophyll synthesis in *Desmarestia aculeata* is found. In addition an influence of the nutrient state previous to the illumination, probably nitrate, on the inductive effect of light quality is observed. The involvement of phytochrome-like photoreceptor in coaction with blue-green photoreceptors on the control of Chl *a* synthesis is proposed. However, more investigations for explaining the mechanisms of control of light and nitrogen on chlorophyll and protein synthesis are necessary.

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