



Interaction Effects of Temperature, Light, Nutrients, and pH on Growth and Competition of *Chlorella vulgaris* and *Anabaena* sp. Strain PCC

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Interaction effects of temperature, light, nutrients, and pH on growth and competition of *Chlorella vulgaris* and *Anabaena* sp. strain PCC were evaluated using an orthogonal design method to elucidate how these environment factors promote the growth of beneficial algae and limit the growth of harmful algae. The optimal conditions for the growth of *C. vulgaris* in the mono-culture system were as follows: temperature, 35°C; light, 660 lx; N concentration, 0.36 mg L⁻¹; P concentration, 0.1 mg L⁻¹; and pH, 9.0; and those for *Anabaena* were as follows: temperature, 30°C; light, 6,600 lx; N concentration, 0.18 mg L⁻¹; P concentration, 0.1 mg L⁻¹; and pH, 7.0. The optimal conditions for the growth of *C. vulgaris* in the co-culture system were as follows: temperature, 25°C; light, 4,400 lx; N concentration, 0.18 mg L⁻¹; P concentration, 0.5 mg L⁻¹; and pH, 6.0; and those for *Anabaena* were as follows: temperature, 35°C; light, 4,400 lx; N concentration, 0.36 mg L⁻¹; P concentration, 0.5 mg L⁻¹; and pH, 6.0. Both competition-inhibition parameters of *Anabaena* against *C. vulgaris* and those of *C. vulgaris* against *Anabaena* were the largest under the following conditions: temperature, 30°C; light intensity, 6,600 lx; N concentration, 0.36 mg L⁻¹; P concentration, 0.025 mg L⁻¹; and pH, 8.0. According to the Lotka–Volterra competition model, *Anabaena* won in the competition in the co-culture system with the following conditions: 1) temperature, 15°C; light, 660 lx; total N (TN), 0.18 mg L⁻¹; total P (TP), 0.025 mg L⁻¹; pH, 6; 2) temperature, 15°C; light, 2,200 lx; TN, 0.36 mg L⁻¹; TP, 0.025 mg L⁻¹; pH, 7; 3) temperature, 15°C; light, 6,600 lx; TN, 3.6 mg L⁻¹; TP, 0.5 mg L⁻¹; pH, 9; 4) temperature, 30°C; light, 4,400 lx; TN, 0.18 mg L⁻¹; TP, 0.05 mg L⁻¹; pH, 9; 5) temperature, 35°C; light, 660 lx; TN, 3.6 mg L⁻¹; TP, 0.05 mg L⁻¹; pH, 8; and 6) temperature, 35°C; light, 2,200 lx; TN, 0.72 mg L⁻¹; TP, 0.025 mg L⁻¹; pH, 9. However, *C. vulgaris* could not win in the competition in the co-culture system under all conditions tested.

Keywords: *Chlorella vulgaris*, *Anabaena* sp. strain PCC, environment factors, interspecies competition, temperature, light, nutrients, pH

INTRODUCTION

Harmful cyanobacterial blooms are becoming increasingly common in eutrophic water bodies, and they may result in a wide range of environmental, social, and economic consequences. For example, cyanobacterial blooms can increase oxygen demand, which may lead to localized incidents of hypoxic or anoxic conditions causing fish deaths (Anderson et al., 2002; Paerl, 2008). Surface blooms can also block light from reaching benthic primary producers, which may adversely affect food web dynamics depending on lake-bottom habitats (Bricelj and Lonsdale, 1997; Gallegos and Bergstrom, 2005). The social and economic effects of cyanobacterial blooms include negative effects on recreational opportunities due to the closure of affected areas, declining local fisheries, and increased water treatment costs (Hoagland et al., 2002; Paerl, 2008). In addition to their wider ecological effects, cyanobacteria are known to produce a suite of secondary metabolites that include hepatotoxins, neurotoxins, and dermatotoxic compounds. These toxins have been linked to reduced water quality and detrimental effects at higher trophic levels (Leonard and Paerl, 2005; Ferrão-Filho et al., 2009), small-animal illness and even mortality (Boyer, 2007; Jacoby and Kann, 2007), and adverse health risks in humans (Paerl, 2008).

Anabaena is a microscopic, bloom-forming, harmful cyanobacterium that has been reported to cause harmful algal blooms (Bouma-Gregson et al., 2017) and produce algal toxins in waters worldwide (Cai et al., 2006; Lawton and Codd, 2010). It also causes ecological damage through high biomass and other related effects (Al-Mamoori et al., 2020). To improve water quality, protect aquatic animals, and ensure the safety and quality of aquatic products, scientists have carried out extensive research on how to control the growth of *Anabaena* in water bodies, especially in aquaculture ponds (Yue et al., 2006; Yu et al., 2016; Peng X. et al., 2020). *Chlorella vulgaris* is a typical microalga in water bodies. It can be easily digested by fish and other aquatic animals and is considered to be useful in water bodies (Meng et al., 2017). Therefore, domination by *C. vulgaris* in a water body is considered an indicator of good water quality (Yang and Lu, 2014; He et al., 2019).

Several environmental factors can influence the growth of algae (Zhao et al., 2014), including abiotic factors such as hydrodynamics (i.e., turbulence, wind-driven currents, and stratification) (Hotto et al., 2007; Fortin et al., 2010), nutrients (Downing et al., 2001; Heisler et al., 2008; Elliott, 2012), temperature (Cires et al., 2011), light availability (Cires et al., 2011; Renaud et al., 2011), and biotic interactions such as competition and grazing (Gobler et al., 2007; Ger et al., 2010). Temperature, light, nutrients, and pH are important ecological factors influencing algal growth (Mao et al., 2007), but there are only a few reports on their interactive effects on *C. vulgaris* and *Anabaena*. Changes in any of the factors may alter the phytoplankton community structure (Mei et al., 2003; Meng et al., 2013). It is important to understand how environmental factors can be manipulated to promote the growth of beneficial algae and limit the growth of harmful algae. Therefore, using an orthogonal design, in this study, we aimed to evaluate whether the interactions between temperature, light, nutrients, and pH influence the growth and competition of *C. vulgaris* and *Anabaena*, and to determine the optimal conditions for the

TABLE 1 | Levels of each factor.

Level	Factor				
	T (°C)	L (lx)	TN (mg·L ⁻¹)	TP (mg·L ⁻¹)	pH
1	15	660	0.18	0.025	6
2	25	2,200	0.36	0.05	7
3	30	4,400	0.72	0.1	8
4	35	6,600	3.6	0.5	9

dominance of *C. vulgaris* over *Anabaena* in water. The results might be valuable in guiding the control of environmental factors in pond and tank aquaculture.

MATERIALS AND METHODS

Algae and Growth Conditions

Chlorella vulgaris and *Anabaena* sp. strain PCC 1042 were obtained from the Institute of Hydrobiology, Chinese Academy of Sciences. All algae were cultured in BG11 medium (Meng et al., 2015) in a plant growth chamber (PGX-150B; Wuxi Woxin Apparatus Co., Ltd., China). The culture conditions were as follows: temperature, 25°C; light intensity, 2.2×10^3 lx (using a fluorescent lamp as the light source); and photoperiod, 12-h: 12-h light/dark.

The experiments were conducted in 250 ml Erlenmeyer flasks with 200 ml of BG11 medium (Meng et al., 2015). The cultures were shaken gently once every 2 h during the light period and allowed to stay still during the dark period. Before sampling, they were shaken again to ensure homogeneous cell distribution.

Experimental Design

An orthogonal array $L_{16} 5^4$ with five environmental factors (temperature (T), light (L), N concentration (TN), P concentration (TP), and pH) and four levels (Table 1) were set using software Minitab 15 (The water temperature that good for the growth of most fish species is higher than 15°C, and the highest water temperature is about 35°C in summer, so the four temperature of 15°C, 25°C, 30°C, 35°C were chosen. The phosphorus concentration of 0.02 mg L⁻¹ is critical point for eutrophication happening (Shi et al., 2004), and that of 0.5 mg L⁻¹ is the first level standard value for the waste water discharged from aquaculture pond (Ministry of Agriculture and Rural Affairs of the PRC, 2007), so the four phosphorus concentrations of 0.025 mg L⁻¹, 0.05 mg L⁻¹, 0.1 mg L⁻¹, 0.5 mg L⁻¹ were chosen. Our other test showed that the nitrogen and phosphorus ratio for the best growth of *Chlorella vulgaris* is 7.2:1 (Wang et al., 2015), so the four nitrogen concentrations of 0.18 mg L⁻¹, 0.36 mg L⁻¹, 0.72 mg L⁻¹, 3.6 mg L⁻¹ were chosen based on the four phosphorus concentrations. According to the “Environmental quality standards for surface water” (Ministry of Ecology and Environment of the PRC, 2002), the pH should be between 6 and 9, so the four pH levels of 6, 7, 8, 9 were chosen. Although the natural light intensity in summer is as high as 100,000 lx in summer, the best light intensity for the growth of most fish species is lower than 7,000 lx (Xu et al., 2014), so the four light

TABLE 2 | The orthogonal test program.

Treatment	T (°C)	L (lx)	TN (mg·L ⁻¹)	TP (mg·L ⁻¹)	pH
1	15	660	0.18	0.025	6
2	15	2,200	0.36	0.05	7
3	15	4,400	0.72	0.1	8
4	15	6,600	3.6	0.5	9
5	25	660	0.36	0.1	9
6	25	2,200	0.18	0.5	8
7	25	4,400	3.6	0.025	7
8	25	6,600	0.72	0.05	6
9	30	660	0.72	0.5	7
10	30	2,200	3.6	0.1	6
11	30	4,400	0.18	0.05	9
12	30	6,600	0.36	0.025	8
13	35	660	3.6	0.05	8
14	35	2,200	0.72	0.025	9
15	35	4,400	0.36	0.5	6
16	35	6,600	0.18	0.1	7

intensity levels of 660, 2,200, 4,400, 6,600 were chosen.); there were 16 groups in total, as shown in **Table 2**. There were three types of algal culture in every group, namely, mono-culture of *C. vulgaris* (treatment C), mono-culture of *Anabaena* (treatment A), co-culture of *C. vulgaris* and *Anabaena* (treatment CA). Three replicates for each group were prepared.

The initial density of *C. vulgaris* and *Anabaena* in each group was 5×10^5 cell ml⁻¹, and the inoculations were carried out according to the method of Meng et al. (2015).

General Analyses

During the algal culture period, the liquid medium in each group was sampled with a 0.45- μ m filter needle to determine total N and total P concentrations. Subsequently, NaNO₃, KH₂PO₄, and ammonia-free water were added to increase the N and P concentrations and liquid medium volume to the initial level according to the determination results.

The cells were counted every 24 h after the beginning of the test. The test was terminated when a negative growth of algae was found, and the density 1 day before the negative growth was used as the maximum density of each algal species. The algal density was determined according to the methods described in the *Standard Methods for the Examination of Water and Wastewater* (Chinese National Environmental Protection Agency, 2002).

Data Analysis Methods

Specific Growth Rate

Specific growth rate was calculated using the following formula (Meng et al., 2012):

$$\ln \frac{N_n}{N_{n-1}} = \mu_n \cdot (t_n - t_{n-1}) \quad (n = 1, 2, 3, 4, \dots) \quad (1)$$

where, μ_n is the growth rate on day n , N is cell density (cells ml⁻¹), and t is the culture time (d). The average specific growth rate (μ) is the algal growth rates from day 1 of the test to the day when the maximum cell density appeared, and μ was used to compare the growth rate of algal cells in different treatments.

Algae Growth Curve Fitting

The growth of algae was fitted by the logarithmic form of a logistic equation, and the least squares method was used for regression analysis to obtain the intercept and slope rate of the equation as estimated values for a and r respectively:

$$\ln \frac{K - N}{N} = a - rt \quad (2)$$

where, N is the biomass of the algae (count the biomass of algae in each treatment every day, and this biomasses are N values), K is the maximum biomass of the algae (using the maximum biomass of the algae in each treatment as its K value), r is the intrinsic growth rate, t is culture time.

Calculation of Competition–Inhibition Parameter

The Lotka–Volterra competition model was adopted to calculate the competition–inhibition parameters of *C. vulgaris* and *Anabaena* (Meng et al., 2012):

$$\frac{N_c, n - N_c, n - 1}{t_n - t_{n-1}} = \frac{r_c N_c, n - 1 (K_c - N_c, n - 1 - \alpha N_a, n - 1)}{K_c} \quad (n = 1, 2, 3, 4, \dots) \quad (3)$$

$$\frac{N_a, n - N_a, n - 1}{t_n - t_{n-1}} = \frac{r_a N_a, n - 1 (K_a - N_a, n - 1 - \beta N_c, n - 1)}{K_a} \quad (n = 1, 2, 3, 4, \dots) \quad (4)$$

where, N_c and N_a are the biomass ($\times 10^4$ cells ml⁻¹) of *C. vulgaris* and *Anabaena* in the co-culture system at time t , respectively; r_c and r_a are the intrinsic growth rate of *C. vulgaris* and *Anabaena* in the mono-culture system, respectively; K_c and K_a are the maximum biomass of *C. vulgaris* and *Anabaena* in the mono-culture system, respectively; α is the competition–inhibition parameter of *Anabaena* against *C. vulgaris* in the co-culture system, and β is the competition–inhibition parameter of *C. vulgaris* against *Anabaena* in the co-culture system.

The restraint beginning point and inhibition parameter were calculated according to Chen et al. (1999).

Statistical Analysis

Statistical analyses were performed using SPSS 15.0. Significant differences in algae biomass caused by the environment factors combination of T, L, TN, TP and pH, that is to say between the different treatments, were analyzed using the one-way analysis of variance (ANOVA), and Tukey's multiple comparisons were used for statistical comparisons. Data were tested for normality of distribution (Shapiro–Wilk test) and homogeneity of variance (Levene's test) before analysis. Data that did not meet the assumptions of normality and homoscedasticity were transformed (lg), and then analyzed using the one-way ANOVA. Student's t -test was used for testing the significance of the coefficients in the regression equations. Results with $p < 0.05$ were considered significant.

RESULTS

Growth of *C. vulgaris* and *Anabaena*

The growth curves of *C. vulgaris* and *Anabaena* are shown in **Figure 1** and their growth rates in **Table 3**. The main effect

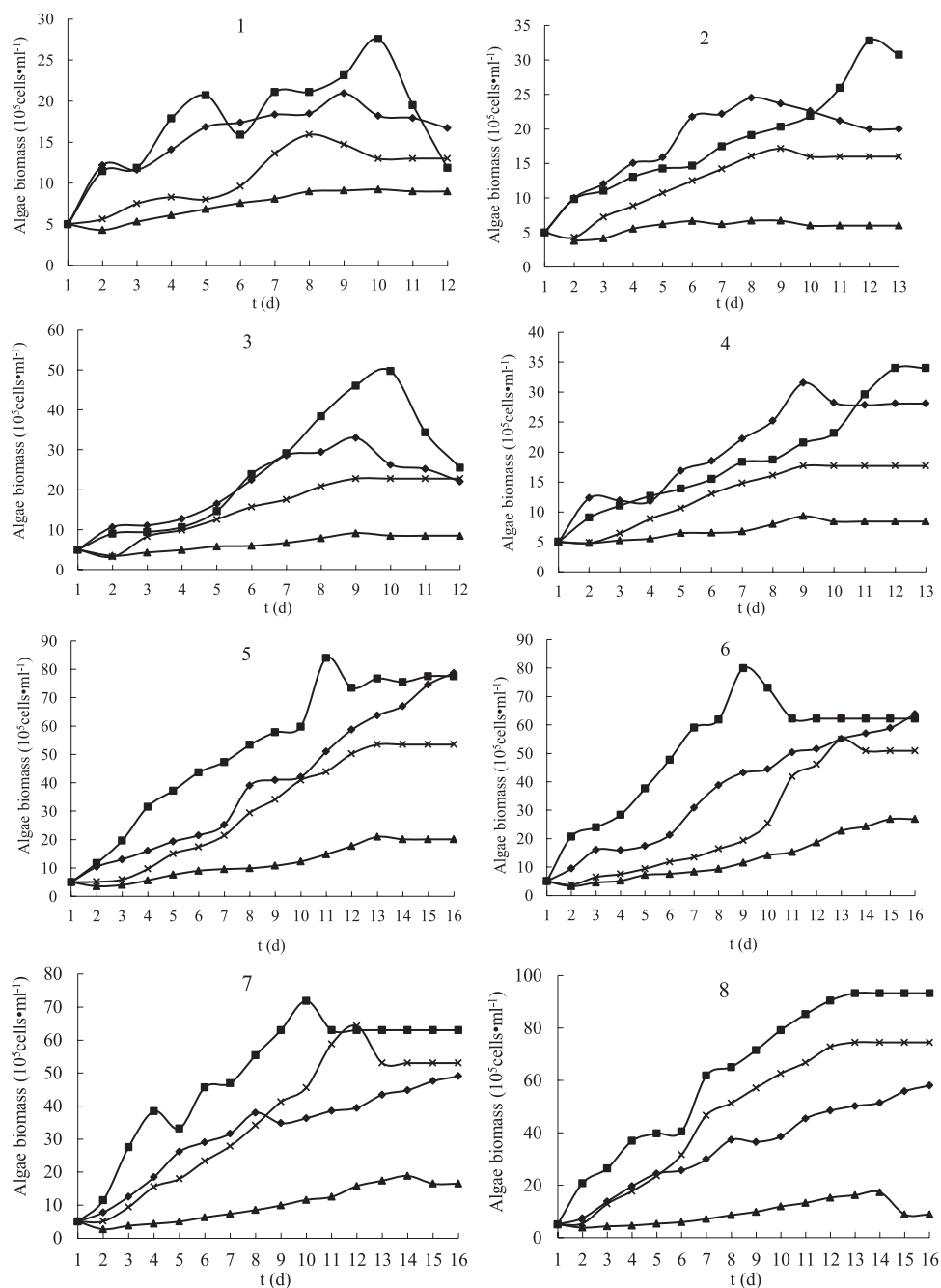
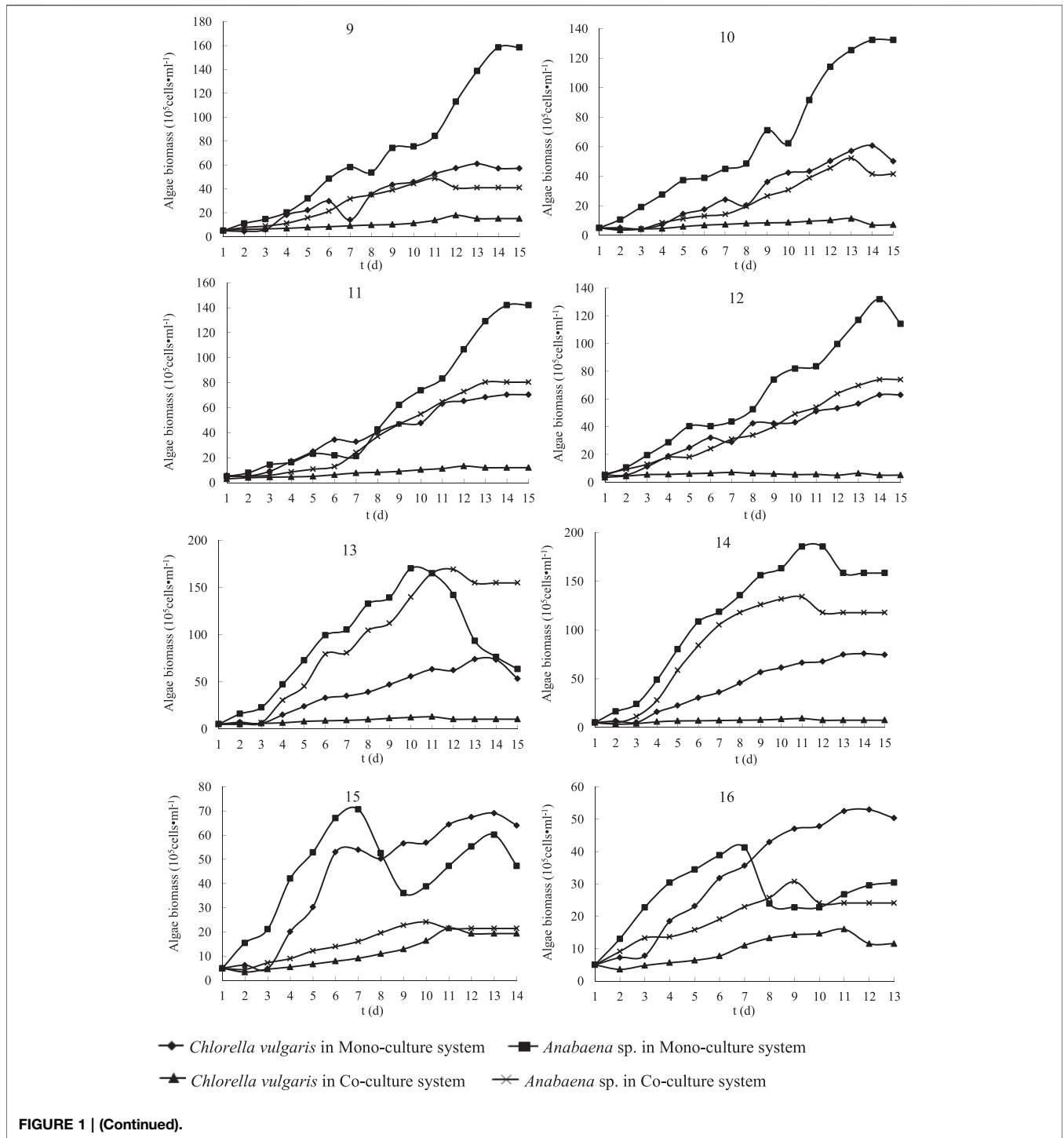


FIGURE 1 | Growth curves of *Chlorella vulgaris* and *Anabaena* sp. strain PCC in mono-culture and co-culture systems at different conditions (from Treatment 1 to Treatment 16).

analysis plots (**Supplementary Figures S1, S2**) showed that the optimal growth conditions for *C. vulgaris* in the mono-culture system were as follows: temperature, 35°C; light intensity, 660 lx; N concentration, 0.36 mg L⁻¹; P concentration, 0.1 mg L⁻¹; and pH, 9.0; and those for *Anabaena* were as follows: temperature, 30°C; light intensity, 6,600 lx; N concentration, 0.18 mg L⁻¹; P concentration, 0.1 mg L⁻¹; and pH, 7.0. As shown in **Supplementary Figures S3, S4**, the optimal growth condition

for *C. vulgaris* in the co-culture system were as follows: temperature, 25°C; light intensity, 4,400 lx; N concentration, 0.18 mg L⁻¹; P concentration, 0.5 mg L⁻¹; and pH, 6.0; and those for *Anabaena* were as follows: temperature, 35°C; light intensity, 4,400 lx; N concentration, 0.36 mg L⁻¹; P concentration, 0.5 mg L⁻¹; and pH, 6.0.

The maximum cell density of *C. vulgaris* in the mono-culture system was observed in treatment 5 (temperature, 25°C; light



intensity, 660 lx; N, 0.36 mg L⁻¹; P, 0.1 mg L⁻¹; pH, 9.0); under these conditions, the maximum cell density was $787.0 \times 10^4 \text{ cells L}^{-1}$. The maximum cell density of *Anabaena* in the mono-culture system was found in treatment 14 (temperature, 35°C; light intensity, 2,200 lx; N, 0.72 mg L⁻¹; P, 0.025 mg L⁻¹; pH, 9.0); under these conditions, the maximum cell density was $1,854.9 \times 10^4 \text{ cells L}^{-1}$. The maximum cell density of *C. vulgaris* in the co-culture system

was in treatment 6 (temperature, 25°C; light intensity, 2,200 lx; N, 0.18 mg L⁻¹; P, 0.5 mg L⁻¹; pH, 8.0); under these conditions, the maximum cell density was $268.5 \times 10^4 \text{ cells} \cdot \text{L}^{-1}$. The maximum cell density of *Anabaena* in the co-culture system was in treatment 13 (temperature, 35°C; light intensity, 660 lx; N, 3.6 mg L⁻¹; P, 0.05 mg L⁻¹; pH, 8.0); under these conditions, the maximum cell density was $1,690.2 \times 10^4 \text{ cells} \cdot \text{L}^{-1}$.

TABLE 3 | Mean specific growth rate (μ) of *Chlorella vulgaris* and *Anabaena* sp. strain PCC at different conditions.

Algae	Treatment	Mean specific growth rate	
		Mono-culture	Co-culture
<i>Chlorella vulgaris</i>	1	0.179	0.096
	2	0.227	0.112
	3	0.236	0.076
	4	0.157	0.094
	5	0.184	0.119
	6	0.200	0.126
	7	0.143	0.138
	8	0.163	0.127
	9	0.208	0.108
	10	0.207	0.106
	11	0.193	0.135
	12	0.192	0.116
	13	0.215	0.106
	14	0.204	0.108
	15	0.218	0.205
	16	0.199	0.166
<i>Anabaena</i> sp.	1	0.213	0.173
	2	0.191	0.167
	3	0.278	0.189
	4	0.174	0.158
	5	0.276	0.198
	6	0.359	0.200
	7	0.247	0.242
	8	0.244	0.243
	9	0.266	0.226
	10	0.241	0.233
	11	0.257	0.231
	12	0.252	0.195
	13	0.392	0.336
	14	0.418	0.369
	15	0.441	0.175
	16	0.352	0.174

The growth curves of both *C. vulgaris* and *Anabaena* in the mono-culture system fitted an “S” shape (Figure 1), indicating that the growth curve of the two algae in the mono-culture system could be fitted with a logistic model, and the inflection point could be calculated using a logistic equation (Supplementary Materials). To calculate the inflection point time, the growth curves of *C. vulgaris* and *Anabaena* in the co-culture system were also fitted by a logistic model (Supplementary Materials).

Competition–Inhibition Parameters Between *C. vulgaris* and *Anabaena*

The competition–inhibition parameters of *C. vulgaris* against *Anabaena* and *Anabaena* against *C. vulgaris* in the co-culture system are shown in Table 4. The results revealed that the competition–inhibition parameters of *Anabaena* against *C. vulgaris* (α) were higher than those of *C. vulgaris* against *Anabaena* (β) in treatments 1, 2, 4, and 11. On the contrary, the competition–inhibition parameters of *C. vulgaris* against *Anabaena* (β) were greater than that of *Anabaena* against *C. vulgaris* (α) in other treatments. Both α and β reached the highest value in treatment 12. As shown in Table 4, the inflection point time of *C. vulgaris* was later than that of *Anabaena* in the mono-

culture system in most treatments, but it was complicated, and there were no change trends for the inflection point time of *C. vulgaris* and *Anabaena* in the co-culture system.

DISCUSSION

Interaction Effects of Environmental Factors on the Growth of *C. vulgaris* and *Anabaena* in Mono-Culture System

The optimal growth conditions are different for different species of algae (Nakajima et al., 2020; Toth et al., 2020; Li et al., 2021). Long et al. (2011) reported that the optimal growth conditions for spring algal species are as follows: temperature, 20°C; light intensity, 4,700 lx; N concentration, 3.5 mg L⁻¹; P concentration, 0.3 mg L⁻¹; and water flow rate, 0.1 m s⁻¹. Our analyses showed that the maximum cell density of *C. vulgaris* increased with temperature (Supplementary Figure S1) and reached the peak point at 35°C. The optimal growth conditions for *C. vulgaris* were as follows: temperature, 35°C; light intensity, 660 lx; N concentration, 0.36 mg L⁻¹; P concentration, 0.1 mg L⁻¹; and pH, 9.0; and those for *Anabaena* were as follows: temperature, 30°C; light intensity, 6,600 lx; N concentration, 0.18 mg L⁻¹; P concentration, 0.1 mg L⁻¹; and pH, 7.0. Song et al. (2013) observed an apparent exponential growth phase of *Chlorella* when the temperature increased to 20°C or 25°C, and its specific growth rate and maximum cell density also increased with the increase in temperature. In the present study, we found a similar relationship between maximum cell density and temperature.

As shown in Supplementary Figure S2, the maximum cell density of *Anabaena* at a light intensity of less than 2,200 lx was below the mean level, indicating that its growth was inhibited under such light conditions. A long period under light-limited conditions could increase the precipitation of *Anabaena* cells and result in cell loss (Wu et al., 2012), which might explain the phenomenon observed in our experiment.

Through regression analysis, Liang et al. (2010) found that water temperature and total P concentration are two key factors affecting the growth of *Anabaena*. Wang et al. (2005) reported that the effect of water temperature on algal biomass is closely related to the nutrient concentration in the water. They found that the algal biomass at a low temperature was greater than that at a high temperature in the water with low nutrient concentrations (inorganic N, 0.2–0.4 mg L⁻¹; organic N, 0.2–0.4 mg L⁻¹; and total P, 0.005–0.01 mg L⁻¹), and the algal biomass at a low temperature was less than that at a high temperature in water with high nutrient concentrations (inorganic N, 0.3–0.65 mg L⁻¹; organic N, 0.4–0.7 mg L⁻¹; and total P 0.01–0.03 mg L⁻¹). We obtained a similar result in our experiment, that is, the maximum cell density of *C. vulgaris* in treatments with a high temperature and low nutrient concentrations was lower than that in treatments with a low temperature and high nutrient concentrations. The activities of the algae increased with the increase in temperature, leading to a higher metabolic rate and greater nutrient consumption; thus, the

TABLE 4 | Inhibition parameters of *Chlorella vulgaris* and *Anabaena* sp. strain PCC after inflection point at different conditions.

Treatment	Inhibition parameter	Time (d)													
		2	3	4	5	6	7	8	9	10	11	12	13	14	Average
1	α	0.89	1.08	1.05	1.09	1.03	0.54	0.72	0.75						0.89
	β		2.10	3.60	0.42	-2.15	-0.02	1.98							0.79
2	α		3.93	0.86	1.59	1.43	1.66	1.05	1.11					1.95	
	β			-1.05	-0.83	-0.02	0.28	0.13	1.16					0.14	
3	α			2.42	1.69	2.04	1.23	0.87	0.73					1.49	
	β			5.43	2.98	2.43	3.84	2.21	2.56					3.24	
4	α	3.89	3.33	1.38	2.30	1.67	0.65	0.57						1.97	
	β			-0.70	-1.49	0.19	0.98	0.43						-0.12	
5	α			2.72	1.89	1.31	1.33	0.90	0.48	0.15				1.25	
	β			-2.13	-9.04	8.70	7.36	5.60	6.25					2.79	
6	α						0.64	0.43	1.34	0.15	0.07	0.51	0.38	0.50	
	β						3.75	0.85	3.39	1.43	0.18			0.57	
7	α				2.17	1.85	1.02	0.54						1.40	
	β	6.84	7.25	5.85	4.37	3.64	3.40							5.23	
8	α				0.32	0.47	0.23	0.41	0.28	0.44	0.40			0.36	
	β			-5.70	3.78	2.27	1.72	1.47	0.66	1.03				0.75	
9	α				2.72	1.89	1.31	1.33	0.90	0.48	0.15			1.25	
	β				-2.13	-9.04	8.70	7.36	5.60	6.25				2.79	
10	α			2.11	2.89	3.32	2.91	2.36	1.85	1.23	1.08	0.77		2.06	
	β							-1.96	5.62	0.85	3.27	3.30		2.22	
11	α				2.50	2.41	2.20	1.30	0.86	0.84	0.51			1.52	
	β						-8.62	1.48	3.89	2.39	3.00	2.50		0.77	
12	α	3.24	1.76	4.11	2.36	2.59	1.70							2.63	
	β							9.30	5.05	1.82	8.55	2.40	6.93	6.26	5.76
13	α		7.74	0.93	1.15	0.70	0.62	0.38	0.43	0.38				1.54	
	β					9.95	-0.01	4.45	-1.55	-2.04	-0.15			1.77	
14	α	-1.63	1.04	1.94	1.54	1.73	2.03							1.11	
	β	5.69	1.67	2.20	1.60									2.79	
15	α						0.96	1.34	0.42	0.67	0.04	0.56		0.66	
	β						4.81	2.91	2.66	1.93	1.36			2.73	
16	α			1.95	1.77	1.66	1.03	0.70	0.54	0.82				1.21	
	β				3.59	3.59	3.38	2.54	1.85	1.58				2.76	

available nutrients in the water depleted and finally limited the algal growth.

Interaction Effects of Environmental Factors on the Competitive Growth of *C. vulgaris* and *Anabaena* in the Co-culture System

Different microalgal species compete with one another for light, nutrients, and other resources (Cao et al., 2012); therefore, competition is a crucial factor promoting changes in the predominant algae in water bodies (Piazzi and Ceccherelli, 2002; Litchman, 2003; Burrows et al., 2021). Our experiment revealed that competition-inhibition parameters of *C. vulgaris* against *Anabaena* and those of *Anabaena* against *C. vulgaris* in the co-culture system differed under different conditions, indicating that the predominant positions of the two algae alternated with the environment. Chen et al. (2010) reported that competition-inhibition parameters between *Oscillatoria* and *Microcystis* changed at 20, 25, and 30°C. Moreover, Chen et al. (2009) showed that *Microcystis* is more competitive than *Scenedesmus* at light intensity of below 6,600 lx, and the vice versa at higher light intensity. In our analyses, the maximum cell densities of both *C. vulgaris* and *Anabaena* in the co-culture system

were lower than in the mono-culture system; this indicated that the growth of both algae was inhibited in the co-culture system.

The algae growing together compete for light, nutrients, and other resources and even secrete growth-inhibition substances to inhibit each other (Xu et al., 2004; Peng Y. et al., 2020; Stn and Bykiik, 2020). When the growth of one algal species is inhibited due to the deficiency of some nutrient elements, another species less dependent on these nutrient elements might grow quickly and become the dominant species (Wang et al., 2010; Xu et al., 2011). Hu et al. (2006) showed that *Chlorella* reduced the N and P concentration in the environment by absorbing them. Therefore, it could be inferred that the growth of *C. vulgaris* changes the N-to-P ratio in a co-culture system to a certain extent. This effect might explain why the competition-inhibition parameters of *C. vulgaris* against *Anabaena* were higher than those of *Anabaena* against *C. vulgaris* in the present study, even when the growth of *C. vulgaris* had been inhibited in treatments 1, 2, 4, 10, 11, 12, 13, and 16. Zhao H. T. et al. (2011) showed that, under non-steady-state conditions, *Microcystis aeruginosa* quickly adopted the dominant position when nutrients were added continuously, but *Scenedesmus obliquus* occupied the dominant position when the nutrient level was low. In

our experiment, the nutrients in the medium were measured and restored to the initial level every 24 h. Under such conditions, the cell density of *Anabaena* was always higher than that of *C. vulgaris*, indicating that *Anabaena* had a greater affinity for nutrients. Zhao X. D. et al. (2011) revealed that under conditions of low N and P concentrations, *M. aeruginosa* became the dominant species. Zhao H. T. et al. (2011) found that *Microcystis* sp. could adapt to low-nutrient conditions by changing cell size. Therefore, it could be inferred that another species of cyanobacteria, namely *Anabaena*, might be able to absorb nutrients and inhibit the growth of *C. vulgaris* by changing cell size according to its cell density and the nutrient concentration in the environment. This would also explain why the competition–inhibition parameters of *Anabaena* against *C. vulgaris* were greater in treatments with lower N and P concentrations.

Competitive Growth of *C. vulgaris* and *Anabaena* in the Co-culture System

According to the algal competition ending described in the Lotka–Volterra competition model (Meng et al., 2012), the relationships between competition–inhibition parameters α , β , and environmental capacities K_c and K_a are shown in Table 5. As shown in Table 5, in treatments 1, 2, 4, 11, 13, and 14, $1/K_a < \alpha/K_c$ and $1/K_c > \beta/K_a$, indicating that *Anabaena* was dominant in the competitions; in treatments 3, 5, 9, 10, 12, 15, and 16, $1/K_c < \beta/K_a$ and $1/K_a < \alpha/K_c$, indicating that *C. vulgaris* and *Anabaena* could coexist, but not stably; in treatments 6, 7, and 8, $1/K_c > \beta/K_a$ and $1/K_a > \alpha/K_c$, indicating that *C. vulgaris* and *Anabaena* could coexist stably (Supplementary Figure S5). The phenomenon in our experiment showed that low phosphorus conditions are good for the victory of *Anabaena* in the competitions, and high phosphorus conditions are beneficial for *C. vulgaris*. Just as *M. aeruginosa*, the other harmful blue-green algae, could become the dominant species under conditions of low

phosphorus concentration by the way of changing cell size to adapt to low-nutrient conditions. So maybe maintain a suitable condition with high phosphorus concentration (no less than 0.1 mg L^{-1}) is useful to promote growth of beneficial algae such as *C. vulgaris* and inhibit growth of harmful algae such as *Anabaena*.

CONCLUSION

The optimal growth conditions for *C. vulgaris* in the mono-culture system were as follows: temperature, 35°C ; light intensity, 660 lx; N concentration, 0.36 mg L^{-1} ; P concentration, 0.1 mg L^{-1} ; and pH, 9.0. The optimal growth conditions for *Anabaena* in the mono-culture system were as follows: temperature, 30°C ; light intensity, 6,600 lx; N concentration, 0.18 mg L^{-1} ; P concentration, 0.1 mg L^{-1} ; and pH, 7.0. The optimal growth conditions for *C. vulgaris* in the co-culture system were as follows: temperature, 25°C ; light intensity, 4,400 lx; N concentration, 0.18 mg L^{-1} ; P concentration, 0.5 mg L^{-1} ; and pH, 6.0. For *Anabaena* in the co-culture system, the optimal growth conditions were as follows: temperature, 35°C ; light intensity, 4,400 lx; N concentration, 0.36 mg L^{-1} ; P concentration, 0.5 mg L^{-1} ; and pH, 6.0. Light was not the most critical factor affecting the growth of *C. vulgaris*, and pH was not the most critical factor affecting the growth of *Anabaena*.

Temperature, light, nutrients, and pH significantly influenced the competition–inhibition parameters of the two algal species. Both competition–inhibition parameters of *Anabaena* against *C. vulgaris* and *C. vulgaris* against *Anabaena* were the highest under the following conditions: temperature, 30°C ; light intensity, 6,600 lx; N concentration, 0.36 mg L^{-1} ; P concentration, 0.025 mg L^{-1} ; and pH, 8.0. According to the Lotka–Volterra competition model, *Anabaena* won in the competition in co-culture system under the following conditions: 1) temperature, 15°C ; light, 660 lx; TN, 0.18 mg L^{-1} ; TP, 0.025 mg L^{-1} ; pH, 6; 2) temperature, 15°C ; light, 2,200 lx; TN, 0.36 mg L^{-1} ; TP, 0.025 mg L^{-1} ; pH, 7; 3) temperature, 15°C ; light, 6,600 lx; TN, 3.6 mg L^{-1} ; TP, 0.5 mg L^{-1} ; pH, 9; 4) temperature, 30°C ; light, 4,400 lx; TN, 0.18 mg L^{-1} ; TP, 0.05 mg L^{-1} ; pH, 9; 5) temperature, 35°C ; light, 660 lx; TN, 3.6 mg L^{-1} ; TP, 0.05 mg L^{-1} ; pH, 8; and 6) temperature, 35°C ; light, 2,200 lx; TN, 0.72 mg L^{-1} ; TP, 0.025 mg L^{-1} ; pH, 9.

TABLE 5 | Parameters of *Chlorella vulgaris* and *Anabaena* sp. strain PCC in Lotka–Volterra Model.

Treatment	$1/K_c$	$1/K_a$	α/K_c	β/K_a
1	0.048	0.036	0.043	0.029
2	0.041	0.030	0.080	0.004
3	0.030	0.020	0.045	0.065
4	0.032	0.029	0.062	-0.004
5	0.013	0.012	0.014	0.017
6	0.016	0.013	0.008	0.007
7	0.020	0.014	0.007	0.003
8	0.017	0.011	0.006	0.008
9	0.016	0.006	0.021	0.018
10	0.016	0.008	0.034	0.017
11	0.014	0.007	0.022	0.005
12	0.016	0.008	0.042	0.044
13	0.014	0.006	0.021	0.010
14	0.013	0.005	0.025	0.009
15	0.014	0.014	0.020	0.074
16	0.019	0.024	0.027	0.059

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/Supplementary Material, further inquiries can be directed to the corresponding authors.

AUTHOR CONTRIBUTIONS

JC, PX, and SM designed the study. SM and XC planned the research activities. SM, XC, and JW performed the study, and collected and analyzed the data. SM wrote the manuscript. LF,

LQ, and YZ revised the manuscript. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fenvs.2021.690191/full#supplementary-material>

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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