

Effects of light intensity and artificial aeration on growth and photosynthetic physiology of marine invasive green alga *Codium fragile* from Bohai Sea, China

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Research Article

Keywords: environmental factors , light intensities , artificial aeration , *Codium fragile* , photosynthetic physiology

Posted Date: August 26th, 2022

DOI: <https://doi.org/10.21203/rs.3.rs-1984458/v1>

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Abstract

Codium fragile has attracted much attention due to its high economic and nutritional values. The light intensity and artificial aeration affect its growth and photosynthetic activity, which in turn affect its economic and nutritional values. The light intensities ($30\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, $60\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, $90\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and aeration regulation are investigated to the effect on the growth and photosynthetic physiology of *C. fragile* collected from the Bohai Sea, China. The results show that different light intensities have a highly significant effect on the maximal photochemical efficiency of PSII(Fv/Fm), photochemical quenching coefficient (qP), and a significant effect on the non-photochemical quenching coefficient (NPQ). They all decreased the least under $60\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. The increase in the relative growth rate(RGR) of *C. fragile* during aeration was greater than that of the non-aeration group. At the same time, the Fv/Fm and qP decreased less than those of the non-aeration group. It shows that the aeration regulation had a highly significant effect on the wet weight, Fv/Fm and qP of *C. fragile*. Among the six groups, only aeration and light intensities of 60 and $90\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ were suitable for the growth of *C. fragile*, because the Fv/Fm decreased less and the qP increased. The result shows that the interaction of the two environmental factors had a significant effect on the Fv/Fm and qP of *C. fragile*, while there was no significant effect on the wet weight and NPQ.

Introduction

The marine invasive green alga *Codium fragile* is composed of a multinucleated tube structure and is widely distributed in intertidal or subtidal zones of tropical and subtropical seas worldwide (Silva 1955). It is noticed for its high nutritional value and becomes a natural health food as its high protein, low fat and low-calorie characteristics in East Asia (Shao 2007). In addition, it has some medical effects such as anti-tumor, detumescence, antipyretic and the destroyer of intestinal parasites (Li 1994; Zhang 2006; Yin 2007). Therefore, international scholars and aquaculture companies have begun to explore its cultivation approach (Pan 1992; Hwang 2005, 2008; Ciancia 2007; Ortiz 2009; Wang 2020).

The growth and development of marine benthic green algae are affected by many environmental factors. In them, some such as temperature, water's movement, and light have been explained separately by previous literatures. However, the combined effect of light intensity and aeration regulation has not been reported. As the main energy source of photosynthetic plants, light intensity is one of the important factors affecting the efficiency of algal photosynthesis (Galmés 2019). *C. fragile* is very sensitive to light intensity (Kenworthy 1996). Its morphogenesis could be observed at a light intensity of $60\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and a water temperature of 10–25°C(Park 1992). However, the effect of light intensities on its photosynthetic properties was not formally reported.

Atmospheric CO₂ concentration has been on the rise in recent years and is predicted up to $550\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ by the middle of the 21st century (Prentice et al. 2001). CO₂ is used as a raw material for photosynthesis by assimilation to satisfy the growth and development of plants (Leakey 2009). When

plants are cultured at high density and grow vigorously, more CO₂ is required. Artificial aeration, as an external CO₂ input approach, will increase the CO₂ flux and dissolved quantity in the water and then affect the growth and development of algae. High CO₂ concentration in water can increase the growth rate of the freshwater green alga (Yang 2001). Whether the approach will affect the growth of *C. fragile* is our concern.

Previous study have shown that *C. fragile* collected in Shantou, Guangdong Province was able to grow in a wide range of light intensities (between 10–120 μmol·m⁻²·s⁻¹) (Wang 2013). However, its antioxidant capacity was reduced at both ends of the range. Changes in environmental factors such as light, temperature, and salinity can also synergistically affect algal photosynthesis (Wang 2013). At the Niantic River estuary, located on Long Island Sound near New London, Connecticut, temperature, and salinity were the main growth-limiting factors, only when the salinity exceeds 27, and the temperature exceeds 16°C, does the highest growth rate of *C. fragile* occurs (Malinowski 1973). It also shows very strong environmental adaptation through changes in reproductive patterns (Wang 2013; Huang and Ding 2016; Ding et al. 2022).

There are some studies on the growth and physiological characteristics of *C. fragile* by light and on the synergistic effects of light and other environmental factors (Hanisak 1979; Ye et al. 2010; Wang 2013; Wei et al. 2021; Ding et al. 2022). However, there are few on the synergistic effects of light and artificial aeration. In recent years, changes in light intensity and atmospheric CO₂ concentration have been reported to seriously affect the physiological and ecological health of algae (Weitzman et al. 2021), which in turn damages the algal culture. Therefore, the effects of light intensities and artificial aeration for the green alga were investigated in this study. To investigate the effects of two environmental factors on the photosynthetic physiology of *C. fragile*, changes in parameters can better reflect the "intrinsic" changes in the algae and the underlying mechanisms of such changes with the help of chlorophyll fluorometry (Demmig-Adams 1996; Zhang 1999). Therefore, changes in chlorophyll fluorescence kinetic parameters can be considered as reference indicators of plant response to different environments (Zhang 2017).

We studied the physiological ecology of this species distributed in Shantou, South China Sea (Wang 2013; Huang and Ding 2016; Ding et al. 2022). In recent years, the pollution of the northern environment causes long-term fog weather, whether they will affect the growth and development of the alga, is still unknown. Therefore, this study uses the samples collected in Qinhuangdao, Bohai Sea to compare the similarities and differences between growth and environmental physiological adaptability. The aim is to try to understand how these two environmental factors effectively regulate its growth process and provide scientific approaches to the culture on different seas of China.

Materials And Methods

Sample collection, processing and temporary cultivation

C. fragile was collected from Shanhaiguan, Qinhuangdao, Hebei Province, China on September 7, 2021. The epiphytes and protozoa were cleaned before the experiment, washed several times with sterilized seawater, and examined microscopically under a dissecting microscope until the surface of the thallus was clean. After that, it was transferred to a 25L culture tank for 3d of temporary artificial aeration. The culture conditions include filtered seawater, salinity 30, water temperature 25°C, an appropriate amount of F/2 formula culture solution, and light intensity $60\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$.

Experimental design

In the experiment, 75 ml of sterilized and filtered seawater was added to a 100 ml triangular conical flask, and the salinity was 30. And the culture solution was added in the ratio of culture solution:seawater=1:1000. Subsequently, a two-factor experimental approach (light and aeration) was used to design experimental groups with a total of six treatments (Table 1). Among them, the light intensity was $30\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, $60\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, $90\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in three groups, and the photoperiod was 12 L:12 D (light hours were 8:00-20:00). Two groups of aeration regulation with a flow rate of 14 L/min and a duration of 24 h in the aeration group and no aeration in the control group. In addition, the culture temperature was 25°C and the culture solution was F/2.

The samples were selected based on the criteria of vigorous growth and full chlorophyll. The branches of the sample were cut into branches of approximately 1cm in length by a scalpel. Each treatment group was randomly placed into three segments and three parallel groups were set up, with a total of 18 replicate groups being created. The incubation process was continuous for one month, with the entire culture solution changed every three days. Wet weight and chlorophyll fluorescence kinetic parameters were measured starting at 8:00 am on the same day.

Table 1

Treatment groups and design

aeration light intensity ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	aeration group (t)	non-aeration group (n)
30(I)	It	In
60(II)	IIIt	IIIn
90(III)	IIIIt	IIIIn

Experimental instruments, equipment and reagents

Electronic balance (accuracy: 0.1mg, model: FA1004, manufacturer: Hua Chao Hi-Tech), PAM (model: DUAL-PAM/F, manufacturer: WALZ)

Reagents: F/2 culture solution, sterilized seawater with salinity 30

Measurement methods

Measurement of relative growth rate (RGR): Absorbent paper was used to absorb water from the surface of the algae, and the fresh weight of the algae was measured accurately with an electronic balance. The RGR of spiny pine algae was calculated according to the following equation:

$$RGR\%d^{-1} = \frac{\ln W_1 - \ln W_t}{\Delta t} * 100\%$$

W1 is the initial fresh weight, Wt is the fresh weight after t days.

Measurement of chlorophyll fluorescence kinetic parameters: The maximal photochemical efficiency of PSII (Fv/Fm), photochemical quenching coefficient (qP), and non-photochemical quenching coefficient (NPQ) of PSII were determined by the PAM modulation fluorescence measurement system. They each reflect the potential maximal photosynthetic capacity, photosynthetic activity, and photoprotective capacity of the plant.

Statistics and analysis

Experimental data were processed by T-test as well as two-factor ANOVA, with $P < 0.05$; graphs were made using GraphPad prism.

Results

Growth and photosynthetic physiology changes of *C. fragile* under light intensities

Growth in *C. fragile* under light intensities

The growth curves of *C. fragile* under three light intensities culture conditions are shown in Figure 1.

According to Figure 1, the RGR of *C. fragile* first increased and then decreased when the light intensity was increased from I to III, but the change in RGR trend was not significant. The light intensity when the RGR was maximal was group II. In conclusion, low light intensity (I) was more favorable to the growth in *C. fragile* than high light intensity (III).

Fv/Fm in *C. fragile* under light intensities

As shown in Figure 2, Fv/Fm values of *C. fragile* decreased under all three light conditions, but the downward trend at low light intensity was slower. When the light intensity was increased to III, the decrease in Fv/Fm was the most significant and the fluctuation was large, especially between the 9th and 12th day was extremely significant. The analysis showed that there was a significant difference between group III and groups I and II.

qP and NPQ in *C. fragile* under light intensities

As can be seen from Figure 3, qP curves varied differently for the three light conditions, but all showed a decreasing trend. Among them, the decrease in group I was 27.7%, while the decrease in group II was smaller at 2.9%. When the light intensity rose to III, the qP curve showed dramatic fluctuations, with distinct peaks and valleys several times, especially the highest measured value at day 12, but the overall showed a smooth downward trend.

According to Figure 4, NPQ showed an overall decreasing trend under the three light conditions, but with some degree of fluctuation. The greatest decrease in NPQ was observed in group I, with 50.7%, and the smallest decrease in group II, with 23.1%. However, the lowest point of NPQ was in group III, which was measured on the third day.

Growth and photosynthetic physiology in *C. fragile* under aeration regulation

Growth in *C. fragile* under aeration regulation

In this experiment, the airflow when artificially aerated for 24 hours was 14 L/min. The wet weight of *C. fragile* was obtained by calculating the average value of each group. Based on Figure 5, it can be seen that the group t grew well, with an increasing trend of fresh weight from 0.1093g to 0.3941g, with a RGR of 1.05%. Group n showed a trend of increasing and then decreasing fresh weight from 0.1113g to 0.1787g and then to 0.1205g, with a RGR of 0.03%. Analysis of Figure 6 shows that there is a significant difference between the effect of artificial aeration and non-aeration on the growth of *C. fragile*.

Fv/Fm in *C. fragile* under aeration regulation

The Fv/Fm of *C. fragile* was affected by artificial aeration or not, as shown in Figure 7. Fv/Fm showed a decreasing trend in both conditions, but the decrease in group t was smaller than that in group n, with a decrease of 11.8% in group t and 14.4% in group n.

qP and NPQ in *C. fragile* under aeration regulation

Figure 8 and Figure 9 show that the qP and the NPQ in *C. fragile* were affected by artificial aeration.

The qP in the group t showed an increasing trend, with an increase at 14.1%. qP curves in the group n fluctuated but showed a decreasing trend overall, with a decrease of 37.4%.

With or without aeration, their NPQ was affected to a certain decrease, 22.1% in the group t and 50.3% in the group n.

Growth and photosynthetic physiology in *C. fragile* under light intensities and aeration regulation

Growth in *C. fragile* under light intensities and aeration regulation

As can be seen from Figure 10, the RGR of group t was better than that of group n at all light intensities. The group It had the best RGR of 1.241%. When aeration was applied, or when the light intensity decreased, the RGR increase was decreasing. When aeration was not applied, the increase in RGR decreased or even became negative when the light intensity was increased.

Fv/Fm in *C. fragile* under light intensities and aeration regulation

Figure 11 shows that the Fv/Fm of all six groups decreased to different degrees under the combined conditions. Among them, the decrease in Fv/Fm was greater in group n compared to group t, and there was a highly significant difference between them ($P < 0.01$). Among the three groups, the decrease in Fv/Fm was the smallest in group II, which was not related to the presence or absence of artificial aeration. The decrease in the Fv/Fm of group III was greater than that of group I.

qP and NPQ in *C. fragile* under light intensities and aeration regulation

As shown in Figure 12, the qP increased in the groups It and IIIt and decreased in the rest of the groups to different degrees. Among them, the decrease of qP was the largest in the group In, and the decrease of qP showed a trend of decreasing and then increasing as the light intensity was gradually increased. The increase in qP was the greatest in group IIIt, reflecting the greatest opening of the PSII reaction center at this time, but the increase in qP decreased as the light intensity was reduced.

As shown in Figure 13, under different light intensities and with or without artificial aeration, the NPQ of all six groups (It, IIIt, IIIt, In, IIIn, IIIn) decreased to different degrees, unlike qP. Among them, the largest

decrease was in the group In, where the NPQ value decreased from 0.129 to 0.043, a decrease of 66.7%. The smallest decrease in NPQ was observed in group II with or without aeration.

Discussion

Changes in the growth and photosynthetic physiology in *C. fragile* under light intensity

The RGR in *C. fragile* was affected by light intensity to produce different changes, in the light intensity range of $30\text{--}90\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, as the light intensity was enhanced, it showed a trend of first increasing and then decreasing. The RGR of group II was the largest, while the Fv/Fm, qP, and NPQ all decreased the least, indicating that the photosynthetic mechanism was the least damaged and the photosynthetic activity was the highest. It can be seen that among the three light intensities, the light intensity of $60\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ was indeed the most suitable for the growth of *C. fragile*.

The Fv/Fm and qP of *C. fragile* show a decrease in light intensities, a phenomenon that is relatively common and occurs in conifers, oleander seedlings, *Arabidopsis thaliana*, and other plants (He 2006; Shi 2018; Carvalho 2015). In this experiment, the greatest decrease in Fv/Fm was observed in group III, indicating that the photosynthetic mechanism of *C. fragile* was most severely damaged and stressed at this time. qP decreased the most in group I, indicating that its photosynthetic activity was the worst at this time. It means that the light environment of both group III and the group I are not suitable for its growth.

The NPQ is the portion of absorbed light energy that cannot be used for photosynthetic electron transfer and is dissipated in the form of heat, reflecting the photoprotective capacity of the plant. Its variation in this experiment is different from the results of previous studies. It was reported that NPQ of *C. fragile* were affected by light intensities with different degrees of increase (Wang 2013), but in this experiment, the NPQ all had different degrees of decrease, with the smallest decrease in group II. It indicated that the ability of *C. fragile* to dissipate excess light energy was the best among the three groups, and the photosynthetic mechanism was the least damaged. The difference in the results of the two studies was considered, and we speculate that this difference reflects some extent the different adaptations of the southern and northern *C. fragile* to light intensity, but the deeper reasons need to be further explored.

Changes in the growth and photosynthetic physiology in *C. fragile* under aeration regulation

In this experiment, the Fv/Fm, qP, and NPQ decreased less in group t than in group n, which is consistent with the change in their RGR, indicating that the non-aeration is a stressful environment for *C. fragile*.

The RGR rose more in group t and less in group n, which is consistent with the growth of cotton seedlings in higher plants (Qi 2016). The decrease in the photosynthetic capacity of plants during artificial aeration may be a phenomenon of photosynthetic adaptation to CO₂ (Gunderson 1994). This phenomenon is currently found in ryegrass, winter wheat, rice, and other crops (Ainsworth et al. 2003; Liao 2002, 2003), where high concentrations of CO₂ cause a large accumulation of carbohydrates in the plant, resulting in

feedback inhibition of photosynthesis, leading to a decrease in photosynthetic rate (Rogers 2004; Delucia 1985). The qP of soybean leaves showed a decreasing trend after the increase of CO₂ concentration (Wang 2015), which is not consistent with the results of this experiment and was analyzed probably because the artificial aeration was to some extent conducive to the nutrient uptake by the *C. fragile* for better growth, thus increasing the photosynthetic activity of the plant.

Changes in growth and photosynthetic physiology in *C. fragile* under different light intensities and aeration regulation

This experiment investigated whether the effect of artificial aeration and light intensities on the growth of *C. fragile*, the plant yield was more significantly affected by enhanced CO₂ concentration when the light was stronger (STITT 1991). The RGR of *C. fragile* were all increased when being artificially aerated, which is consistent with the results of a study on *Spirulina maxima* (Xia 2001), where the RGR rise was significantly greater at high light intensities and less at low light intensities. Chlorophyll fluorometry measurements showed that the largest differences in half-saturation light intensity I_k between photosystem II and photosystem I among the six treatment groups were in the groups II_n and III_n, with more than three times the difference, and also only these two groups had negative relative growth rates. The smaller differences in half-saturation light intensity I_k between photosystem II and photosystem I were in the two groups II_t and III_t, with a difference of three times and less, but their relative growth rates were positive. This indicates that in this experiment, even the presence of cyclic electron transport in the absence of artificial aeration could not moderate the damage caused by high light intensity to the *C. fragile*.

The Fv/Fm decreased to different degrees in all six treatment groups, but the decrease was most pronounced in the group n. The group II_t had the lowest decrease in Fv/Fm. When no environmental stress was present, the change in Fv/Fm was small (Xu 1992), indicating that the absence of artificial aeration is environmental stress on the growth of *C. fragile*. Only the qP increased in the groups II_t and III_t, indicating that the photosynthetic machinery was least damaged and suitable for its growth under these two environmental conditions.

The NPQ reflects the strength of the photoprotective ability of plants (Xu 1990). The decrease of NPQ of the groups t was all smaller than that of the groups n. When artificially aerated and at low light intensities, the NPQ showed the smallest decreasing trend, indicating the strongest photoprotection capacity under this condition. However, the non-aeration and high light intensity are destructive to the photoprotective ability of *C. fragile*.

In summary, the presence of artificial aeration regulation can make the *C. fragile* better adapted to high light intensity, and moderate the damage of light intensity stress on its growth and photosynthetic physiology. However, the mechanisms of the interactive effects of changes in atmospheric light intensity and the introduction of artificial airflow on the photosynthetic physiology of *C. fragile* need to be

understood in greater depth in the future, to cope with future changes in the growth of *C. fragile* under complex environmental changes.

Declarations

Acknowledgements Special thanks to Wang XueCong, Yan PanZhu, Qin JiaNan at Tianjin Normal University for their support during the study.

Funding This study was financially supported by the National Natural Science Foundation of China, grant numbers 31970216.

Data availability The data are available from the authors upon reasonable request.

Conflict of interest The authors declare no competing interests.

Author Contributions

All authors contributed to the study, with conceptualization by Bingxin Huang, methodology by Lanping Ding and Bingxin Huang, formal analysis and investigation by Lanping Ding, Jing Yan, Yao Zhang, Bingxin Huang, Junxia Liang, Youxuan Guo and Yue Chu, experimental process by Lanping Ding, Jing Yan, Yao Zhang, Bingxin Huang, Junxia Liang and Youxuan Guo, writing - original draft preparation by Lanping Ding, Jing Yan and Bingxin Huang, Writing - review and editing by Lanping Ding, Jing Yan, Bingxin Huang and Yue Chu, funding acquisition by Lanping Ding and Bingxin Huang, resources by Lanping Ding and Bingxin Huang, and supervision by Lanping Ding and Bingxin Huang, respectively.

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Figures

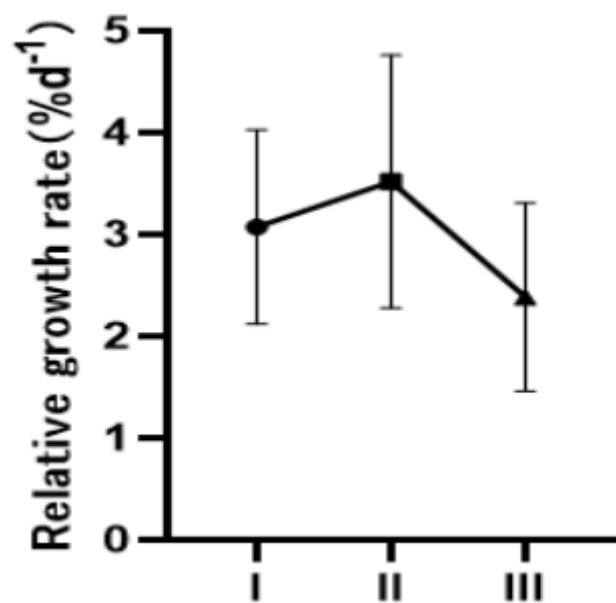


Figure 1

Growth in *C. fragile* under light intensities

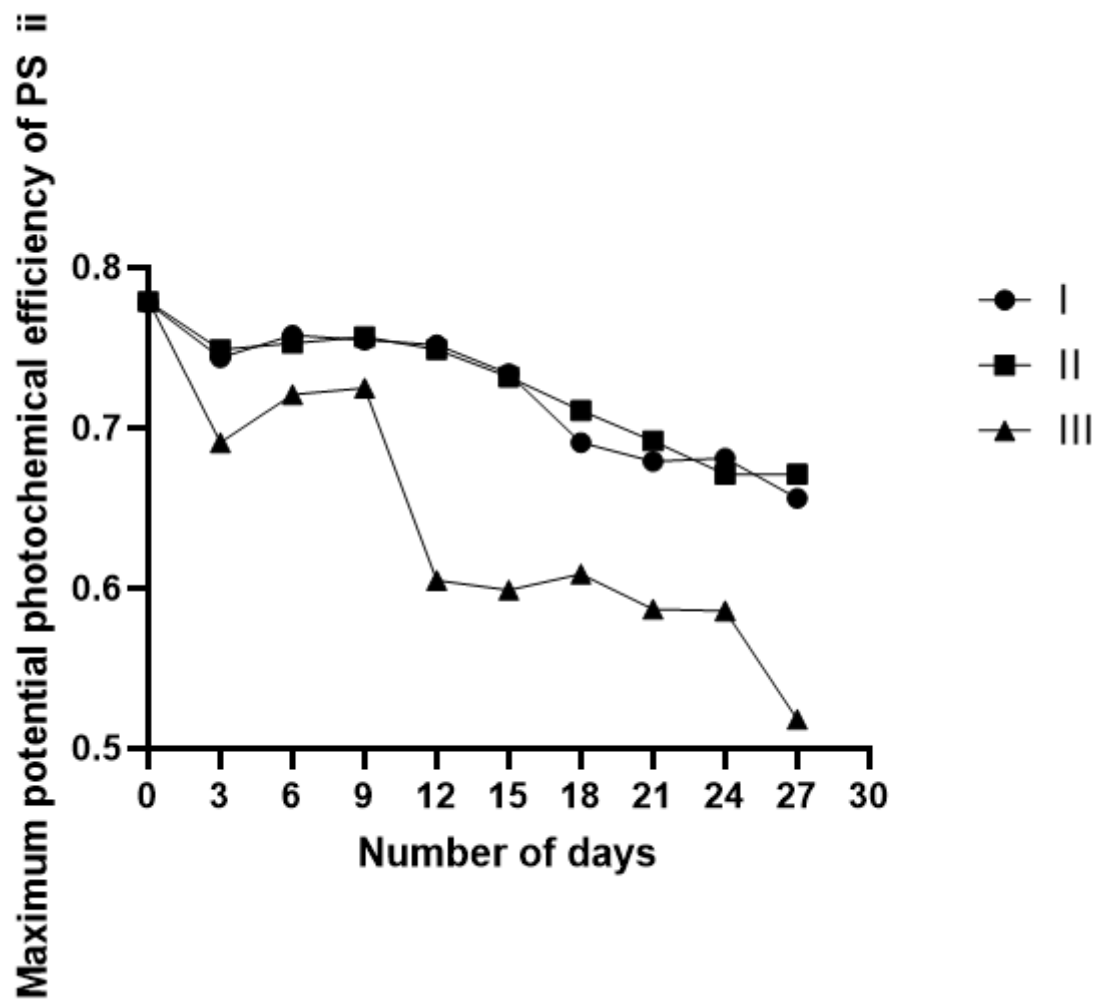


Figure 2

Variation curve of PSII F_v/F_m in *C. fragile* under light intensities

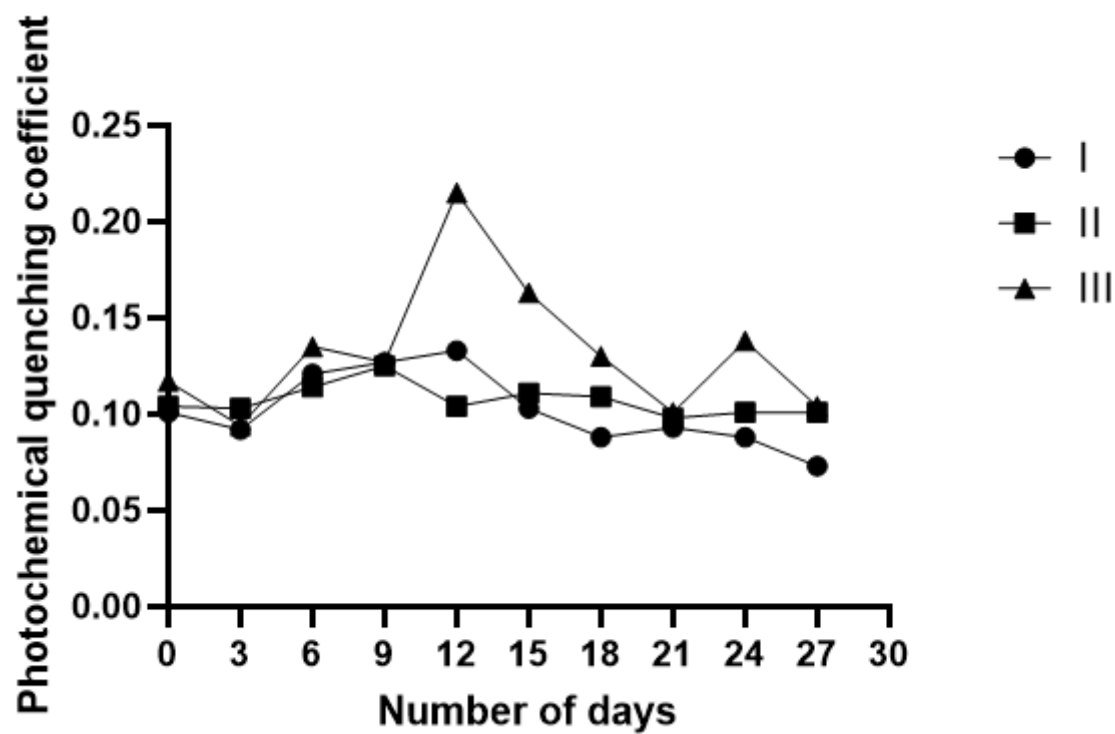


Figure 3

Variation curve of qP in *C. fragile* under light intensities

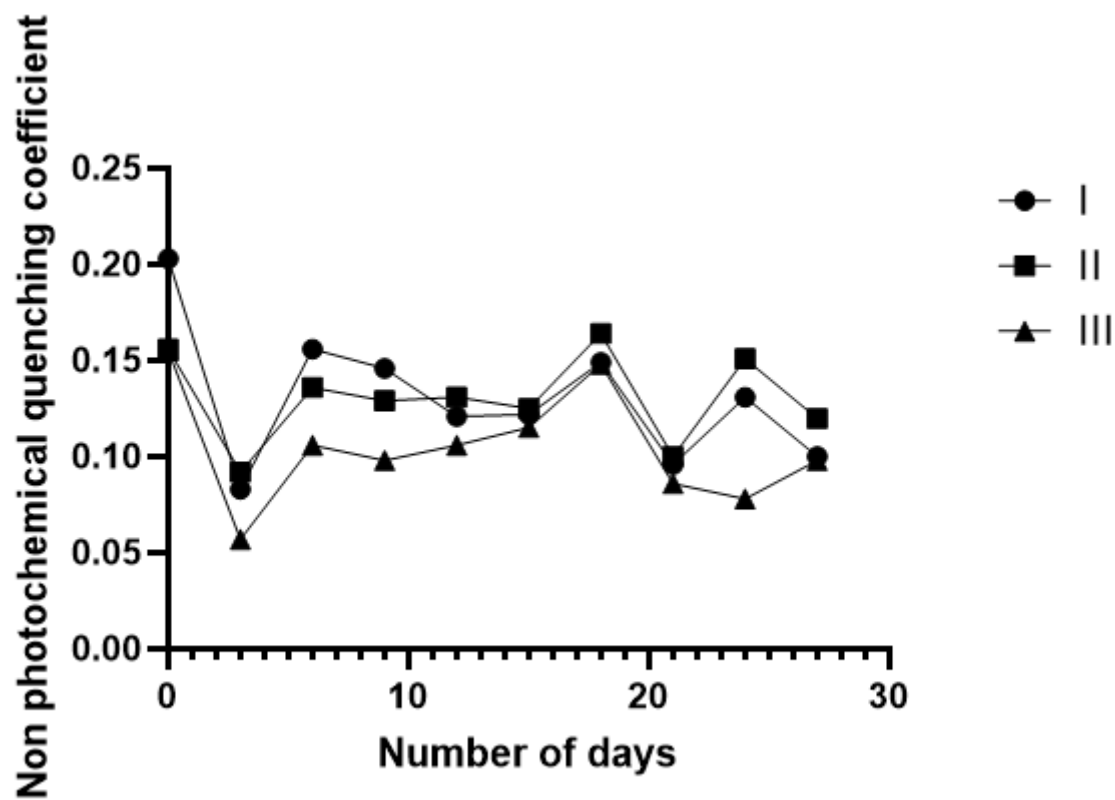


Figure 4

Variation curve of NPQ in *C. fragile* under light intensities

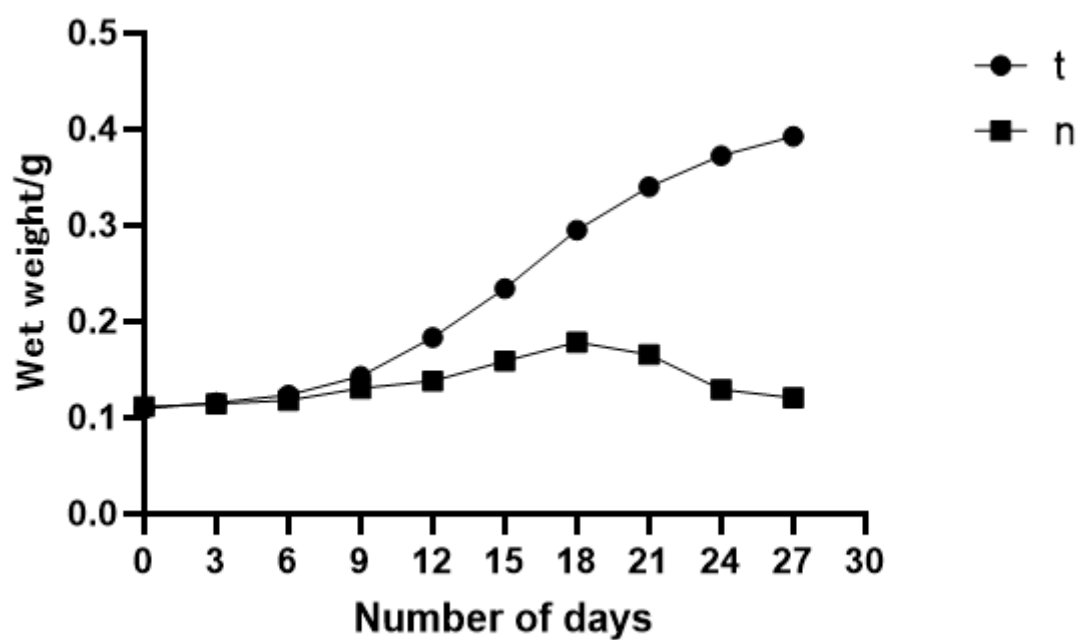


Figure 5

Variation curve of growth in *C. fragile* under aeration regulation

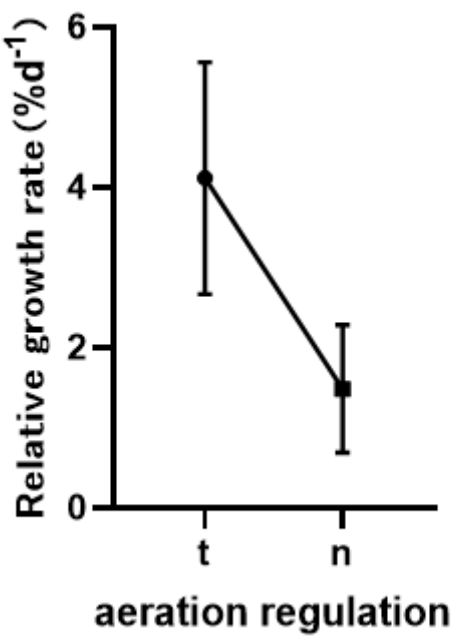


Figure 6

RGR in *C. fragile* under aeration regulation

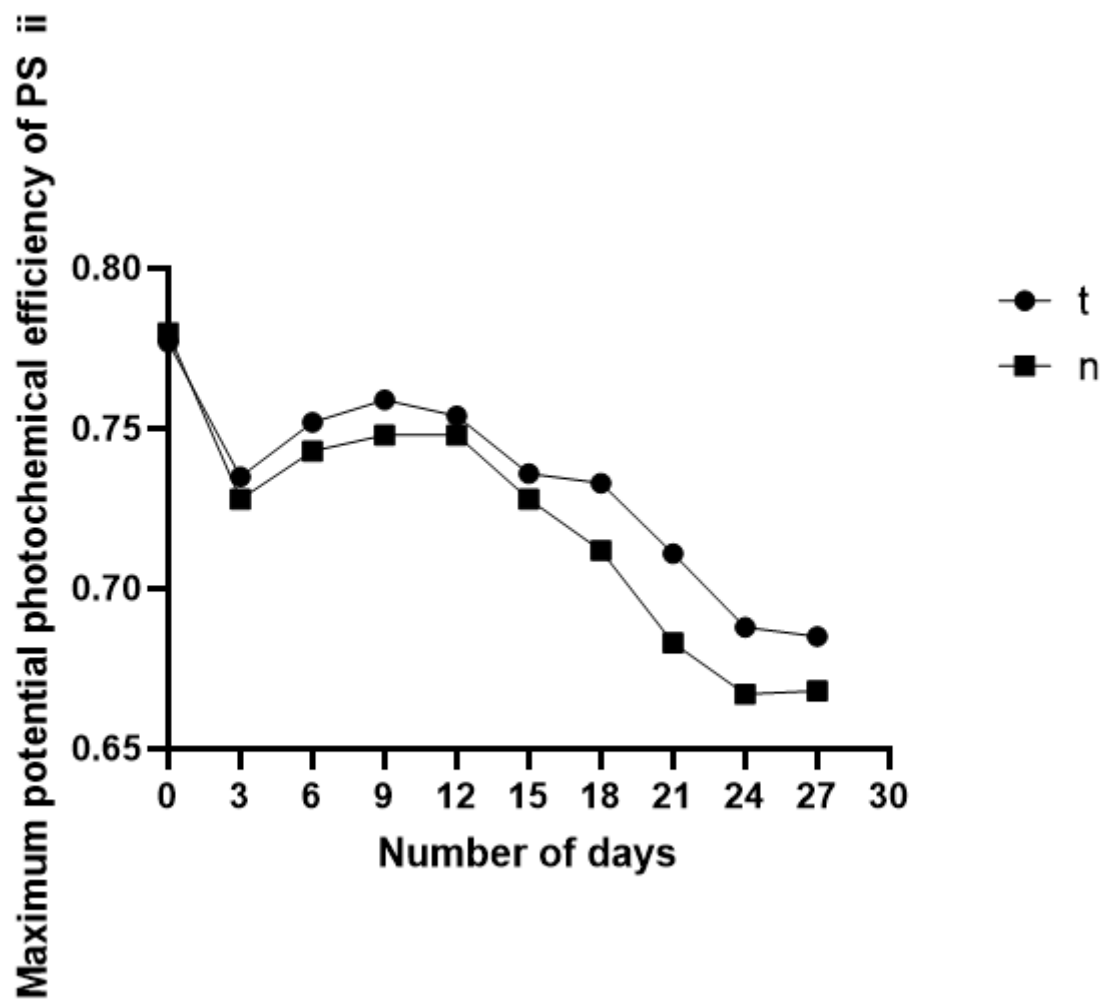


Figure 7

Variation curve of PSII Fv/Fm in *C. fragile* under aeration regulation

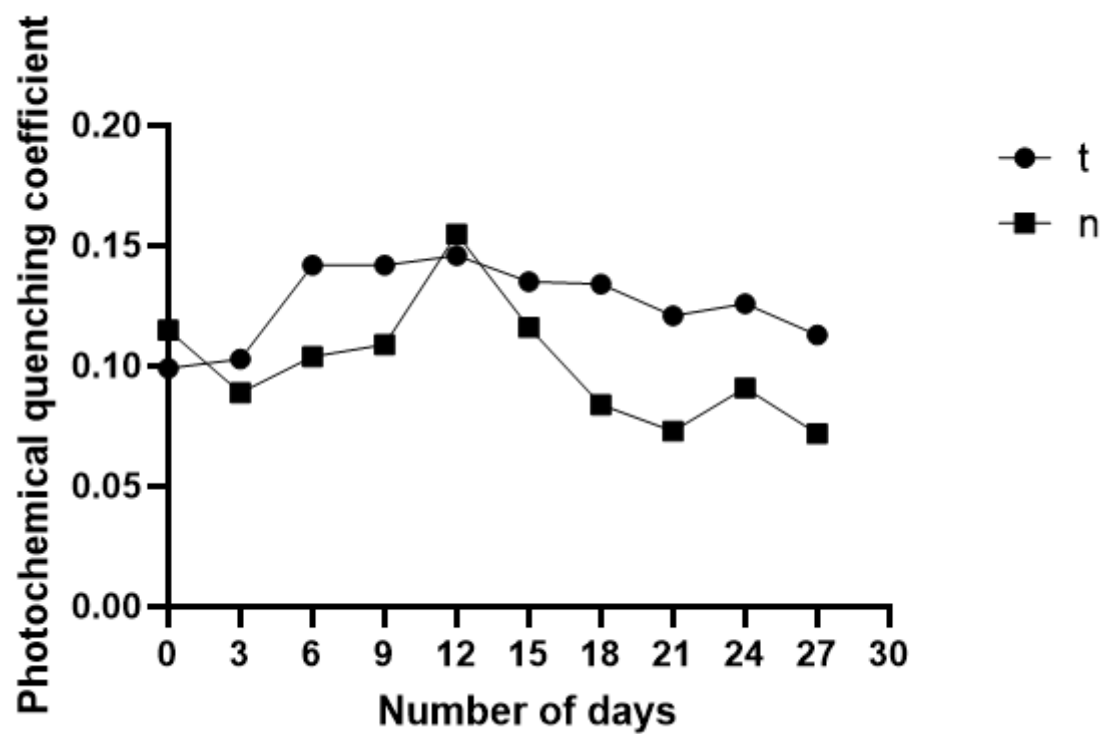


Figure 8

Variation curve of qP in *C. fragile* under aeration regulation

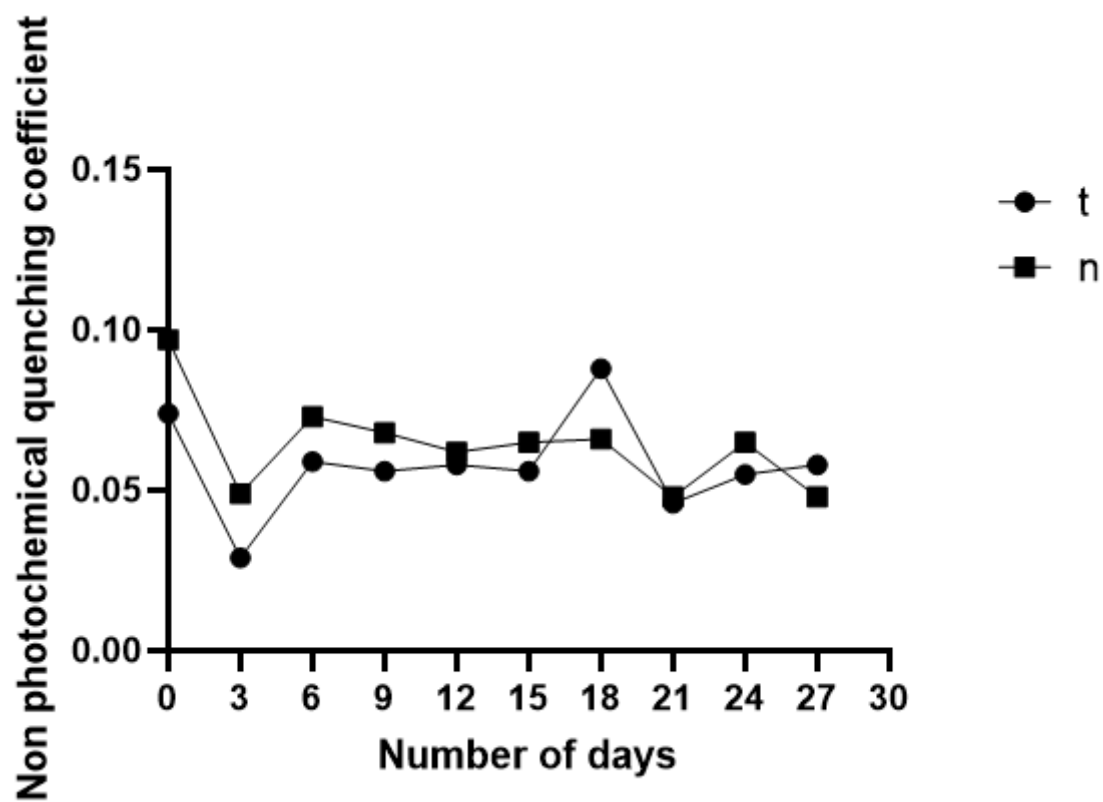


Figure 9

Variation curve of NPQ in *C. fragile* under aeration regulation

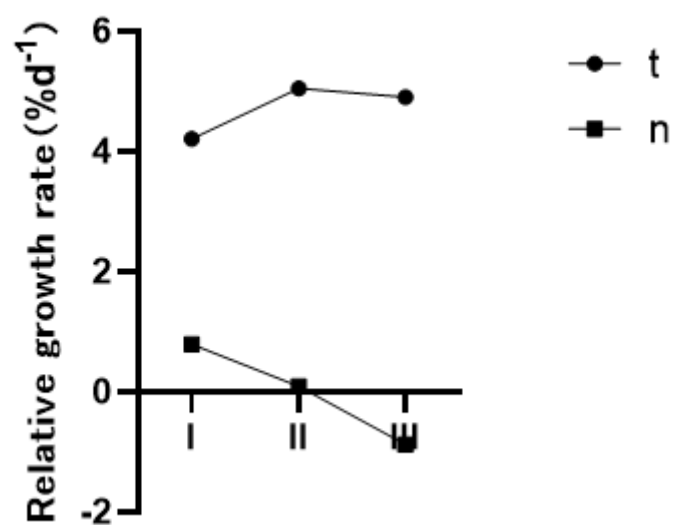


Figure 10

RGR in *C. fragile* under light intensities and aeration regulation

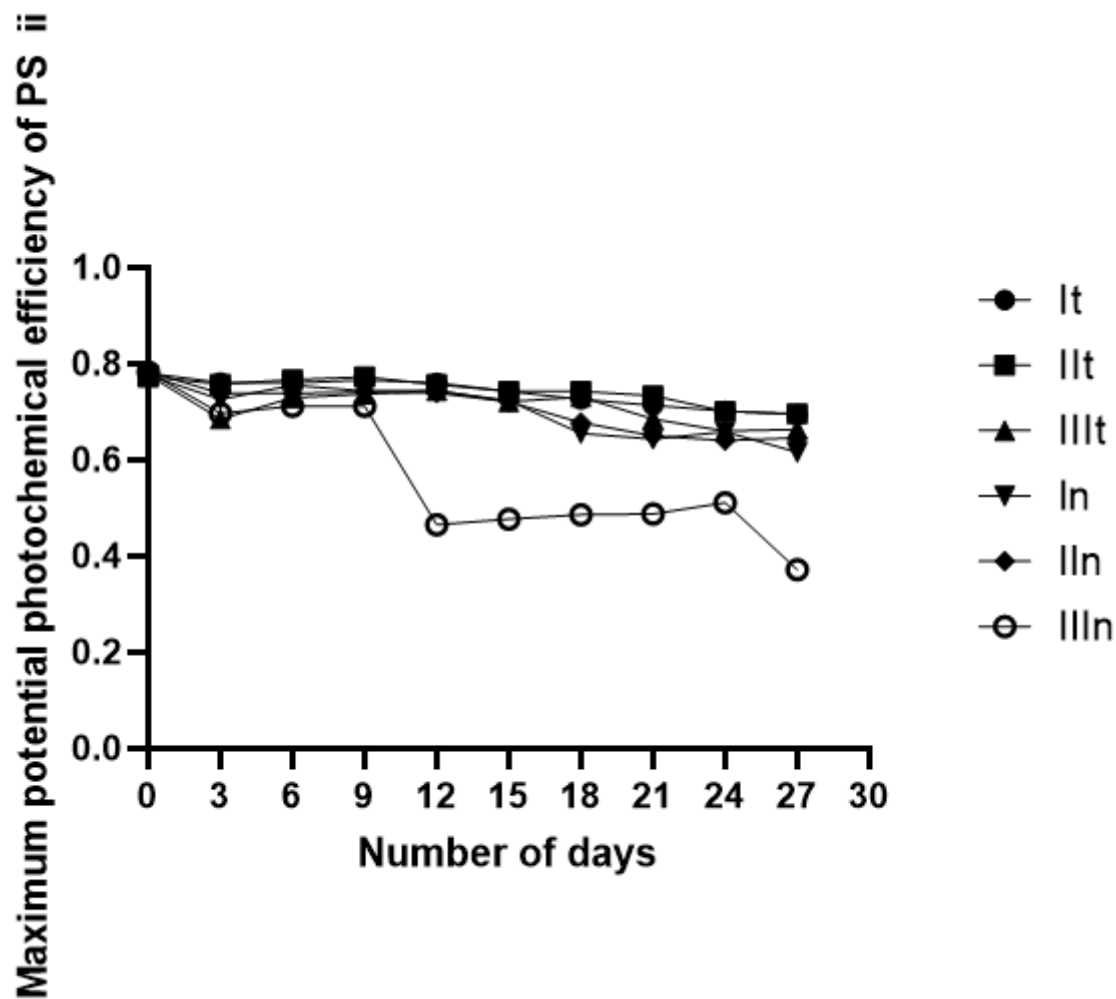


Figure 11

Variation curve of Fv/Fm in *C. fragile* under light intensities and aeration regulation

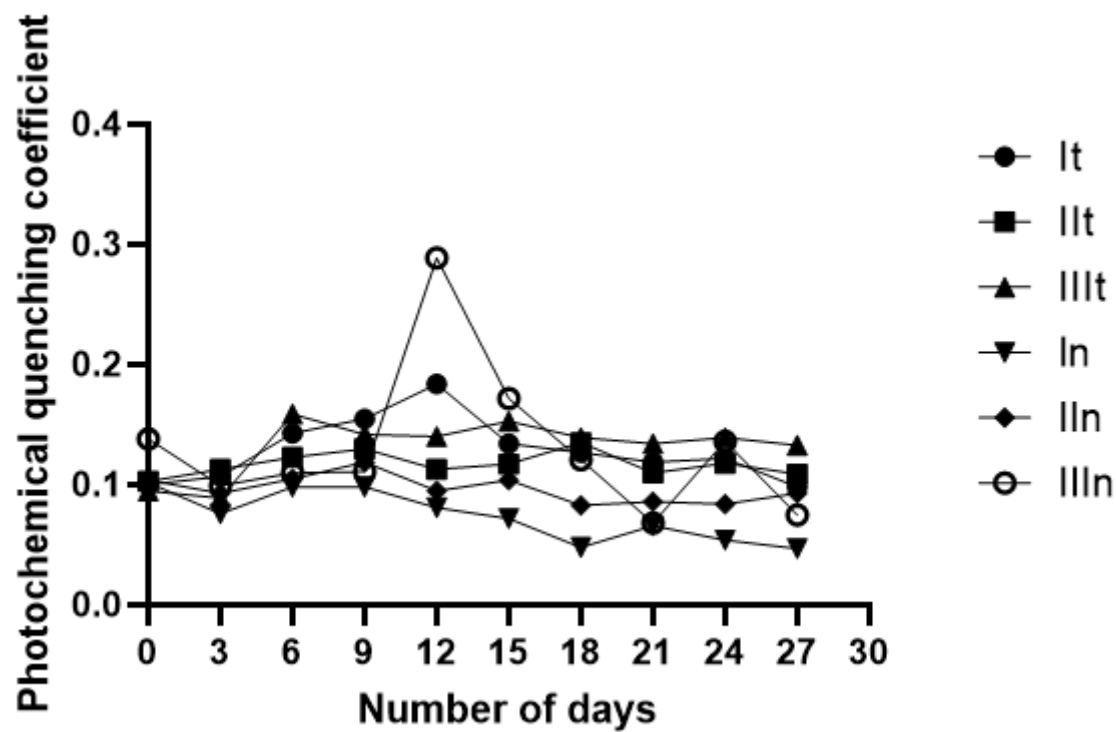


Figure 12

Variation curve of qP in *C. fragile* under light intensities and aeration regulation

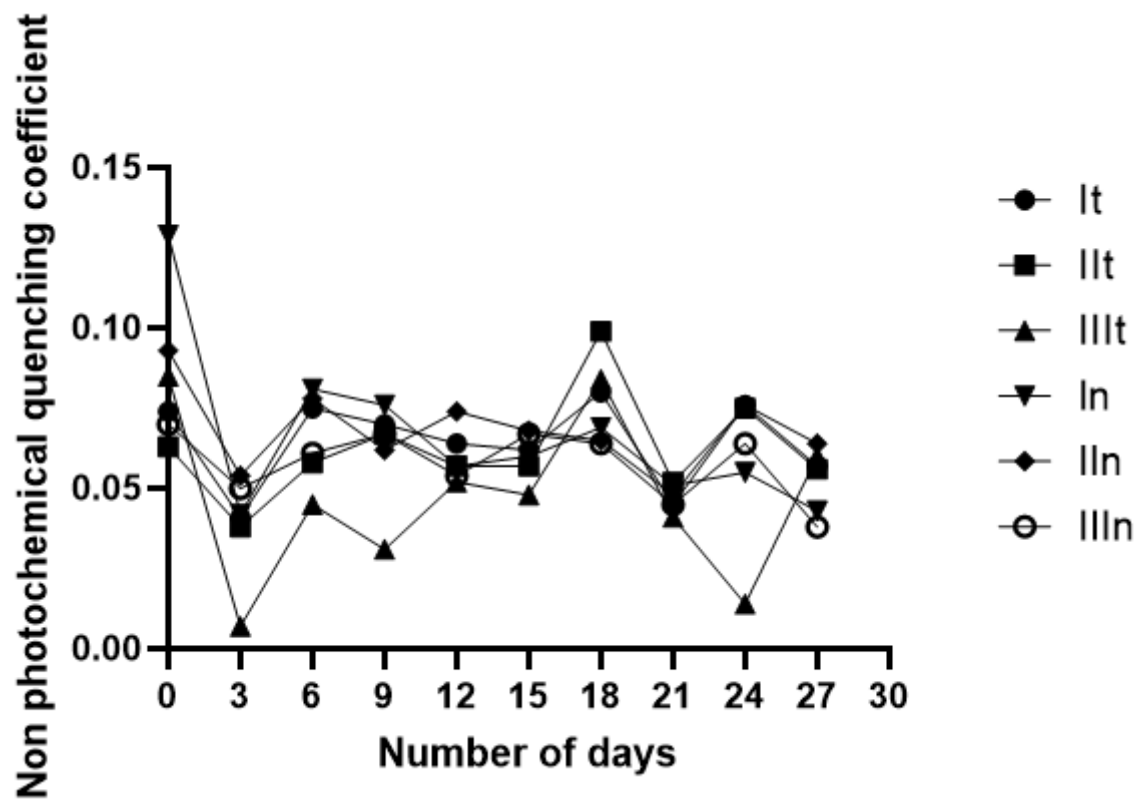


Figure 13

Variation curve of NPQ in *C. fragile* under light intensities and aeration regulation