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RESEARCH ARTICLE

Light and temperature as triggers for surface filamentous green algal blooms in shallow freshwater systems

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Abstract

Blooms of filamentous green algae (FGA) form dense mats at the surface of shallow freshwaters and have multiple negative impacts on aquatic ecosystem functions, services, and aesthetics. Although nutrient enrichment in freshwaters is a primary driver of excessive FGA growth, much less is known about other abiotic factors controlling bloom growth rate, extent, and timing. We performed a series of indoor mesocosm (Limnotron) experiments to investigate the effects of photosynthetically active radiation irradiance, photoperiod, and water temperature on the growth and surface bloom formation of FGA using underwater and surface photography. The results revealed that a minimum daily light integral of ~ 13.2 mol m^{-2} d^{-1} (a combination of photosynthetically active radiation irradiance measured at the water surface and daylength) was required for bloom formation and substantial FGA growth. Surface blooms did not occur at short daylengths (i.e., 8 h), whereas a long daylength (i.e., 16 h) allowed more time for photosynthetically derived gas bubbles to accrue in the FGA masses, making them rise to the water surface through buoyancy. We also found that temperatures between 16°C and 22°C were optimal for FGA to form surface blooms. As freshwater ecosystems are increasingly impacted by climate change, our study sheds new light on factors affecting the occurrence of surface blooms and helps identify when waterbodies may be at risk of FGA blooms in the future.

Filamentous green algal (FGA) blooms are a threat to shallow freshwaters (Messyasz et al. 2018; Gladyshev and Gubelit 2019; Vadeboncoeur et al. 2021), causing negative ecological, economic, and social impacts. Dense FGA mats shade the aquatic environment below, reducing the biodiversity of other photosynthetic organisms (Pikosz et al. 2017). FGA dominance can also negatively impact food web dynamics and the subsequent transfer of energy to higher trophic levels (Page et al. 2022). FGA decompose rapidly, which can cause anoxia, leading to macrofaunal die-offs (Green and Fong 2016) and increased release of bioavailable phosphorus (P) from lake sediments (Søndergaard et al. 2003). Surface blooms of FGA are also unsightly, have unpleasant odors, and can pose a health risk by harboring pathogens (Dodds et al. 2009; Byappanahalli et al. 2009), impeding recreational use and compromising the benefits of freshwater bodies to people's health and well-being (Suplee et al. 2009). FGA blooms are often considered an indicator of deteriorating water quality (European Commission 2014) and result in economic losses to water industries (Higgins et al. 2008b). Effective management and control of FGA blooms is therefore a pressing issue but is hindered by incomplete understanding of the spatiotemporal patterns and drivers of FGA growth and blooms.

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Common bloom-forming FGA genera in shallow freshwater bodies include *Cladophora*, *Ulva*, *Spirogyra*, *Hydrodictyon*, *Mougeotia*, and *Oedogonium* (Messyasz et al. 2018). FGA grow either free-floating in the water column or attached to benthic substrates, depending on the genus and growth conditions (Pikosz et al. 2017). Blooms form when FGA rise to the surface of waterbodies, creating thick mats (Gladyshev and Gubelit 2019). Unlike ephemeral blooms of planktonic algae, surface blooms of FGA can persist from spring to late summer, with species composition often varying intra-annually (Berry and Lembi 2000). The mechanisms that cause FGA to rise in the water column and form blooms can vary among genera, although relevant studies are largely restricted to *Spirogyra* and *Cladophora*. *Spirogyra* and other free-floating FGA trap gas within their biomass, including oxygen released from rapid photosynthesis (Mendoza-Lera et al. 2016) and ebullitive methane (Liang et al. 2016), making them buoyant and causing them to rise to the water surface where growth continues (Hillebrand 1983; Berry and Lembi 2000). *Cladophora* grows attached to a substrate and usually reaches peak biomass in mid-summer, after which sloughing (breakage or tearing from their substrate) occurs (Higgins et al. 2008b), when filaments weaken due to a combination of factors, including self-shading, nutrient limitation, and temperature stress (Canale and Auer 1982; Dodds and Gudder 1992; Higgins et al. 2006). Once detached, *Cladophora* behaves similarly to other floating FGA, trapping gas and rising to the surface to form blooms (Hillebrand 1983).

Nutrient enrichment (especially with nitrogen [N] and P) is a known driver of excessive growth and bloom occurrence for many FGA genera (Planas et al. 1996; Auer et al. 2010; Gladyshev and Gubelit 2019). Much less is understood of how other abiotic factors, such as light availability and temperature, control FGA growth, and whether they act as triggers of bloom formation. Daily light integral (DLI), the total light energy delivered as a combination of photosynthetically active radiation irradiance and photoperiod (daylength), has been shown to determine the extent of benthic FGA growth and seasonal succession of FGA species in the littoral zone of shallow freshwater bodies (Hillebrand 1983; Messyasz et al. 2018). *Cladophora* spp. generally require high irradiances to grow and have physiological adaptations that allow for a high photosynthetic rate (Dodds and Gudder 1992). With increased photoperiod and higher irradiance in the summer in northern temperate regions, floating FGA mats can dominate at the water surface while the biomass of attached FGA filaments decreases as they are shaded and out-competed (Berry and Lembi 2000; Pikosz et al. 2017). However, excessive irradiance can cause photoinhibition (Rattanasaensri et al. 2020).

Water temperature affects rates of biogeochemical reactions, including photosynthesis and respiration, which in turn influence the overall biomass production of FGA. The optimum temperature for growth varies vastly across FGA taxa and locations, and can depend on other environmental factors, including light availability (Pitawala et al. 2023) and carbon dioxide concentrations (Andersen and Andersen 2006). For example, optimum growth temperature ranges of *Cladophora* sp. in 500 mL bottle experiments are reported as 13–20°C (Bellis and McLarty 1967) as well as much higher ranges of 25–30°C (Lester et al. 1988). The greatest net photosynthesis rate of *Spirogyra* sp. has been measured at 25°C, but the genus often forms blooms in late spring when water temperatures are as low as 8–12°C (Graham et al. 1995; Berry and Lembi 2000). Hoffmann and Graham (1984) found that temperature had a significant effect on the induction of zoosporogenesis in *Cladophora* sp. between 15°C and 20°C, but maximum biomass production was recorded at 25°C, highlighting the importance of increasing temperatures through the growing season from spring to summer. At high water temperatures, often later in the summer, FGA start to decay, producing toxic or noxious compounds (NH_3, H_2S) and anoxia (Fong and Zedler 1993).

While there is good evidence that temperature directly affects FGA growth, temperature may also modify ecological interactions at the ecosystem level via phenological mismatches (Cushing 1990; Winder and Schindler 2004; Thackeray 2012), resulting in changes to seasonal windows of "clear water" phases (Sayer et al. 2010; van Gerven et al. 2015). Whether similar relationships exist between FGA and other freshwater organisms is not yet known. However, the timing of these "clear water" phases could be crucial for providing FGA the opportunity and light availability to compete and dominate within freshwaters.

Considering the increasing impact of climate change on freshwaters, this study aims to understand how light availability and temperature affect FGA growth and surface bloom formation. Specifically, in a series of indoor mesocosm experiments, we investigated the effects of (1) photosynthetically active radiation surface irradiance delivered as low, medium, and high (129, 232, and 451 μmol m^{-2} s^{-1}); (2) photoperiod delivered as short (8 h) and long (16 h) daylength; and (3) different temperatures delivered along a gradient between 8°C and 24°C. We hypothesized that higher irradiance would lead to greater FGA growth due to increased photosynthesis, but that there could be critical limits to growth due to photosystem saturation. We expected greater FGA growth and surface blooms to occur at the longer daylength treatment because the longer photoperiod extends the photosynthetically active time for gas accrual and buoyancy within FGA masses. Lastly, we hypothesized there would be an optimum temperature range in which maximum FGA growth and surface bloom formation will occur, dictated by species-specific physiological optima for photosynthesis.

Materials and methods

Experimental setup

We carried out three experiments to assess the effects of irradiance, daylength, and temperature on FGA growth. These

were conducted in nine cylindrical, indoor mesocosms known as Limnotrons (diameter = 0.97 m, depth = 1.35 m, volume = 988 L) at the Netherlands Institute of Ecology (NIOO-KNAW) (Verschoor et al. 2003) (Fig. 1; Supporting Information Fig. S1). Before the start of each experiment, each Limnotron was cleaned and filled with ~ 60 L of homogenized natural sediment taken from a small pond in Wageningen, The Netherlands (51.98781°N, 5.66835°E) and filled with ~ 920 L of pretreated (aerated) ground water (1.1 m depth). To limit the extent of phytoplankton growth, water was circulated at a rate of ~ 346 L d^{-1}, fully replacing the water in the Limnotrons every 3 d, using a greenhouse drip and overflow system. A mesh guard on the overflow pipe prevented FGA from flushing from the system. Limnotrons were spiked with $NaNO_3$ and KH_2PO_4 at the Redfield ratio (Redfield 1960) to achieve a starting concentration of 1.6 mg L^{-1} of NO_3-N and 0.1 mg L^{-1} of PO_4-P, typical conditions of lowland eutrophic water bodies in northern Europe (Nikolaidis et al. 2022). To maintain high nutrient conditions and reduce the likelihood of nutrient limitation in the FGA, NO_3-N and PO_4-P were supplied to match the flushing rate of the Limnotrons using individually calibrated Gilson Minipuls 3 peristaltic pumps, which delivered 500 mL of $NaNO_3$ and KH_2PO_4 known concentration solution over each 24-h period.

At the start of each experiment, Limnotrons were inoculated with ~ 100 g wet weight of spring-blooming FGA made

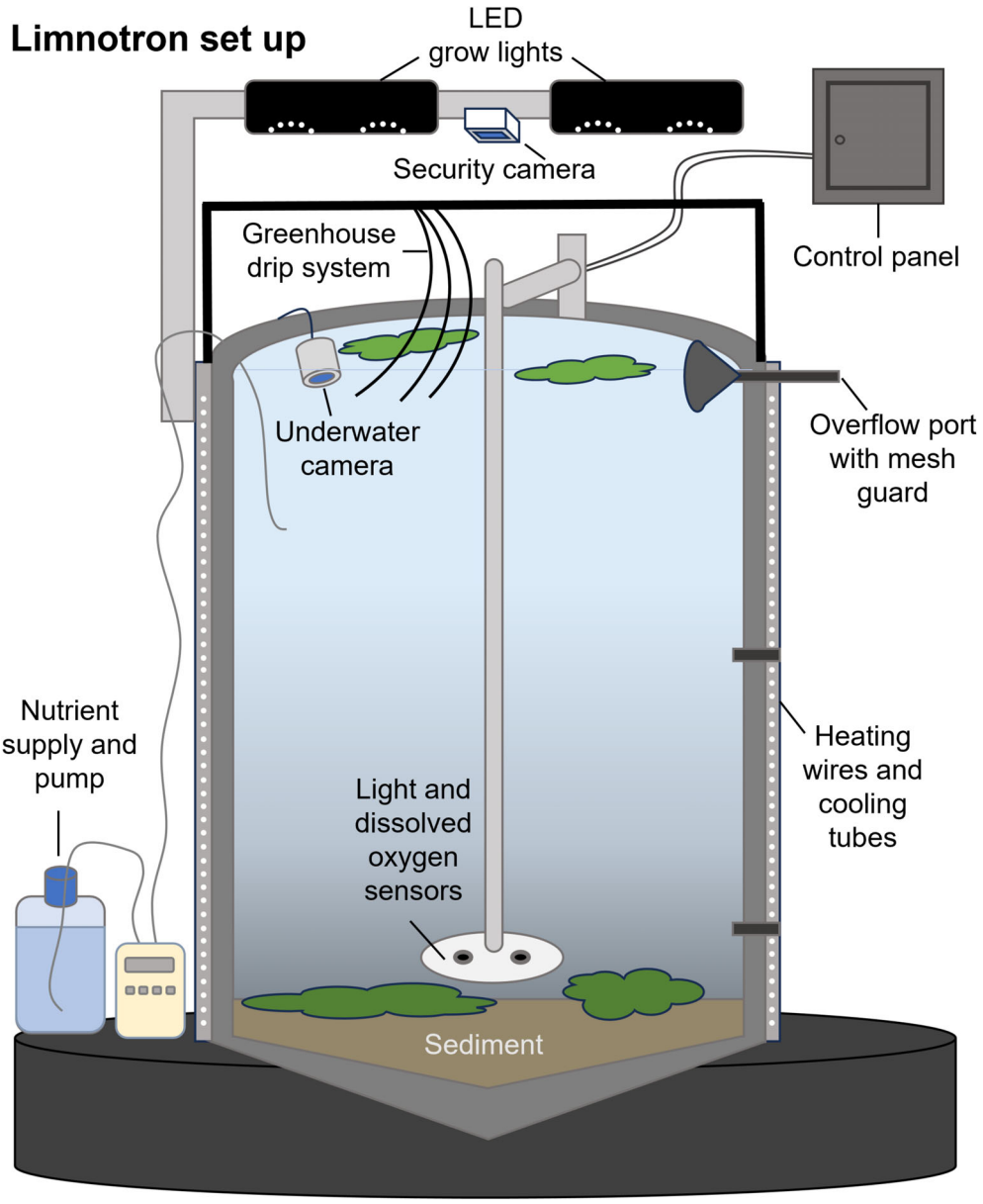

Fig. 1. Schematic drawing (lateral transection) of a Limnotron as used in these experiments.

up of two distinct samples: (1) sample A containing *Mougeotia* sp. and *Oedogonium* sp. from NIOO ponds (Experiment 1 located at 51.98809°N, 5.67348°E, Experiments 2 and 3 at 51.98680°N, 5.67110°E); (2) sample B containing *Spirogyra* sp. and *Hydrodictyon* sp. from Binnenveldse Hooilanden Nature Reserve (51.99562°N, 5.60295°E). These four genera of benthic FGA can all survive and grow free floating in the water column. FGA inoculated into each Limnotron contained 50 g wet weight of each sample A and B in Experiments 1 and 2, but 20 g of sample A and 85 g of sample B in Experiment 3. Prior to inoculation, FGA samples were cleaned using tap water to remove macrobenthos, epiphytes, and detritus. Images of FGA at multiple magnifications depending on algal cell size were taken (Cell*D or Leica DMI3000 microscope) for identification purposes.

Experimental treatments

Three consecutive experiments were carried out in the Limnotrons from March to July 2022. Experiments 1 and 2 tested the effects of irradiance and photoperiod, and Experiment 3 tested the effects of temperature, on FGA growth and bloom formation at the surface and bottom of the Limnotrons (i.e., their air–water and sediment–water interfaces, respectively; Table 1).

Experiment 1 used a short daylength of 8 h, equivalent to winter photoperiod conditions in a known FGA-affected lake in the UK (Clumber Park Lake, 53.26615°N, 1.05485°W), and Experiment 2 used a long daylength of 16 h, equivalent to summer photoperiod conditions for the same location. Water temperature was maintained at 14°C in both experiments using a custom-made climate control system (SpecView 32/859; SpecView Ltd.) (Supporting Information Fig. S2), typical of spring surface water temperatures in lowland northern European lakes (Ptak et al. 2019). In both experiments, three different irradiance treatments, low, medium, and high (129, 232, and 451 μmol m^{-2} s^{-1}), were applied in triplicate across the nine Limnotrons (Table 1) using LED grow lights (Sunfactor II Smart Series, Hortilight Systems) that were mounted 80 cm directly above the water surface. To quantify the irradiance delivered, a mean ($n = 3$) of each treatment was taken during setup at the water surface in the center of the Limnotron (Irradiance; Table 1), using a LI-250A Light Meter (LI-COR). The light was delivered in the 400–700 nm spectral range (photosynthetically active radiation) as a combination of white, red, and blue light at a ratio of 1.25 : 1 : 1 (Table 1). Although white light alone supports highest overall productivity in FGA, the additional red and blue wavelengths were delivered to maximize biomass production and increase photosynthetic efficiency, respectively (Webb et al. 2020). Both experiments were designed to enable comparisons among light treatments based on DLI, calculated as a combination of irradiance and daylength (DLI classification; Table 1). The irradiances and DLIs delivered to the FGA were within seasonal annual ranges experienced at latitudes similar to the FGA-affected Clumber Park Lake, UK. Experiments 1 and 2 ran for 26 and 24 d, respectively, based on the availability of the Limnotron facilities.

Experiment 3 ran for 14 d (again reflecting Limnotron availability). Each of the nine Limnotrons was randomly assigned a different water temperature treatment from 8°C to 24°C, increasing in increments of 2°C (controlled as explained earlier; Supporting Information Fig. S3). A DLI of 14.6 mol m^{-2} d^{-1} was delivered using the LED grow lights set to a 12 : 12 h light : dark cycle and a water surface irradiance of $\sim$ 338 μmol m^{-2} s^{-1} (Experiment 3; Table 1). Note that although the duration of each experiment was different due to access/availability constraints, this paper focuses on bloom formation at the early stages of each experiment; differences in experiment length are therefore unlikely to have influenced our results.

Experimental sampling

To quantify nutrient concentrations, 2 L water samples were taken at the start, middle, and end of Experiments 1 and 2 from the surface and bottom of each Limnotron. Water was filtered through GF/F filters ($\sim$ 0.7 μm pore size, Whatman), and the filtrate was stored in the dark at −20°C until analysis. Concentrations (mg L^{-1}) of dissolved inorganic nitrogen (DIN) (NO_2^-, NO_3^-, NH_4^+) and soluble reactive phosphorus (SRP) (PO_4^{3-}) were measured on a Skalar SAN++ Autoanalyzer (SKALAR). Planktonic chlorophyll *a* (Chl *a*) concentrations (μg L^{-1}) were measured in a known volume of integrated water sample taken from each Limnotron at the start, middle, and end of Experiments 1 and 2, and analyzed spectrophotometrically on a Thermo Helios Alpha UV/Vis Spectrophotometer (Thermo Fisher Scientific) following the method by Jeffrey and Humphrey (1975). Sensors at the bottom of the Limnotrons measured dissolved oxygen (DO) (mg L^{-1}) (PreSence) every minute for the duration of each experiment. Midday DO and DO amplitude (max and min DO values within 24-h period either side of midday recording) were extracted for analyses. At the end of each experiment, FGA was harvested from the surface and bottom of each Limnotron and dried to constant weight to compare final dry weight (DW) (g) among treatments.

Quantifying FGA area via in situ imaging

To quantify the change in FGA biomass over time at the surface and bottom of Limnotrons, FGA area was measured from images taken by cameras (Supporting Information Fig. S4). TP-Link Tapo TC60/C100 IP cameras mounted 80 cm above each Limnotron were used to photograph the whole water surface to measure surface bloom formation, while a Barlus B2G5MPBX10 Super Wide-Angle Underwater IP Cameras mounted immediately below the water surface provided images of FGA growth on the sediment. Images were acquired automatically every 15 min, but the series was subsampled at midday, twice a week (intervals of 3–4 d) for analyses. Each image was scaled to size using the Limnotron width, and total

Table 1. Experimental design of the three consecutive Limnotron experiments, including experimental parameters and aims. In Experiments 1 and 2, each irradiance treatment was applied in triplicate across the nine Limnotrons ($n = 3$). In Experiment 3, a different temperature treatment was applied to each of the nine Limnotrons ($n = 1$). Irradiance was measured at the water surface in the center of the Limnotron. Spectral composition describes the ratio of light delivered by the light-emitting diode (LED) grow lights—ratios were 1.25 : 1.00 : 1.00 for white, red, and blue, where the values are a % of maximum output. Letters A, B, C, and D indicate treatments based on daily light integral (DLI). Treatments with the same letters received the same DLI but as different combinations of irradiance and daylength (i.e., B, ~ 7.1 mol m^{-2}; C, ~ 13.2 mol m^{-2}).

Parameters	Experiment 1			Experiment 2				Experiment 3
Length of treatment (d)	26 (Apr 22 to May 17, 2022)			24 (May 24 to Jun 16, 2022)				14 (Jun 23 to Jul 7, 2022)
Temperature (°C)	14			14				Gradient across nine Limnotrons: 8, 10, 12, 14, 16, 18, 20, 22, 24
Daylength (h)	8	8	8	16	16	16		12
Daylength description	Short	Short	Short	Long	Long	Long		Equal
Irradiance (μmol m^{-2} s^{-1})	129	232	451	129	232	451		338
Irradiance description	Low	Medium	High	Low	Medium	High		Medium-high
Spectral composition (%)	25 : 20 : 20	50 : 40 : 40	100 : 80 : 80	25 : 20 : 20	50 : 40 : 40	100 : 80 : 80		75 : 60 : 60
DLI (mol m^{-2} d^{-1})	3.72	6.68	12.99	7.43	13.36	25.98		14.60
DLI classification	A	B	C	B	C	D		NA
Experimental aim	Assess effects of irradiance under short-daylength (winter) conditions over time.			Assess effects of irradiance under long-daylength (summer) conditions over time.				Assess effects of temperature under medium-daylength and medium-high irradiance conditions over time.

FGA area (cm^2) of each image was estimated by tracing FGA masses using ImageJ (version 1.53t: 2022). If an image was not of suitable quality for tracing (e.g., camera view obstructed by air bubbles), the next closest-acquired image (in time) was instead selected for analysis.

Data analysis

Data were analyzed using R (version 4.3.2) (R Core Team 2023). Data were tested for normality (Shapiro–Wilk test and Q–Q plots) and homogeneity of variances (Levene's test), and outliers were identified using the *rstatix* package (Kassambara 2023). Non-normal data were Box-Cox transformed using the *MASS* package (Venables and Ripley 2002). To evaluate the effect of irradiance over time on FGA area, DO, Chl *a*, and dissolved nutrient concentrations under two daylength conditions, respectively, 9 two-way repeated measures ANOVAs were performed on datasets collected in Experiments 1 and 2. The response variables included: (1) surface FGA area, (2) bottom FGA area, concentrations of (3) midday DO, (4) DO amplitude, (5) Chl *a*, (6) surface SRP, (7) bottom SRP, (8) surface DIN, and (9) bottom DIN. The predictor variables were irradiance, time (length of treatment in days), and their interaction. When the interaction factor was statistically significant ($p \leq 0.05$), a post hoc test was performed to test for the significance of the irradiance treatment (simple main effect) on specific days. When the irradiance treatment was statistically significant, simple pairwise comparisons (paired *t*-tests) were performed. All *p*-values were Bonferroni-corrected.

Two-way ANOVAs tested the effects of irradiance, daylength, and their interactions on the final surface and bottom FGA DW, respectively, followed by Tukey Honestly Significant Difference (HSD) multiple comparison test where appropriate. Simple linear models of FGA area over time were run to determine whether FGA growth rate at the surface and bottom was significantly different from 0 and among DLI treatments, using the *emmeans* package (Lenth 2023). Custom pairwise contrasts were used to compare FGA growth rate between the pairs of treatments receiving the same DLI (B and C: Table 1).

For Experiment 3, simple linear models and pairwise contrasts of FGA growth rates in the different temperature treatments were run to assess whether growth rate was significantly different from 0 and among treatments using the *emmeans* package (Lenth 2023). Two-way ANCOVAs were performed to investigate the effect of temperature (categorical independent variable) and time (covariate: length of treatment in days) on (1) surface and (2) bottom FGA area and (3) midday DO concentrations.

Results

Effects of light availability and temperature on FGA area

Under short daylength (8 h; Experiment 1), no FGA growth occurred at the surface apart from one Limnotron in the high

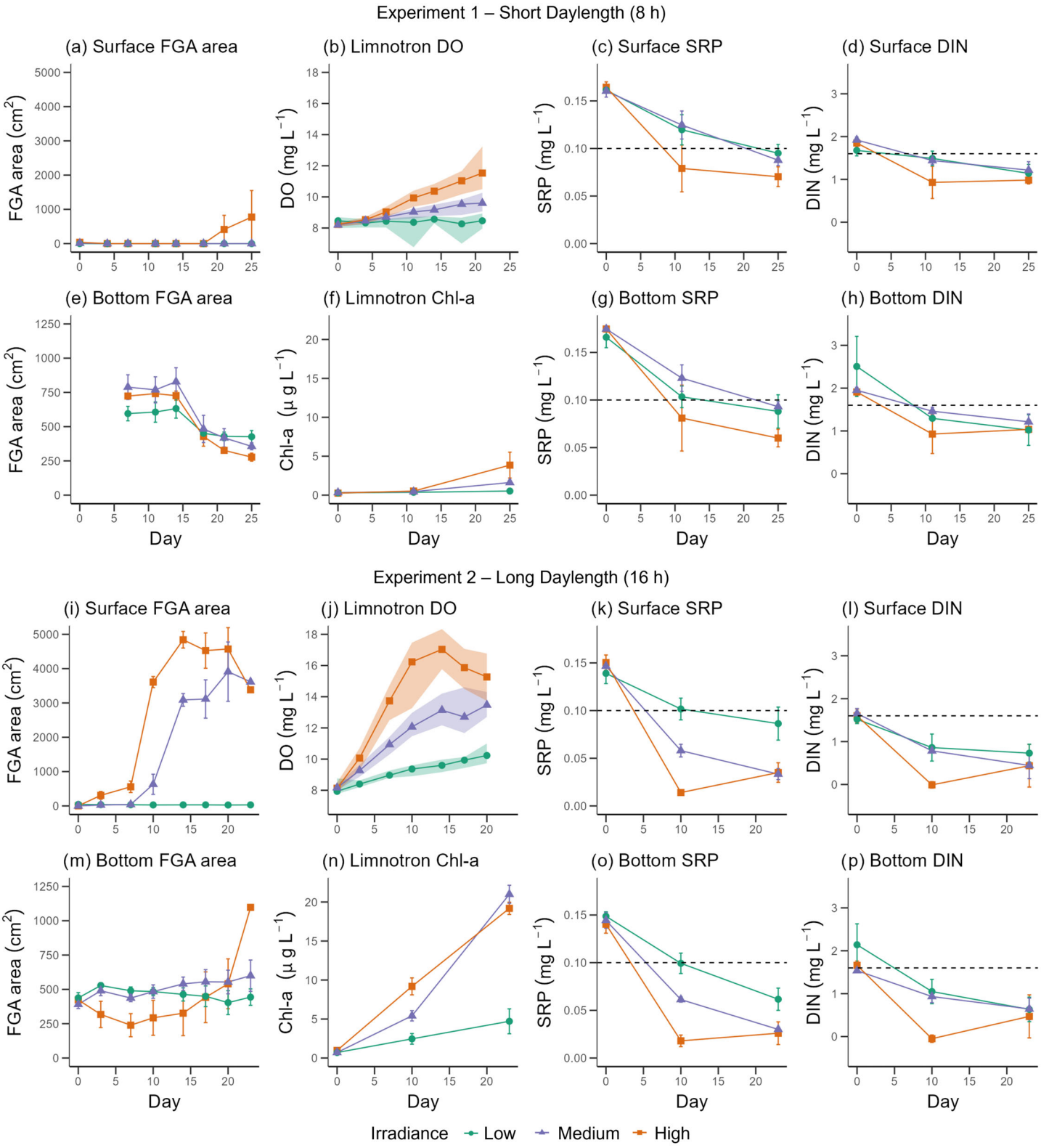

Fig. 2. Time series from Experiment 1—short daylength (**a**–**h**) and Experiment 2—long daylength (**i**–**p**) of measured variables: filamentous green algae (FGA) area calculated from image analysis; midday dissolved oxygen (DO) concentration with a ribbon showing maximum and minimum DO values from that 24 h period; and chlorophyll *a* (Chl *a*), soluble reactive phosphorus (SRP) and dissolved inorganic nitrogen (DIN) concentrations in the water. Surface

(Figure legend continues on next page.)

irradiance treatment (Fig. 2a), and surface FGA area was not significantly affected by irradiance or time (Table 2). Bottom FGA area decreased significantly over time, was not significantly affected by irradiance directly (Fig. 2e, Table 2), but was significantly affected by the irradiance-time interaction. Decreases in bottom FGA area from the start of Experiment 1 were greatest at high irradiance (61.7%) and lowest at low irradiance (28.3%) (Fig. 2e).

Under long daylength (16 h; Experiment 2), substantial growth of surface FGA occurred at both high and medium irradiance but not at low irradiance (Fig. 2i). Overall, surface FGA area was significantly affected by irradiance, time, and the irradiance-time interaction (Table 2). At high irradiance, surface FGA area increased from day 0, rapidly between days 7 and 10, and reached a maximum mean area on day 14. On days 10–17, surface FGA area was significantly greater in high- compared to low-irradiance treatments (post hoc paired *t*-tests: $p < 0.05$). At medium irradiance, surface FGA area followed a similar growth pattern but did not increase until day 7, reaching a maximum on day 20, and was significantly different from the low irradiance treatment only on day 14 (post hoc paired *t*-test: $p < 0.05$). Bottom FGA area at long daylength was only significantly affected by the irradiance-time interaction (Fig. 2m, Table 2).

Under different water temperatures (8–24°C; Experiment 3), surface and bottom FGA area were significantly affected by temperature and time, with bottom FGA area also being significantly affected by the temperature–time interaction (Table 3). A clear thermal optimum for surface FGA bloom formation occurred between 16°C and 22°C (Fig. 3a). Surface daily growth rates at 16–22°C were significantly different from 0 $cm^{-2}\ d^{-1}$ (linear model *t*-test; $p < 0.001$) and significantly different from those at all other temperature treatments (pairwise contrasts: $p < 0.05$; Fig. 3b). Bottom FGA growth was greatest at 14°C (Fig. 3c) and bottom daily growth rates were significantly different from 0 $cm^{-2}\ d^{-1}$ in all temperature treatments apart from 8°C and 12°C (linear model *t*-test; $p < 0.05$; Fig. 3d).

Effects of light availability and temperature on FGA biomass

The linear relationship between FGA DW biomass and FGA area calculated from images found FGA area to be a representative measure of FGA growth (Supporting Information Fig. S5). Surface FGA biomass (measured as DW) at the end of Experiments 1 and 2 was significantly affected by irradiance (two-way ANOVA: $F_{2,12} = 8.99$, $p = 0.004$) but not daylength (two-way ANOVA: $F_{1,12} = 4.62$, $p = 0.052$). Surface FGA biomass was significantly greater at the high irradiance-long daylength treatment than at all other treatments apart from the high irradiance-short daylength treatment (Fig. 4; Tukey HSD multiple comparison test: $p < 0.05$). Bottom FGA biomass at the end of Experiments 1 and 2 was significantly affected by daylength (two-way ANOVA: $F_{1,12} = 8.84$, $p = 0.011$), with a longer daylength yielding slightly higher biomasses. However, there was no significant difference in the yield of bottom FGA biomass between all irradiances at either daylength (Tukey HSD multiple comparison test) (Fig. 4). Surface FGA biomass at the end of Experiment 3 was greatest (i.e., 3.1–4.0 g DW) between the 16°C and 22°C treatments but comprised < 1 g of DW at all other temperatures (Fig. 3f). The final bottom FGA biomass was greater than the surface FGA biomass in all treatments apart from 18°C to 22°C. The greatest end DW biomass of 8.9 g was harvested from the bottom of the 14°C treatment.

Effects of DLI on FGA growth

Our experiments were designed to enable comparisons among light treatments with the same DLI, as a combination of different irradiance and daylength (Table 1). Surface FGA growth did not differ between the treatments receiving a DLI of ~ 7.1 mol $m^{-2}\ d^{-1}$, regardless of the combination of irradiance and daylength delivery. However, surface FGA growth was significantly greater in the long daylength with medium irradiance treatment compared to the short daylength with high irradiance treatment, both receiving a DLI of ~ 13.2 mol $m^{-2}\ d^{-1}$ ($t = -10.86$, df = 127, $p < 0.001$). Significant bottom FGA growth only occurred in the treatment receiving a DLI of 26.0 mol $m^{-2}\ d^{-1}$; the long daylength with high irradiance treatment ($t = 3.28$, df = 110, $p = 0.001$).

Effects of light availability and temperature on water column parameters

At both short and long daylength, dissolved nutrient concentrations generally decreased over time (Fig. 2). This decrease was significant for SRP at short daylengths and for SRP and DIN at long daylengths (Table 2). SRP concentration at the bottom of the Limnotrons at long daylength was significantly lower at high irradiance compared to low and medium irradiance on day 10 (post hoc paired *t*-test: $p < 0.05$).

At short daylengths, DO concentrations were significantly affected by time and the irradiance-time interaction (Table 2). DO concentrations at high irradiance increased at twice the rate measured at medium irradiance (Fig. 2b). Time and the irradiance-time interaction had a significant effect on DO

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and bottom denote the air–water and sediment–water interfaces in the Limnotron, respectively, and Limnotron denotes data representative of the whole mesocosm system. Color and shape denote the three different irradiance treatments delivered in triplicate to the nine Limnotrons: high, medium, and low (Table 1). In all but Fig. 2b, j, values denote means ± SE ($n = 3$) for each irradiance treatment. Water temperature was maintained at 14°C. Dashed lines indicate target nutrient concentrations.

Table 2. Results from two-way repeated measures ANOVAs, performed to evaluate the effects of irradiance (treatments), time (length of treatment in days), and the interaction between irradiance and time on (1) surface and (2) bottom filamentous green algae (FGA) area, concentrations of (3) midday dissolved oxygen (DO), (4) DO amplitude, (5) chlorophyll *a* (Chl *a*), (6) surface, and (7) bottom soluble reactive phosphorus (SRP), and (8) surface and (9) bottom dissolved inorganic nitrogen (DIN). Values in bold denote a significant effect on FGA area; $p \leq 0.05$ and * indicates the level of significance ($p \leq 0.001$***, $p \leq 0.01$**, $p \leq 0.05$*).

		Short daylength (8 h)			Long daylength (16 h)		
Parameter	**Effect**	**df**	***F*-value**	***p*-value**	**df**	***F*-value**	***p*-value**
Surface FGA area (cm^2)	Irradiance	2	1.75	0.284	2	110.45	< **0.001*** **
	Time	7	0.73	0.652	6	55.22	< **0.001*** **
	Interaction	14	0.85	0.615	12	38.94	< **0.001*** **
Bottom FGA area (cm^2)	Irradiance	2	0.54	0.622	2	1.32	0.363
	Time	5	40.16	< 0.001***	6	1.27	0.340
	Interaction	10	8.25	< 0.001***	12	2.47	**0.029***
Midday DO ($mg\ L^{-1}$)	Irradiance	2	6.47	0.056	2	46.84	**0.002****
	Time	6	43.97	< 0.001***	6	207.41	< **0.001*** **
	Interaction	12	7.98	< 0.001***	12	7.21	< **0.001*** **
DO amplitude ($mg\ L^{-1}$)	Irradiance	2	3.02	0.158	2	36.82	**0.003****
	Time	6	11.58	< 0.001***	6	14.16	< **0.001*** **
	Interaction	12	4.38	0.001**	12	1.67	0.137
Chl *a* ($\mu g\ L^{-1}$)	Irradiance	2	4.99	0.082	2	17.33	**0.011***
	Time	2	38.86	0.002**	2	134.14	< **0.001*** **
	Interaction	4	5.25	0.023*	4	20.63	< **0.001*** **
Surface SRP ($mg\ L^{-1}$)	Irradiance	2	3.97	0.112	2	6.98	**0.050***
	Time	2	14.19	0.015*	2	199.87	< **0.001*** **
	Interaction	4	3.72	0.054	4	13.48	**0.001****
Bottom SRP ($mg\ L^{-1}$)	Irradiance	2	1.93	0.259	2	23.32	**0.006****
	Time	2	37.67	0.003**	2	85.25	< **0.001*** **
	Interaction	4	0.61	0.669	4	13.14	**0.001****
Surface DIN ($mg\ L^{-1}$)	Irradiance	2	1.70	0.292	2	2.46	0.201
	Time	2	4.98	0.082	2	8.80	**0.034***
	Interaction	4	1.99	0.190	4	5.72	**0.018***
Bottom DIN ($mg\ L^{-1}$)	Irradiance	2	1.95	0.257	1	14.85	0.061
	Time	2	4.99	0.082	2	10.37	**0.026***
	Interaction	4	0.58	0.685	4	1.67	0.248

amplitude (Table 2), which increased over Experiment 1 at high and medium irradiances. At long daylength, there was a significant effect of irradiance, time, and the irradiance-time interaction on DO concentrations (Table 2) which increased at all irradiances (Fig. 2j). After day 14, DO concentrations started to decrease at high and plateau at medium irradiances. Irradiance and time had a significant effect on DO amplitude at long daylength (Table 2), which increased over time at high and medium irradiance but remained small and consistent at low irradiance. In Experiment 3, DO concentrations were significantly affected by temperature, time, and the temperature–time interaction (Table 3). Concentrations increased at all temperatures over the first 7 d (Fig. 3e; Supporting Information Fig. S6), with the greatest increase at 14°C and 8°C.

At short daylength, planktonic Chl *a* concentrations were significantly affected by time and the irradiance-time interactions (Table 2). Chl *a* concentrations remained very low ($< 0.44\ \mu g\ L^{-1}$) for the first half of the experiment, increasing to $1.62\ \mu g\ L^{-1}$ at medium irradiance and $3.85\ \mu g\ L^{-1}$ at high irradiance by day 25 (Fig. 2f). At long daylengths, Chl *a* concentrations were significantly affected by irradiance, time, and the irradiance-time interactions (Table 2), with Chl *a* concentrations increasing rapidly over the duration of the experiment (Fig. 2n).

Discussion

Effects of light and temperature on FGA growth

Our experiments allowed us to assess irradiance, photoperiod, and their combined effect measured as DLI ($mol\ m^{-2}\ d^{-1}$), on the growth and surface bloom formation of FGA. Significant surface FGA growth only occurred with a minimum DLI of $\sim 13.2\ mol\ m^{-2}\ d^{-1}$, as a combination of a longer daylength (16 h), typical of long summer days in northern Europe, and a

Table 3. Results from two-way ANCOVAs, performed to evaluate the effect of different temperature treatments, time (length of treatment in days), and the interaction between temperature and time on (1) surface and (2) bottom filamentous green algae (FGA) area, and (3) midday dissolved oxygen (DO) concentration. Values in bold denote a significant effect on FGA area, $p \leq 0.05$, and * indicates the level of significance ($p \leq 0.001$***, $p \leq 0.01$**, $p \leq 0.05$*).

Parameter	Effect	df	*F*-value	*p*-value
Surface FGA area (cm^2)	Temperature	8	41.23	< **0.001*** **
	Time	1	40.63	< **0.001*** **
	Interaction	8	1.47	0.216
Bottom FGA area (cm^2)	Temperature	8	16.23	< **0.001*** **
	Time	1	133.50	< **0.001*** **
	Interaction	8	8.02	< **0.001*** **
Midday DO ($mg\ L^{-1}$)	Temperature	8	9.03	< **0.001*** **
	Time	1	172.11	< **0.001*** **
	Interaction	8	3.27	**0.018***

minimum irradiance of $\sim 232\ \mu mol\ m^{-2}\ s^{-1}$. Significant FGA surface blooms did not form in the comparable DLI treatment that received $\sim 13.2\ mol\ m^{-2}\ d^{-1}$ as a combination of short daylength (8 h), typical of northern European winter conditions, and a high irradiance of $\sim 451\ \mu mol\ m^{-2}\ s^{-1}$. These results can be explained in part by the longer daylength and thus, greater cumulative photosynthetically active time allowing for gas bubbles to accrue in the FGA mass (Mendoza-Lera et al. 2016), making them rise to the water surface through buoyancy. It is also likely that over a short daylength with high irradiance, the FGA photosystems were saturated and/or damaged by photoinhibition, resulting in less cumulative photosynthesis and thus reduced biomass production (Rattanasaensri et al. 2020). Much of the vertical FGA movement to form surface blooms occurred within the first week of the experiments, followed by the floating FGA masses increasing in areal extent throughout the duration of the experiments. Once at the surface, FGA have a competitive advantage over phytoplankton and macrophytes, as their growth is unlimited by light and their presence shades photosynthetic organisms below (Han et al. 2009; Dong et al. 2015).

Although it is common to find some FGA in freshwater bodies during the winter (Lavery and McComb 1991; Berry and Lembi 2000; Ensminger et al. 2000), we are unaware of any reports of FGA surface bloom formation during the winter season in temperate regions. We observed a decrease in bottom FGA area over time and no significant FGA surface blooms at a short daylength (8 h), regardless of irradiance, indicating that conditions were not viable for FGA growth. Reported minimum irradiance requirements for FGA growth range from $29\ \mu mol\ m^{-2}\ s^{-1}$ for *Cladophora* sp. (Lorenz et al. 1991) to $60\ \mu mol\ m^{-2}\ s^{-1}$ for both *Oedogonium* spp. (Rattanasaensri et al. 2020) and *Spirogyra* spp. (Berry and Lembi 2000). Although light attenuation was not measured in the Limnotrons, irradiance at the sediment was likely to meet these requirements, in even the lowest irradiance treatment ($129\ \mu mol\ m^{-2}\ s^{-1}$), as the water was clear of phytoplankton growth. The species used in our experiments may have different light requirements than those reported in the literature. However, the decrease in FGA biomass is likely due to a low DLI, driven by the short photoperiod, reducing photosynthetic rates, which results in a decrease in FGA biomass as resources for growth, maintenance, or repair are reduced (Pitawala et al. 2023; Jiang et al. 2025). Microscopic examination (Supporting Information Table S1 and Fig. S7) of the final FGA harvest at short daylength supports this interpretation because *Mougeotia* and *Spirogyra* filaments were partially decomposed with broken cell walls and evidence of epiphytic growth. Shorter photoperiods can induce FGA reproduction, resulting in less energy for biomass production (Jiang et al. 2025). At short daylength with low irradiance, there were several examples of sexual reproduction with the existence of conjugations between *Spirogyra* filaments and the formation of zygotes, thus providing another hypothesis for the observed decrease in FGA biomass.

Our temperature experiment identified a clear thermal optimum between 16°C and 22°C for the formation of FGA surface blooms, with the peak at 20°C. Within this temperature range, the gross photosynthetic rate of FGA increases due to increased enzyme activity. However, when temperatures exceed the optimum, heat stress can lead to a decline in photosynthetic efficiency (Pitawala et al. 2023). Bottom FGA growth and final biomass were greatest at 14°C. This treatment was evidently warm enough for efficient photosynthesis, although not enough for gas accrual and surface bloom formation. It is also possible that bottom FGA received higher irradiances in the 14°C treatment than in the 16–22°C treatments because there was no surface bloom to cause shading to the water column below. The optimum temperatures we identified are toward the lower end of those reported in other experimental studies, ranging from 15°C to 30°C (Lester et al. 1988; Graham et al. 1995; Berry and Lembi 2000; Rattanasaensri et al. 2020). However, temperature preferences can vary greatly among FGA genera and species within the same genus, resulting in a succession of species throughout a seasonal cycle (Hillebrand 1983; Graham et al. 1995; Berry and Lembi 2000). The FGA inoculum for our experiments was formed of the dominant species sampled between mid-April and mid-June in the Netherlands. It is likely that our FGA samples had lower temperature optima than FGA species that dominate later in the summer, as they are adapted to grow during the cooler spring. Despite this, we were able to establish that FGA growth and surface bloom formation are greatest within an optimum water temperature range, independent of light availability at the mesocosm scale. The combination of both of these abiotic factors is most critical for the growth of FGA blooms in situ.

Our results show that seasonal changes in irradiance, photoperiod, and temperature are crucial for the movement of

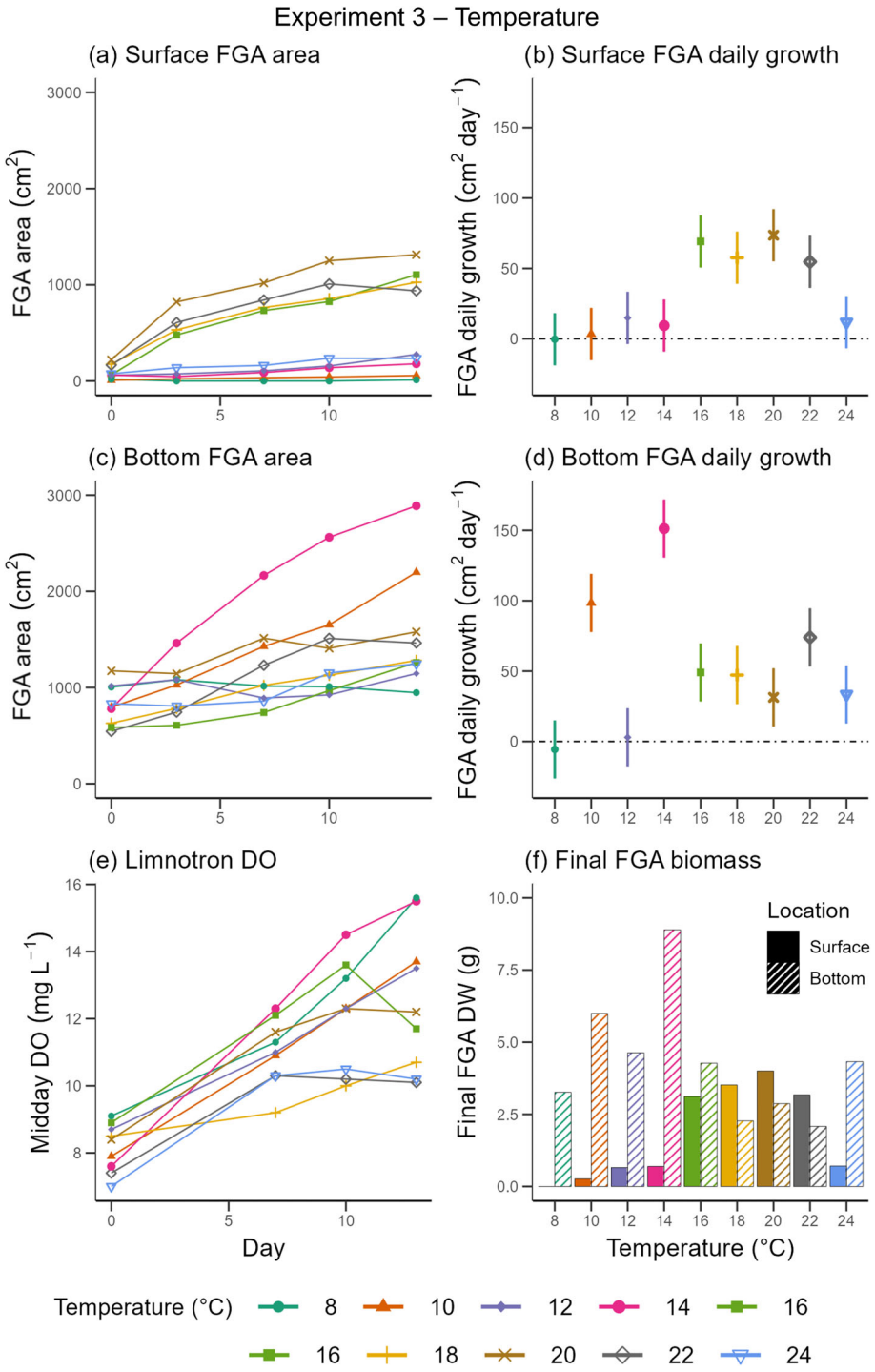

Fig. 3. Results from Experiment 3—temperature: (**a**) surface and (**c**) bottom filamentous green algae (FGA) area over time calculated from image analysis; (**b**) surface and (**d**) bottom plots of FGA area daily growth rate with 95% confidence limits; (**e**) midday dissolved oxygen (DO) concentrations over time; and (**f**) final dry weight (DW) biomass of FGA harvested from the surface and bottom of the Limnotrons. Surface and Bottom denote the air–water and sediment–water interfaces in the Limnotron, respectively, and Limnotron denotes a data representative of the whole mesocosm system. Color and shape denote the nine different temperature treatments each delivered to a Limnotron; 8–24°C at 2°C intervals. Light delivered at an irradiance of 338 μmol m^{-2} s^{-1} over a 12-h photoperiod.

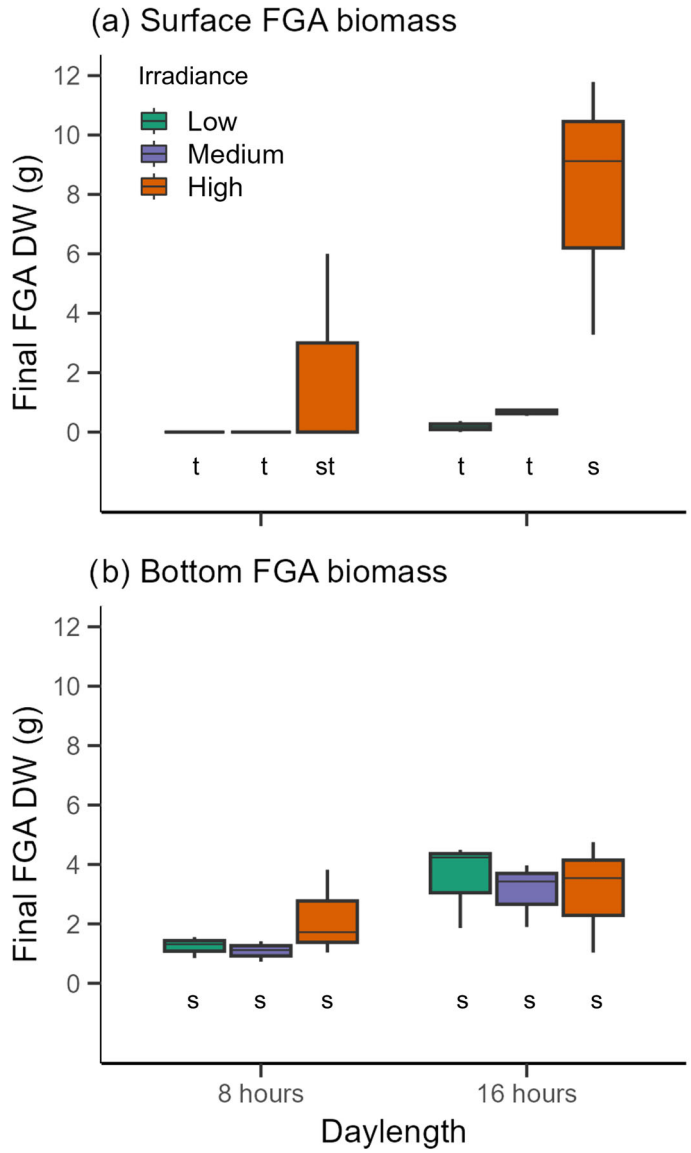

Fig. 4. Dry weight (DW) biomass of final filamentous green algae (FGA) harvested from (**a**) the surface and (**b**) bottom of Limnotrons after 24–26 d exposure to high, medium, and low irradiances delivered for 8 and 16-h, respectively (Table 1). Different letters (s and t) indicate statistically significant differences between groups in Tukey HSD multiple comparison test ($p < 0.05$), carried out on both surface and bottom data independently.

FGA biomass to the water surface. However, light availability at the sediment for FGA growth can be influenced by turbidity changes caused by seasonal phytoplankton dynamics (Sayer et al. 2010). Despite rapidly flushing the Limnotrons, significant phytoplankton growth occurred in treatments with long daylength and medium-high irradiance. This indicates how phytoplankton in less heavily flushed systems could be crucial in moderating light availability at the sediment surface to limiting levels for FGA growth. Lake water temperatures are increasing globally with climate change, altering spring phenological patterns and leading to trophic mismatches (Winder and Schindler 2004). This could result in changes to the timing of spring phytoplankton blooms and subsequent "clear-water" phase (Lampert et al. 1986; Meis et al. 2009; Thackeray 2012), which in turn could alter FGA growth dynamics.

Influence of FGA on water column parameters

Freshwater FGA are highly successful at sequestering nutrients due to their fast growth rates and physical adaptations, such as increased cell size and broad environmental tolerances (Hoffmann 1990; Higgins et al. 2005). When FGA blooms peak, the available nutrient concentrations in the water column reach seasonal lows, potentially limiting growth of other algae and floating plants (Dalsgaard 2003). In this study, both SRP and DIN concentrations reduced dramatically with FGA growth in the light experiments, despite constant delivery of nutrients to match the Limnotron flushing rate. As freshwater FGA start to decompose, they supply nutrients to the water column (Paalme et al. 2002; Higgins et al. 2008b). During the long daylength experiment, we observed an increase in SRP and DIN concentrations, as FGA biomass at the surface was beginning to plateau and decrease in the medium and high irradiance treatments, respectively. The critical role that FGA play in modifying nutrient cycling in freshwater systems by storing nutrients and then releasing them later in the season when decomposing has implications for the seasonal availability of nutrients and therefore the seasonal succession of phytoplankton in aquatic systems (Winder and Schindler 2004; Sommer et al. 2012).

Freshwaters experiencing FGA blooms see vast fluctuations in diurnal DO concentrations, resulting in nocturnal hypoxia when community respiration exceeds daytime photosynthesis, which can be harmful to biota (Hillebrand 1983; Engström-Öst and Isaksson 2006). In our experiments, DO concentration and daily amplitude increased over time with increasing light availability and FGA biomass. However, DO concentrations did not fall below 7.3 mg L^{-1} in Limnotrons with surface blooms, exceeding concentrations that are harmful to other aquatic organisms. However, the potential for hypoxia increases when FGA subsequently decompose, which can lead to mass deaths of benthic invertebrates (Havens et al. 2001), and a shift in the benthic community structure toward hypoxia-resistant taxa (Green and Fong 2016). In the Limnotrons experiencing high irradiance and long daylengths, DO concentrations decreased from day 15, coinciding with the decrease in surface FGA area. This suggests that the FGA were starting to decompose, likely due to overexposure and photoinhibition in the top layers of the FGA bloom, or conversely, self-shading by the upper layers of the bloom causing decomposition in the lower layers (Graham et al. 1995; Pikosz et al. 2017).

Implications for FGA outside of mesocosms

In these experiments, complex food web effects were avoided by removing macroinvertebrates preinoculation and rapidly flushing the Limnotrons to remove phytoplankton buildup. Freshwater managers usually have less control over water residence time and the trophic interactions, so the importance of these factors and the timing of "clear water" phases would have a much greater impact on the timing and proliferation of FGA blooms (Sayer et al. 2010). However, many small and artificial waterbodies are heavily regulated, presenting opportunities for FGA management through hydrological manipulation. Macroinvertebrate grazing pressures on FGA in the Limnotrons were limited and could provide bottom-up control of FGA in freshwater ecosystems (Sturt et al. 2011). We did not test the effects of competition with floating-leaved plants, free-floating macrophytes, or buoyant cyanobacterial blooms, which would otherwise compete with FGA in freshwaters (Scheffer and van Nes 2007). Weather-related factors such as wind and rain can also affect FGA surface bloom presence (Higgins et al. 2008a; Kasprzak et al. 2017). Our experiments did not test the effects of light spectral composition, which naturally varies across latitudes, seasons, and days, and could affect FGA growth and blooms due to altering the rate of photosynthesis (Webb et al. 2020). It is important to consider the potential impact of these variables on FGA growth and blooms in situ, and incorporate them alongside our experimental results for future freshwater management strategies.

FGA blooms predominantly occur in temperate regions that experience seasonal changes in temperature and light availability (Hillebrand 1983). We observed a rapid growth of FGA at 14°C, but surface blooms were noticeably absent. However, significant surface blooms of FGA occurred between 16°C and 22°C. This suggests that the seasonal thermal window provided in temperate climates allows FGAs to increase in biomass and gain a competitive advantage over other photosynthetic organisms. Afterwards, surface FGA blooms may form in the spring and summer, as both temperature and light availability increase. Global lake water temperatures are increasing due to climate change (Maberly et al. 2020), which could result in FGA blooming earlier in the year than previously observed. However, changes to the seasonal thermal patterns in waterbodies will also impact the wider trophic cascade, and in turn FGA bloom occurrence. Experimental results alongside weather and climate data can be used to help predict when FGA blooms are likely to occur, enabling a more focused management response. The inclusion of more physical and biotic environmental factors alongside light and temperature in the modeling and forecasting of FGA blooms is essential for prediction and management.

Conclusions

Our mesocosm experiments demonstrate the importance of irradiance, photoperiod (and their combine effect as DLI) and temperature on FGA growth and surface bloom formation. FGA are evidently very successful at growing and forming blooms when provided with a window of opportunity that combines both optimum light and temperature conditions with clear water at the start of the growing season. Predicting how aquatic systems and trophic relationships will respond to more extreme and unpredictable weather conditions due to climatic change is difficult and requires research into the physical demands of different freshwater FGA species and their relationships within aquatic systems. In addition to mitigation measures such as reducing nutrient loading, this work will help managers of freshwater bodies to predict when FGA blooms will occur and reduce their negative impacts by enabling a more focused management response.

Author Contributions

Hannah R. Kemp: conceptualization (equal); data curation (lead); formal analysis (lead); funding acquisition (equal); investigation (equal); methodology (equal); visualization (lead); writing—original draft preparation (lead); review and editing (equal). Alexandra Zieritz: conceptualization (equal); supervision (supporting); writing—review and editing (equal). Stephen J. Dugdale: conceptualization (equal); supervision (supporting); writing—review and editing (equal). Nico R. Helmsing: conceptualization (supporting); investigation (equal); methodology (equal); resources (equal). Suzanne Wiezer: conceptualization (supporting); investigation (equal); resources (equal). Stephen C. Maberly: conceptualization (supporting); writing—review and editing (supporting). Lisette N. de Senerpont Domis: conceptualization (supporting); writing—review and editing (supporting). Martyn Kelly: conceptualization (supporting); writing—review and editing (supporting). Suzanne McGowan: conceptualization (equal); funding acquisition (equal); investigation (equal); methodology (equal); supervision (lead); writing—review and editing (equal).

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Conflicts of Interest

None declared.

Data Availability Statement

The data that support the findings of this study are openly available in at Zenodo: https://dio.org/10.5281/zenodo.15669103.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

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