Research Article

Changes of Photosynthetic Behaviors in Kappaphycus alvarezii Infected by Epiphyte

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Epiphytic filamentous algae (EFA) were noted as a serious problem to reduce the production and quality of K. alvarezii. The morphological studies revealed that the main epiphyte on K. alvarezii was Neosiphonia savatieri in China. Though the harmful effects of EFA on the production of K. alvarezii have been reported, the detailed mechanism of the N. savatieri in limiting the production of K. alvarezii has not been studied yet. The present paper studied the effects of N. savatieri infection on photosynthetic behaviors in K. alvarezii by detecting chlorophyll fluorescence transient in vivo. The results revealed that damage of oxygen-evolving complex (OEC), decrease of active reaction centers (RCs), and the plastoquinone (PQ) pool as well as significant reduction in the performance indexes (PI) of PSII were caused by the infection of N. savatieri. The influence of N. savatieri on photosynthetic activity of K. alvarezii should be one of the important reasons to reduce the production of K. alvarezii infected by N. savatieri.

1. Introduction

Kappaphycus alvarezii (Solieriaaceae, Rhodophyta) have been farmed as raw materials for carrageenan production in many countries since 1970s [1]. However, the carrageenan industry was faced with raw material problems relating to quality and quantity [2]. Epiphyte infection was one of the main reasons causing the decrease of quality and quantity of raw materials.

Epiphytic filamentous algae (EFA) were noted as a serious problem to reduce the production and quality of K. alvarezii. The morphological studies revealed that the main epiphyte on K. alvarezii was Neosiphonia savatieri in China. Though the harmful effects of EFA on the production of K. alvarezii have been reported, the detailed mechanism of the N. savatieri in limiting the production of K. alvarezii has not been studied yet. The present paper studied the effects of N. savatieri infection on photosynthetic behaviors in K. alvarezii by detecting chlorophyll fluorescence transient in vivo. The results revealed that damage of oxygen-evolving complex (OEC), decrease of active reaction centers (RCs), and the plastoquinone (PQ) pool as well as significant reduction in the performance indexes (PI) of PSII were caused by the infection of N. savatieri. The influence of N. savatieri on photosynthetic activity of K. alvarezii should be one of the important reasons to reduce the production of K. alvarezii infected by N. savatieri.
2. Materials and Methods

2.1. Materials. Both infected and healthy green K. alvarezii were collected from Lian Bay, Hainan province, China (18°27'N, 110°5'E). Detritus on the materials were cleaned by seawater. Sections and dominant epiphytes were removed by a razor blade and then transferred to microscope slides. Slides were viewed at 100x magnification under optical microscope. Images were taken using an attached Cannon digital camera to investigate the morphological characters of epiphyte.

EFA-infected green K. alvarezii were precleaned with a soft brush to remove all the epiphytes and contaminants and then brought to our laboratory beside the bay accompanied with the healthy ones to carry out the physiological studies.

2.2. Chl a Fluorescence Measurement. Algal thalli, about 3-4 mm in diameter and 3 cm in length, were selected, respectively, from infected and healthy green K. alvarezii. Each thallus was transferred into one capped transparent glass vial filled with seawater, and subsequently the vial was incubated at room temperature in darkness for 15 min. Chl a fluorescence of dark-adapted sample was measured by a plant efficiency analyzer (Handy PEA, Hansatech UK) and a single vial adapter for liquid-phase samples (HPEA/LPA2 Hansatech, UK). Red light of 650 nm wavelength (1500 μmol m⁻² s⁻¹) was continuously provided for 1 s. The fluorescence transients were recorded in a time span from 10 μs to 1 s. For the first 300 μs, fluorescence was sampled at 10 μs intervals. The time resolution of digitization was then switched to slower acquisition rates as the kinetics of the fluorescence signal slow. Each group of experiments was done for four times.

2.3. Analysis of OJIP Chl a Fluorescence Induction Transient. Each transient was analyzed according to JIP-test [15–18] by utilizing the following data: the minimal fluorescence intensity (F₀) when all RCs are open, the maximal fluorescence intensity (Fₘ), assuming that excitation intensity is high enough to close all the RCs of PSII, and the fluorescence intensities at times 300 μs (Fₓ), 2 ms (Fᵧ), and 30 ms (Fᵧ). Based on the above data, the following parameters were then calculated: the relative variable fluorescence intensity at the J-step, Vⱡ ≡ (F₁ - F₀)/(Fₘ - F₀); the relative variable fluorescence intensity at the K-step, Vₖ ≡ (Fₖ - F₀)/(Fₘ - F₀); the approximated initial slope of the fluorescence transient, M₀ ≡ 4(Fₓ - F₀)/(Fₘ - F₀); the total complementary area above the O-J-I-P transient, Area = \int_{t₀}^{tₚ} (Fₘ - F₁) dt.

The normalized total complementary area above the O-J-I-P transient (reflecting single-turnover QA reduction events) is Sₘ = (Area)/(Fₘ - F₀); the times of QA have been reduced to Qₐ⁻ in the time span from t₀ to tₚ, N = Sₘ × M₀ × (1/V₁).

The maximum quantum yield of primary photochemistry is \( \varphi_{P₀} = TR_G/ABS = [1 - (F₀/Fₘ)] \); the probability that a trapped exciton moves an electron into the electron transport chain beyond Qₐ⁻ is \( \psi_O ≡ ET_O/TR_O = (1 - V₁/F₁) \); the quantum yield for electron transport is \( \varphi_{E₀} ≡ ET_O/ABS = [1 - (F₀/Fₘ)] \times \psi_O \).

The specific energy fluxes (per Qₐ⁻ reducing PSI2 reaction center (RC)) for the energy absorbed is ABS/RC = M₀ × (1/V₁) × (1/\varphi_{P₀}); the energy trapped is TR₂/RC = M₀ × (1/V₁); the electron transported is ET₂/RC = ET₀/RC × M₀ × (1/V₁) × \( \psi_O \); and the energy dissipated is DI₂/RC = (ABS/RC) - (TR₂/RC).

Phenomenological energy fluxes (per excited cross-section (CS)) for absorption (ABS/CS), trapping (TR₂/CS), electron transport (ET₂/CS), and dissipation (DI₂/CS) were calculated by the following equations: ABS/CS₀ = F₀ (at \( t = t₀ \)); ABS/CSₘ = Fₘ (at \( t = t_{Fₘ} \)); TR₂/CS₀ = \( \varphi_{P₀} \times (ABS/CS₀) \) (at \( t = t₀ \)); TR₂/CSₘ = \( \varphi_{P₀} \times (ABS/CSₘ) \) (at \( t = t_{Fₘ} \)); ET₂/CS₀ = \( \varphi_{E₀} \times (ABS/CS₀) \) (at \( t = t₀ \)); ET₂/CSₘ = \( \varphi_{E₀} \times (ABS/CSₘ) \) (at \( t = t_{Fₘ} \)); DI₂/CS₀ = (ABS/CS₀) - (TR₂/CS₀) (at \( t = t₀ \)); DI₂/CSₘ = (ABS/CSₘ) - (TR₂/CSₘ) (at \( t = t_{Fₘ} \)).

The density of reaction centers per exited cross-section was computed by the equations below: RC/CS₀ = \( \varphi_{P₀} \times (V₁/M₀) \times (ABS/CS₀) \) (at \( t = t₀ \)); RC/CSₘ = \( \varphi_{P₀} \times (V₁/M₀) \times (ABS/CSₘ) \) (at \( t = t_{Fₘ} \)).

The performance indexes for absorption (PI_ABS) and per excited cross-section (PI_CS) were calculated as follows: PI_ABS = (RC/ABS) × \( \varphi_{P₀} \times (V₁/M₀) \times (ABS/CS₀) \) (at \( t = t₀ \)); PI_ASSIGN = (RC/CS₀) × \( \varphi_{P₀}/(1 - \varphi_{P₀}) \) × \( \varphi_{E₀}/(1 - \varphi_{E₀}) \) (at \( t = t₀ \)); PI_ASSIGN = (RC/CSₘ) × \( \varphi_{P₀}/(1 - \varphi_{P₀}) \) × \( \varphi_{E₀}/(1 - \varphi_{E₀}) \) (at \( t = t_{Fₘ} \)).

2.4. Chlorophyll a Measurement. Cleaned algal thalli, 3-4 mm in diameter and 0.5 g fresh weight, were selected, respectively, from infected and healthy green K. alvarezii. The thalli were homogenized in 5 mL of 95% ethanol for 15 min then were centrifuged at 1000 rpm for 5 min. After centrifugation, 4 mL supernatant was transferred into a colorimetric tube and diluted to 25 mL with 95% ethanol. Absorbance was measured by 722 s spectrophotometer (Shanghai precision & scientific instrument CO., LTD) at 665 nm and 649 nm. Each group of experiments was done for 3 times. Pigment concentration was calculated according to Wintermans and de Mots [19],

\[
\text{Chl a (μg/g)} = \frac{(13.70D_{665} - 5.76D_{649}) \times \text{dilution rate}}{0.5g}.
\]

2.5. Phycobiliprotein Measurement. Cleaned algal thalli, 3-4 mm in diameter and 0.5 g fresh weight, were selected, respectively, from infected and healthy green K. alvarezii. The thalli were chopped into 3 mm⁴ and then homogenized in 3 mL of 10 mM CaCl₂ solution, which was stocked in 4°C for 12 hours prior to the experiment, for 15 min. Subsequently,
the homogenized solution was transferred into a colorimetric tube then diluted to 25 mL with 10 mM CaCl₂. After that, the colorimetric tubes were incubated at 4°C in dark for 48 hours. Absorbance of the supernatant at 562 nm, 615 nm, and 652 nm was measured by 722 s spectrophotometer. Each group of experiments was done for 3 times. Phycobiliproteins were calculated according to Venkataraman [20] as below:

\[
\text{Phycocyanin (PC)(mg/g)} = \frac{(\text{OD}_{615\text{nm}} - 0.474\text{OD}_{652\text{nm}})}{5.34} \times \frac{\text{dilution rate}}{0.5\text{ g}},
\]

\[
\text{Phycoerythrin (PE)(mg/g)} = \frac{(\text{OD}_{562\text{nm}} - 2.41\text{PC} - 0.849\text{APC})}{9.62} \times \frac{\text{dilution rate}}{0.5\text{ g}},
\]

\[
\text{Allophycocyanin (APC)(mg/g)} = \frac{(\text{OD}_{562\text{nm}} - 0.208\text{OD}_{615\text{nm}})}{5.09} \times \frac{\text{dilution rate}}{0.5\text{ g}},
\]

\[
\text{Phycobiliprotein (PEP)(mg/g)} = \text{PC} + \text{APC} + \text{PE}.
\]

2.6. Statistics. Statistical analyses were performed using SPSS 13.0 software (SPSS Inc., Chicago, USA). Independent sample t-test at \( P < 0.05 \) was used to test the significant differences between the infected and the healthy controls.

3. Results

3.1. Dominant Epiphytes on the \( K. \) alvarezii. The dominant epiphytes are brownish red and rigid and have percurrent main axes that reach 2–15 mm. The epiphyte thalli grow on the surface of \( K. \) alvarezii solitary and close to each other in the peak season (Figure 1(a)). A basal attachment system of the axis is at first composed of a primary rhizoid only (Figure 1(b)), and later forms a tuft of rhizoids by the production of secondary rhizoids that cut off from the pericentral cells of lower segments (Figure 1(c)). The primary rhizoid often penetrates through the outer cortical cells of \( K. \) alvarezii to medullary layer (Figure 1(b)). The main axes are 60–250 µm in diameter, with segment length 0.5–1.0-fold of diameters. The axes abruptly taper at the apices. Each vegetative segment consists of 4 pericentral cells and lacks cortical cells. The axis produces vegetative trichoblasts or first-order branches from each segment in a spiral manner. Tetrasporangia are formed in the distal segments, one per segment, in a spiral manner. Mature tetrasporangia are 90–110 µm in diameter and protuberant (Figure 1(d)). Procarpal trichoblasts replace vegetative trichoblasts or lateral branches and appear on the distal portion of branches. Each procarpal trichoblast produces a single procarp on the suprabasal segment. The procarp consists of a three-celled carposporangial branch and initials of two sterile groups, one two-celled and lateral, and the other one-celled and basal (Figure 1(e)). Mature cystocarps are broadly ovoid or napiform with 200–350 µm × 200–300 µm in size. Spermatangia are produced on a lateral of fertile trichoblasts that issues from the suprabasal segment. Mature spermatangial branches are conical with 130–200 µm × 45–60 µm in size. They have a one-celled sterile suprabasal branch and the basal segment embedded in the parental branch (Figure 1(f)).

Rhizoids cut off from the pericentral cells of the lower segments, the production of lateral branch in a spiral arrangement, three-celled carposporangial branches, spermatangial trichoblasts with a sterile lateral, and spiralled tetrasporangia found in the epiphyte ally it with Neosiphonia than Polysiphonia [21]. In addition to these features, the morphology and size of the main axes, tetrasporangia, carposporangial, and spermatangial all ally it with \( N. \) savatieri than \( N. \) apiculata [22, 23]. Therefore, based on the results above the dominant EFA in Lian Bay, Hainan province, China are \( N. \) savatieri.

3.2. Fast Chl a Fluorescence Kinetics, O-JIP. Figure 2 showed the fast Chl a fluorescence induction kinetics of both the healthy and the infected \( K. \) alvarezii. When the thalli of \( K. \) alvarezii are exposed to saturating actinic light, the Chl a fluorescence curves start from the initial \( F_0 \) intensity and increase to a peak (\( P \) or \( F_m \)). When the curves were plotted on logarithmic scale, two intermediate steps \( F_v \) (about 2 ms) and \( F_I \) (about 30 ms) can be found between \( F_0 \) and \( F_m \). To visualize the comparative effects of \( N. \) savatieri infection on each step, the curves were replotted as relative variable fluorescence, \( V_t = (F_I - F_0)/(F_m - F_0) \) in the insert chart of Figure 2. Based on the insert chart in Figure 2, certain increases in the peaks at \( K \)-, \( J \)-, and \( I \)-steps were found in the \( N. \) savatieri-infected \( K. \) alvarezii compared with the healthy seaweed.

3.3. Donor and Acceptor Side of PSII Reaction Center. Increase amplitude in \( K \)-step was used as a specific indicator of damage to the oxygen-evolving complex (OEC) [12, 17, 24, 25]. The amplitude in the \( K \)-step of \( K. \) alvarezii, expressed as the ratio \( V_K \), was shown in Table 1. An obvious increase in \( V_K \) was observed in \( N. \) savatieri-infected \( K. \) alvarezii, which reflected that the OEC of host was at least partly damaged. Meanwhile, the number of RCs per excited cross-section (RC/CS₀ or RC/CSₘ) was reduced in \( K. \) alvarezii after \( N. \) savatieri infection. \( V_J \) was used as an indicator of the proportion of active reaction centers (RCs) [12, 15, 17]. The increase of \( V_J \) (Table 1) further indicated that the number of active RCs in the \( N. \) savatieri-infected seaweed obviously decreased.

The approximated initial slope of the fluorescence transient (\( M_0 \)), a profile of the maximal reduction rate of QA, increased by 89.5% in \( N. \) savatieri-infected \( K. \) alvarezii (Table 1). However, the normalized total complementary area above the O-I-I-P transient (\( S_m \)), the energy needed to reduce all the QA, decreased by 29.5% (Table 1). The increase in \( M_0 \) and decrease in \( S_m \) was one indicator of the decrease in the plastoquinone (PQ) pool [12, 15, 17, 25]. Therefore, the changes of the \( M_0 \) and \( S_m \) in \( K. \) alvarezii, after \( N. \) savatieri
infection showed the plastoquinone (PQ) pool of the host decreased. What is more, \( N \equiv S_m \times M_O \times (1/V_J) \), the negligible change (2.7%) in the turnover number of \( Q_A(N) \) were induced by the integrated effects of changes in \( M_O \), \( V_J \), and \( S_m \).

3.4. Energy Distribution via PSII Reaction Center. After \( N. savatieri \) infection, the energy fluxes via PSII reaction centers (RCs) in \( K. alvarezii \) significantly changed. The light energy for absorption (ABS/RC) and trapping (TR\(_O/RC\)) in \( N. savatieri \) infected \( K. alvarezii \)-increased by 49.5% and 50% (Table 2). However, the specific energy fluxes (per \( Q_A \)-reducing PSII reaction center (RC)) for the energy dissipated (DI\(_O/RC\)) increased significantly (Table 2), and the energy for electron transported per reaction center (ET\(_O/RC\)) in the \( N. savatieri \)-infected \( K. alvarezii \) did not change so significantly. Therefore, most of the energy trapped was not used for photosynthesis but dissipated by the reaction centers.

Similarly, the energy distribution was further expressed via excited cross-section. Regardless of Chl a fluorescence at \( t_{F_0} \) or \( t_{F_m} \), the phenomenological energy fluxes per excited cross section (CS) for absorption (ABS/CS), trapping (TR\(_O/CS\)), and dissipation (DI\(_O/CS\)) in \( K. alvarezii \) increased by 27% (Table 3) after \( N. savatieri \) infection. The increase in the DI\(_O/CS\) acted as a counterbalance to the increase in TR\(_O/CS\). Therefore, the change of electron transport per excited cross section (ET\(_O/CS\)) in \( K. alvarezii \) after \( N. savatieri \) infection was negligible (Table 3).

### Table 1: Profiles reflecting the donor and acceptor side of PSII in the healthy and infected \( K. alvarezii \).

<table>
<thead>
<tr>
<th></th>
<th>Healthy</th>
<th>Infected</th>
<th>RV</th>
</tr>
</thead>
<tbody>
<tr>
<td>( V^K )</td>
<td>0.14 ± 0.03</td>
<td>0.27 ± 0.06</td>
<td>1.929</td>
</tr>
<tr>
<td>RC/CS(_O)</td>
<td>299 ± 61</td>
<td>259 ± 30</td>
<td>0.866</td>
</tr>
<tr>
<td>RC/CS(_m)</td>
<td>695 ± 150</td>
<td>606 ± 70</td>
<td>0.872</td>
</tr>
<tr>
<td>( V^J )</td>
<td>0.49 ± 0.08</td>
<td>0.61 ± 0.07</td>
<td>1.245</td>
</tr>
<tr>
<td>( M_O )</td>
<td>0.57 ± 0.11</td>
<td>1.08 ± 0.26</td>
<td>1.895</td>
</tr>
<tr>
<td>( S_m )</td>
<td>23.73 ± 2.29</td>
<td>16.73 ± 4.54</td>
<td>0.705</td>
</tr>
<tr>
<td>( N )</td>
<td>27.52 ± 2.08</td>
<td>28.25 ± 3.59</td>
<td>1.027</td>
</tr>
</tbody>
</table>

Values present mean ± SE of four replicates, *indicates significant differences at \( P < 0.05 \) between the healthy and infected \( K. alvarezii \), and RV indicates the relative value of infected sample to the healthy sample.

\( V^K \ast = V^K \times N \ast \)
Table 2: Profiles reflecting energy flux per reaction center in the healthy and infected K. alvarezii.

<table>
<thead>
<tr>
<th></th>
<th>ABS/RC*</th>
<th>TR_0/RC*</th>
<th>DI_0/RC*</th>
<th>ET_0/RC*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Healthy</td>
<td>2.04 ± 0.08</td>
<td>1.16 ± 0.05</td>
<td>0.88 ± 0.04</td>
<td>0.59 ± 0.07</td>
</tr>
<tr>
<td>Infected</td>
<td>3.05 ± 0.50</td>
<td>1.74 ± 0.29</td>
<td>1.30 ± 0.24</td>
<td>0.66 ± 0.13</td>
</tr>
<tr>
<td>RV</td>
<td>1.495</td>
<td>1.500</td>
<td>1.477</td>
<td>1.119</td>
</tr>
</tbody>
</table>

Values present mean ± SE of four replicates, *indicates significant differences at P < 0.05 between the healthy and infected K. alvarezii, and RV indicates the relative value of infected sample to the healthy sample.

Table 3: Profiles reflecting energy flux per excited cross section in the healthy and infected K. alvarezii.

<table>
<thead>
<tr>
<th></th>
<th>ABS/CS</th>
<th>TR_0/CS</th>
<th>DI_0/CS</th>
<th>ET_0/CS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Healthy</td>
<td>t = 0</td>
<td>614 ± 147</td>
<td>349 ± 86</td>
<td>264 ± 61</td>
</tr>
<tr>
<td>Infected</td>
<td>t = 0</td>
<td>778 ± 68</td>
<td>445 ± 33</td>
<td>333 ± 41</td>
</tr>
<tr>
<td>RV</td>
<td>t = 0</td>
<td>1.267</td>
<td>1.275</td>
<td>1.261</td>
</tr>
<tr>
<td>Healthy</td>
<td>t = t_Fm</td>
<td>1427 ± 354</td>
<td>812 ± 207</td>
<td>614 ± 147</td>
</tr>
<tr>
<td>Infected</td>
<td>t = t_Fm</td>
<td>1821 ± 140</td>
<td>1042 ± 94</td>
<td>778 ± 68</td>
</tr>
<tr>
<td>RV</td>
<td>t = t_Fm</td>
<td>1.276</td>
<td>1.283</td>
<td>1.267</td>
</tr>
</tbody>
</table>

Values present mean ± SE of four replicates and RV indicates the relative value of infected sample to the healthy sample.

Figure 2: Changes of the fluorescence kinetics, O-J-I-P, plotted on logarithmic time scale from 10 μs to 1 s of N. savatieri-infected K. alvarezii (the original data without any normalization). In the insert chart, a relative variable fluorescence, \( V_t = (I_t - F_o)/(F_m - F_o) \) from 10 μs to 1 s, is shown. Values present mean of four replicates.

3.5. Performance Indexes (PI) and Quantum Yields. The probability that trapped exciton moves an electron into the electron transport chain beyond \( Q_A \) (\( \psi_0 \)) and the quantum yield for electron transport (\( \phi_{P0} \)) decreased by 23.5% and 24.1% in N. savatieri-infected K. alvarezii comparing with the healthy control (Table 4). No significant changes in the maximum quantum yield of primary photochemistry (\( \phi_{P0} \)) were found in the infected K. alvarezii compared with the control. However, the comprehensive performance indexes (PI) significantly decreased (Table 4). The average PI_ABS, PI_CS, and PI_CS, in N. savatieri-infected K. alvarezii decreased by 57.7%, 44%, and 42.9%, respectively, compared with the healthy control (Table 4).

3.6. Photosynthetic Pigments. Chl a and phycobiliprotein content in K. alvarezii changed significantly (Table 5) after the seaweed was infected by N. savatieri (\( P < 0.05 \)). The content of Chl a, phycocyanin (PC), phycoerythrin (PE), allophycocyanin (APC), and phycobiliprotein (PBP) in N. savatieri-infected K. alvarezii increased about 56.4%, 104.5%, 146.2%, 139.4%, and 130.9% compared with the healthy control, respectively (Table 5). The pigments increase in N. savatieri-infected K. alvarezii (Table 5) was much higher than the increase of ABS/CS and TR_0/CS (Table 4). The above results indicated a relative decrease in the light energy absorbed per pigment.

4. Discussion

The changes in PSII performance of the photosynthetic apparatus caused by environmental stress or senescence have been explored widely by applying the chlorophyll fluorescence technique in higher plants [8, 26–31]. However, there is not detailed knowledge on the influence of epiphyte on the photosynthetic activity of its host. In the present study, we have demonstrated the response of PSII of K. alvarezii to N. savatieri infection. The Chl a fluorescence transient recorded with high time resolution was analyzed by the JIP-test in order to quantify the PSII behaviors in K. alvarezii after N. savatieri infection.

\( \phi_{P0} \) changed slightly; however, PI decreased significantly in N. savatieri-infected K. alvarezii. The PI was calculated from three components, which depend on the reaction center density, the trapping efficiency, and the electron transport efficiency. The above changes of PI showed that photosynthesis in the infected K. alvarezii was inhibited which could partly explain the phenomenon of stunted, rough, and poorly branched carrageenan producing seaweed arisen by epiphyte infection [7]. Moreover, our results proved that PI is more sensitive to environmental change than \( \phi_{P0} \).
and correlates well with plant vigor and performance again that agrees with the research by Hermans et al. [32]. Chlorophyll and phycoliprotein content in N. savatieri-infected K. alvarezii was increased to 156% and 230% (Table 5). Therefore, the energy fluxes for absorption and trapping in N. savatieri-infected K. alvarezii were increased (Tables 2 and 3). However, the negligible changes of ET/CS (Table 3) and $\varphi_{P0}$ (Table 4) indicated that the trapped energy was not efficiently used for electron transport. The damage of OEC, decrease in RC number, and reduction of PQ pool could further explain why the light trapped in N. savatieri-infected K. alvarezii was not sufficiently consumed timely for photosynthesis.

The side impacts of epiphyte on K. alvarezii growth were not only limited to photochemical reactions. Largo et al. [33] reported that light intensity of less than 50 $\mu$mol photon m$^{-2}$ could induce the decay of K. alvarezii. N. savatieri occupied the outsurface of K. alvarezii and shielded the host from getting enough light. Moreover, both N. savatieri and K. alvarezii all belonged to Rhodophyta species and owned similar types of photosynthetic pigments that aggravated the competition of light absorption between them. The competition between N. savatieri and K. alvarezii seriously decreased the ambient light. However, the infected K. alvarezii tried to acclimate itself to the low-light conditions by increasing its photosynthetic pigments, especially phycoliprotein (Table 5). Unfortunately, the adaptive regulation seemed to be meaningless for EFA-infected K. alvarezii because of the decrease in active RC number, damage of OEC, and reduction of PQ pool as mentioned above. Glenn and Doty [34] reported that culture of K. alvarezii required high levels of water motion provided by strong and consistent trade winds. N. savatieri, covered on the surface of K. alvarezii, were bound to reduce the water motion nearby the K. alvarezii as well as the materials exchange between K. alvarezii and external environment. Therefore, the production of oxygen by the photosynthesis of N. savatieri and K. alvarezii was easy to cause the surplus of oxygen during the daytime. Moreover, the consumption of oxygen by the respiration of N. savatieri and K. alvarezii was easy to cause the insufficiency of oxygen during the nighttime. In addition, the epiphyte N. savatieri competed with host K. alvarezii for absorbing nutrients (N, P, CO$_2$, and other mineral elements). Most of the nutrients dissolving in the water body were first filtered by N. savatieri before reaching to K. alvarezii, and so nutrient deficiency inevitably occurred in K. alvarezii after EFA infection. Dense N. savatieri were severe stress for the metabolism of K. alvarezii by shading, high O$_2$ concentrations in the light, anoxic conditions in the dark, and competition of nutrients. Therefore, heavy decay in K. alvarezii was usually found when the seaweed was infected by N. savatieri.

In conclusion, the dominant EFA on K. alvarezii in Lian Bay, Hainan province were N. savatieri. Damage of OECs, decrease of active RCs and the PQ pool and significant reduction in the performance indexes (PI) of PSII were caused by the infection of N. savatieri although the seaweed acclimated itself to the low-light condition by increasing its photosynthetic pigments to absorb more light energy. The influence of N. savatieri on photosynthetic activity of K. alvarezii was one of the important reasons to reduce the production of K. alvarezii.

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