台灣生物多樣性研究(TW J. of Biodivers.) 18(4): 295-309, 2016

Light Limitation and Phytoplankton Biomass in the Coastal Wetlands of Southern Taiwan

台灣南部海岸溼地浮游藻之光限制與生物量

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Abstract

The biomass of phytoplankton in an aquatic ecosystem is highly unpredictable due to complicated interactions between algal communities and the physicochemical environment. However, given enough observed data, relationships between phytoplankton biomass and certain limiting resources can be established. In this study, a resource-based model was adopted for the simulation of light-limited phytoplankton biomass in coastal wetlands of southern Taiwan. A total of 22 waterbodies, including three tidal wetlands and 19 closed impoundments were surveyed during a year-long study. Light-limiting data were identified and analyzed for the determination of model parameters, including *minimum light requirement* and *critical light requirement*. Results indicate that, light utilization efficiency of the phytoplankton communities in these saline coastal waterbodies were similar to those of freshwater lakes, with critical light requirement ranged from 0.077 to 0.165 mol-photon day^{-1} mg-Chl-a^{-1} m and minimum light requirement ranged from 2.51 to 2.72 mol-photon day^{-1} m^{-1}. Impoundments were more productive and more efficient in light utilization than tidal wetlands. Algal cells accounted for 66.9% of water column light attenuation under light-limiting conditions, as compared with 39.6% for non-light-limiting situations. Self-shading presented a major regulating mechanism on the algal biomass of highly eutrophic coastal waterbodies. Under a light-limited condition, algal biomass can be managed to prevent ecosystem deterioration caused by excessive eutrophication through the control of light availability. Measures such as surface shading using wetland plants, and water depth augmentation through hydrological manipulation, can be employed for wetland management purposes. An enhanced water circulation can also lower wetland productivity, as shown in the case of Spoonbill Reserve of this study.

摘要

光限制水體的藻類生物量受到藻類群聚光照需求，以及水體混合水深與光衰減特性等複雜因素影響，其預測相當困難。然透過大量調查數據的分析，可以判別光限制情況，並使用這些數據建立藻類生物量與光照之相關模式。本研究運用此一概念，探討台南地區海岸溼地浮游藻的光限制，並建立光限制下的浮游藻生物量模式。所選定的水體共 22 個，包括 19 個封閉的池塘與 3 個潮汐濕地，在一年期間每水體進行 2 到 4 次調查，篩選出光限制數據，並據以決定藻類生物量模式參數，包括最小光照(*minimum light requirement*)與臨界光需求(*critical light requirement*)。結果顯示，濱海水體藻類群聚的光利用效率與淡水湖泊相當，臨界光需求在 0.077 與 0.165 mol-photon day^{-1} mg-Chl-a^{-1} m 之間，最小光照在 2.51 與 2.72 mol-photon day^{-1} m^{-1} 之間。封閉池塘的初級生產力以及藻類光利用效率皆高於開放的潮汐濕地。藻類自蔭作用(self-shading)在這些水體的光限制扮演重要角色，藻細胞構成 66.9%的光衰減，遠高於非光線限制水體的 39.6%。初級生產過高可導致水域生態劣化，濱海濕地營養鹽濃度高，其初級生產一般無法透過營養鹽進行控制。瞭解浮游藻的光線限制，可以經由光照調節來維持合適的初級生產，方法包括以濕地植物進行遮光，或透過水文操作提高濕地水位。促進水流循環亦可降低濕地初級生產，如本研究所調查的黑面琵鷺保護區濕地。

Key words: Light limitation, Phytoplankton biomass, Coastal waterbodies, Taiwan

關鍵詞：光限制、浮游藻生物量、海岸濕地、台灣

Received: June 08, 2016 Accepted: August 12, 2016

收件日期：2016 年 06 月 08 日 接受日期：2016 年 08 月 12 日

Introduction

The biomass of phytoplankton in a waterbody is regulated by a number of environmental and biological factors, with the most important factors being species composition (Domingues *et al.* 2005), water temperature (Boyd *et al.* 2013; Pan *et al.* 2016), and the availability of nutrients and light (Heckey and Kilham 1988; Iachetti and Llames 2015; Pan *et al.* 2016). Predicting phytoplankton biomass of a waterbody is difficult due to complicated interactions between these factors. Two general approaches are usually adopted for the determination of phytoplankton biomass in a waterbody. In a population dynamic approach, physicochemical and biological processes are used to describe the growth and decay of an algal community (e.g. Roelke *et al.* 1999; Siegel *et al.* 2002). On the other hand, the resource-based approach uses simple mathematical equations to relate algal biomass with one or a few numbers of limiting resources (e.g. Grover 1990; Reynolds and Maberly 2002). The phosphorus loading equation is a well-known example of the resource-based model (e.g. Vollenweider 1976; Reynolds and Maberly 2002).

Light limitation occurs regularly in eutrophic aquatic ecosystems where phytoplankton biomass is limited primarily by the availability of light (Cloern 1987; Gameiro *et al.* 2011). The determination of light availability and its relationship with phytoplankton biomass involve a set of bio-optical and hydrodynamic parameters (eg. Kirk 1994; Huisman 1999; Diehl *et al.* 2002; Huisman *et al.* 2004). Loiselle *et al.* (2007) illustrated that the mixed-layer integrated phytoplankton biomass (W, mg-Chl-*a* m^{-2}) of a light limited waterbody can be related linearly to the mixed-layer integrated light energy (Q_t, mol-photon day^{-1} m^{-1}) using:

$$W = \frac{1}{\Psi}(Q_t - Q_{\min}) \qquad (1)$$

where ψ (mol-photon day^{-1} mg-Chl-*a*$^{-1}$ m) is the *critical light requirement* defined as a ratio between mixed-layer intgrated light energy and phytoplankton biomass. Q_{min} is the *minimum light requirement* analagous to a compensation irradiance under which the productivity of an algal community balances its repspiration. A Lambert-Beer model (Kirk 1976) was assumed for underwater light distribution with the total light attenuation (K_d, m^{-1}) being divided into the attenuation caused by algal cells ($k\omega$, m^{-1}), and a background attenuation (K_{bg}, m^{-1}) accounting for attenuation from all other sources:

$$I_z = I_o e^{-(k\omega + K_{bg})z} \qquad (2)$$

where I_o (mol-photon day^{-1} m^{-2}) is surface irradiance, I_z (mol-photon day^{-1} m^{-2}) is the solar irradiance at a depth z, k (m^{-1} mg-Chl-*a*$^{-1}$ m^{3}) is the specific attenuation coefficient for algal cells, and ω (mg-Chl-*a* m^{-3}) is the phytoplankton biomass presented using chlorophyll-*a*. A mixed-layer integrated irradiance can be obtained by integrating equation (2) over depth of the mixed-layer:

$$Q_t = \int_0^{z_{mix}} I_z dz = \frac{I_0}{(k\omega + K_{bg})}(1 - e^{-(k\omega + K_{bg})z_{mix}}) \quad (3)$$

Through sustituting Q_t in equation (1) with equation (3), a light-limited phytoplankton biomass model can be derived:

$$W = 1/\psi\left[\frac{I_o}{k\omega + K_{bg}}(1 - e^{-(k\omega + K_{bg})z_{mix}}) - Q_{\min}\right] \quad (4)$$

The values of ψ and Q_{min} in Eq (4) are evaluated using observed data. In a method proposed by Loiselle *et al.* (2007), data of water column integrated phytoplankton biomass is plotted against light energy. An envelope line is then drawn for the data points, as illustrated in Figure 1. Data points adjecent to the envelope line are considered as under light limitation. For data points below the envelope line, algal growth is limited by factors other than light energy, such as the availability of limiting nutrients. The slope of the envelope line is the critical light requirement (ψ) in equation (4), and its intercept with the x-axis is the minimum light requirement (Q_{min}).

The procedures provide a practical approach for the determination of phytoplankton biomass under light limitation. It has been previously applied for the modeling of light-limitted phytoplankton biomass in highly eutrophic Lake Victoria in Africa (Loiselle *et al.* 2007, 2008; Cornelissen *et al.* 2014). Coastal wetlands are ususally nutrient rich and highly productive where light-limitation occurs quite commonly. Therefore the development of a light-limited algal biomss model is of great interest in the study of this particular type of ecosystem. Therefore, the major purposes of this study was to examine the applicability of resourced based models for the predction of phytoplankton biomass in coastal wetlands, and to evaluate light utilization efficiecy of the algal communities in these waterbodies.

Materials and methods

1. Study area

The study area (Figure 2) situates in the coastal region of Tainan in southern Taiwan. The area is covered primarily by aquaculture ponds, together with coastal lagoons, tidal rivers, and other natural impoundments. A total of 22 waterbodies, including three tidal wetlands and 19 closed impoundments, were surveyed over a period of 12 months. With a surface area of 117.6 ha, Spoonbill Reserve is the largest waterbody included in this study. The wetland situates near the coastline and is connected with the sea through a manmade channel. Exchange of water between the wetland and the coastal sea was substantial due to tidal flushing. Si-Cao and Ding-Shan are two smaller tidal wetlands that were not well circulated. The 19 close impoundments were chosen among natural and manmade ponds based on their sizes, representativeness, and accessibility. Dimensions of the studied waterbodies are provided in Table 1.

2. Field survey and lab analysis

The three tidal wetlands were monitored monthly for a period of 12 months, while the 19 impoundments were each surveyed twice during the period of study. In each survey, the depth and transparency (secchi depth) of each waterbody were measured. Water temperature, salinity, pH, and dissolved oxygen were monitored using a multi-parameter water quality analyzer (YSI-556, Yellow Spring Instruments, USA). Water samples were also taken for laboratory analysis of turbidity, chlorophyll-*a*, total phosphorous (TP), total nitrogen (TN), and total silicate (Si). The diffusive attenuation coefficient of photosynthetic active radiation (PAR) was derived using a non-linear model (Padial and Thomaz 2008):

$$K_d = 2.00 \times SD^{-0.76} \tag{5}$$

For waterbodies where secchi depth was greater than total depth, light attenuation coefficient was determined from turbidity measurements (T, NTU) using an equation proposed by Lin *et al.* (2009) for turbid marine environments:

$$K_d = 0.142 \times T + 0.07 \tag{6}$$

3. Solar irradiance

Monthly averaged daily solar irradiance (*SI*, kJ m^{-2} day^{-1}) derived by Ou *et al.* (2008) was adopted for this study. The data was derived using records of the Tainan Meteorological Station located approximately 15 km from the study area. A factor of 0.473 was used to convert solar irradiance into photosynthetic active radiation (kJ m^{-2} day^{-1}) (Papaioannou *et al.* 1993). The calculated PAR energy was further converted to photon flux (μmol m^{-2} s^{-1}) using a factor of 1.83 (Sudhakar *et al.* 2013). Monthly averaged values of PAR are given in Table 2. Mixed-layer integrated solar irradiance was calculated for each waterbody from the PAR using equation (3). Since the studied waterbodies were relatively shallow, a mixed-depth equals to total depth was assumed.

4. Determination of model parameters

The mixed-layer integrated solar irradiance as calculated were plotted against mixed-layer integrated phytoplankton biomass. A visually determined envelope line of the data points was then drawn. Light limited data were identified based on their proximity to the envelope line. A linear regression for the light limited data was then performed. The *critical light requirement* (ψ) in Eq (4) was determined from the slope of the regression line. The *minimum light requirement* (Q_{min}) was also determined from the intercept of the regression line with x-axis. The parameters were derived separately for tidal wetlands, closed impoundments, and the pooled data.

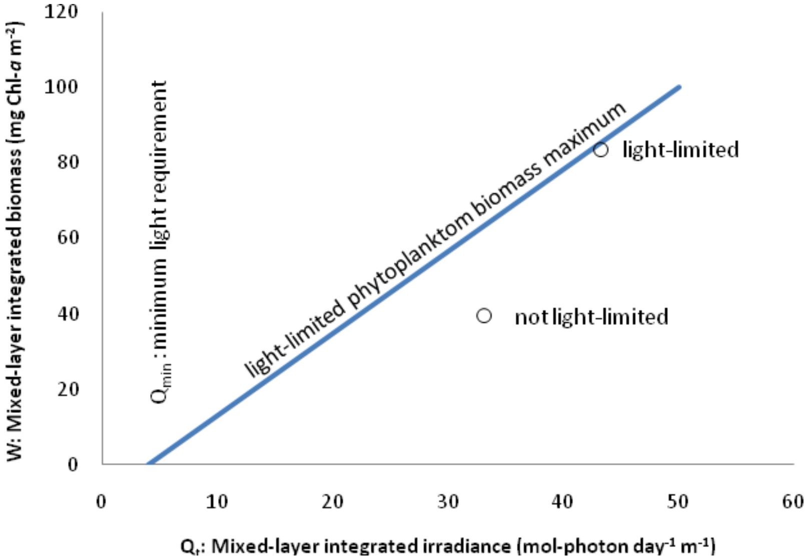

Figure 1. Illustration of a phytoplankton biomass envelop line and the light-limiting and non-light-limiting data points (after Loiselle et al. 2007).

圖 1. 藻類生物量之包絡直線以及光照限制與非光照限制水體判定(摘自 Loiselle et al. 2007)。

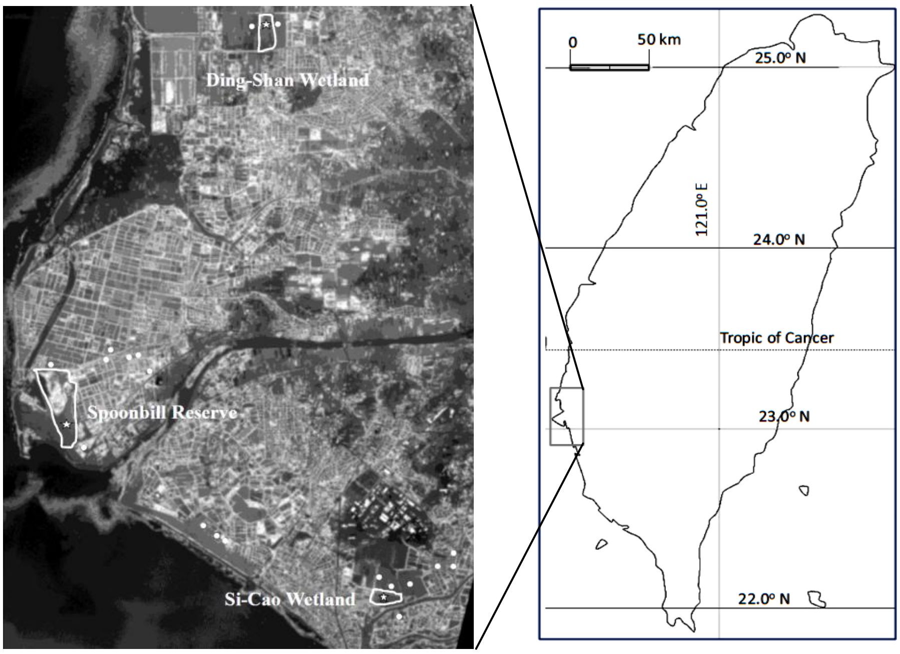

Figure 2. Map of the study area showing locations of studied waterbodies.

圖 2. 調查區域與水體位置。

Table 1. Dimensions of studied waterbodies
表 1. 調查水體之特性

Waterbody	Type	Surface Area (ha)	Depth (m)
Si-Cao Wetland	Tidal wetland	27.8	0.86
Spoonbill Reserve	Tidal wetland	117.6	1.29
Ding-Shan Wetland	Tidal wetland	35.5	0.44
13 impoundments [average (range)]	Closed impoundment	1.29 (0.11-3.58)	0.53 (0.23-1.46)

Table 2. Monthly averaged daily solar irradiance and photosynthetically active radiation (*PAR*) of the study area
表2. 調查區域每月平均日照與光合作用有效輻射

Month	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Solar irradiance (MJ/m^2-day)	6.70	7.52	8.27	9.49	13.92	13.67	13.57	11.36	12.44	13.36	12.26	9.69
PAR (MJ/m^2-day)	3.17	3.56	3.91	4.49	6.58	6.46	6.42	5.37	5.88	6.32	5.80	4.58
PAR (photon) (mol/m^2-day)	20.88	23.43	25.77	29.57	43.38	42.60	42.29	35.40	38.76	41.63	38.20	30.20

Results and discussion

Depth integrated phytoplankton biomass was plotted against depth integrated solar irradiance as shown in Figure 3 through Figure 5, respectively for all data, tidal wetlands, and closed impoundments. Light-limiting data were identified, and values of critical light requirement and minimum light requirement were determined from the regression lines of the selected data points. The numbers derived from this study were compared in Table 3 with those of Lake Victoria reported in two separate studies (Loiselle *et al.* 2007; Cornelissen *et al.* 2014).

1. Critical light requirement

Critical light requirement is a ratio between mixed-layer integrated solar irradiance and phytoplankton biomass. It can be used as the indicator for light utilization efficiency of an algal community. As shown in Table 3, the critical light requirement was 0.084 mol-photon day^{-1} mg-Chl-*a*$^{-1}$ m when all waterbodies were considered. The values were respectively 0.165 and 0.077 for tidal wetlands and closed impoundments. Critical light requirement of the impoundments was comparable with those of 0.067 and 0.064 mol-photon day^{-1} mg-Chl-*a*$^{-1}$ m for Lake Victoria, reported respectively by Loiselle *et al.* (2007) and Cornelissen *et al.* (2014). The critical light requirement for tidal wetlands was much higher than that of the impoundments, suggesting a lower photosynthetic efficiency of the wetlands. As shown in Table 4, phytoplankton biomass of the three tidal wetlands differed significantly. The Si-Cao Wetland was highly productive while the Spoonbill Reserve was particularly low in algal biomass due to significant tidal flushing.

2. Minimum light requirement

Comparable vales of minimum light requirement were obtained for the two groups of waterbodies. The numbers were 2.51 and 2.72 mol-photon day^{-1} m^{-1} respectively for the tidal wetlands and the impoundments, and 2.65 for the pooled data. These values are greater than 1.2 as reported by Loiselle *et al.* (2007) but much smaller than a value of 9.01 mol-photon day^{-1} m^{-1} as reported by Cornelissen *et al.* (2014), both using data from Lake Victoria. The minimum light requirement, when divided by mixing-depth, is equivalent to the compensation irradiance. Using average depths respectively for the three groups of data, the compensation irradiance were respectively 4.11, 7.00, and 5.38 mol-photon m^{-2} day^{-1} for the tidal wetlands, the closed impoundments, and the pooled data. These numbers are much higher than a value of 1.1 ± 0.4 mol-photon m^{-2} day^{-1} as reported by Regaudie-de-Gioux and Duarte (2010) using data based on literature review and their experiment conducted at the ocean, where the average light compensation depth averaged 36 ± 9 m. The numbers are also higher than a value of 1.3 reported by Sommer *et al.* (2011) using mesocosm studies conducted at the Baltic Sea. A much lower range of 0.1-0.3 mol-photon m^{-2} day^{-1} was reported by Marra (2004) using literature review and his study at the north Atlantic. In yet another study, Dielh *et al.* (2015) reported a compensation irradiance of 3.2 mol-photon m^{-2} day^{-1} for algal communities in the oligotrophic Lake Brunnsee. The values obtained in this study were consistently higher than those of the ocean and freshwater lakes.

3. Algal self-shading

Planktonic cells constitute significant light attenuation in highly productive waterbodies (Gikuma-Njuru and Hecky 2005; Nicolausi *et al.* 2013). A specific light attenuation is commonly used to relate light attenuation with the density of algal cells in water. A range between 0.01 and 0.02 m^{2} mg-Chl-a^{-1} have been proposed for lakes (Priscu 1983; Lee and Rast 1997). Taking a value of 0.02 m^{2} mg-Chl-a^{-1}, the light attenuation coefficient from algal self-shading were calculated for light-limiting and non-light-limiting data sets. As shown in Table 5, self-shading constitutes 66.9% of total water column light attenuation (K_d, m^{-1}) under light-limiting conditions, as compared with 39.6% for the non-light-limiting data.

4. Nutrient levels

The growth of phytoplankton in fresh waterbodies is frequently limited by phosphorus (P) and nitrogen (N). Silicon (Si) can also be limiting, particularly in coastal and marine environments (Dortch and Whitledge 1992; Gobler *et al.* 2006). Light limitation occurs when none of the essential nutrients are in short supply. As such, higher nutrient levels are expected for light-limiting waterbodies. Figure 6 compares the nutrient levels of light-limiting and non-light-limiting waterbodies. As can be seen from the figure, the concentrations of N, P, and Si in light-limiting waterbodies were consistently higher than those of the non-light-limiting waterbodies. The differences were statistically significant ($p<0.05$) for all of the three nutrients.

Table 3. Values of light requirement parameters for different types of waterbodies
表 3. 不同類型水體之光需求參數值

Parameter	**This study (Coastal waterbodies)**			**Lake Victoria (Freshwater lake)**	
	All data	**Closed impoundments**	**Tidal wetlands**	**Loiselle *et al.* (2007)**	**Cornelissn *et al.* (2014)**
Critical light requirement (mol-photon day^{-1} mg-Chl-a^{-1} m)	0.084	0.077	0.165	0.067	0.064
Minimum light requirement (mol-photon day^{-1} m^{-1})	2.65	2.72	2.51	1.2	9.01

Table 4. Chlorophyll-*a* concentrations of the studied waterbodies
表 4. 調查水體之葉綠素-*a* 濃度

Waterbodies	**Impoundments**	**Tidal wetlands**			
		All data	**Ding-Shan Wetland**	**Si-Cao Wetland**	**Spoonbill Reserve**
Chl-*a* (mg m^{-3})	54.2 ± 38.2	44.0 ± 40.4	38.8 ± 21.4	88.1± 30.1	5.1± 4.5

*numerical numbers are Mean ± SD.

Table 5. Significance of algal self-shading under light-limiting and non-light-limiting conditions
表 5. 光照限制與非光照限制水體之藻類自蔭作用顯著性

Type of data	**Total attenuation K_d (m^{-1})**	**Attenuation from algal self-shading* $k\omega$(m^{-1})**	**Percent attenuation from algal self-shading $k\omega$ / K_d (%)**
Light-limiting (n=13)	3.18(±1.32)	2.03(±0.73)	66.9(±23.8)
Non-light-limiting (n=58)	2.03 (±0.65)	0.81 (±0.64)	39.6 (±28.5)

*calculated based on ω = 0.020 m^2 mg-Chl-a^{-1}

*numerical numbers are Mean ± SD.

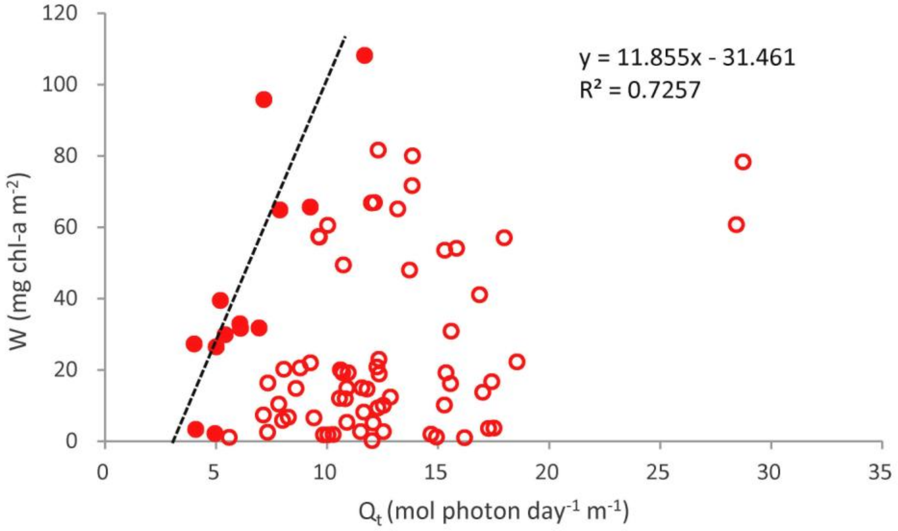

Figure 3. Relationships between depth-integrated irradiance (Q_t) and phytoplankton biomass (*W*) – all data (closed circles are light-limited data points).

圖 3. 混合層光照量(Q_t)與藻類生物量(*W*)之關係—所有數據 (實心圓爲光限制數據點)。

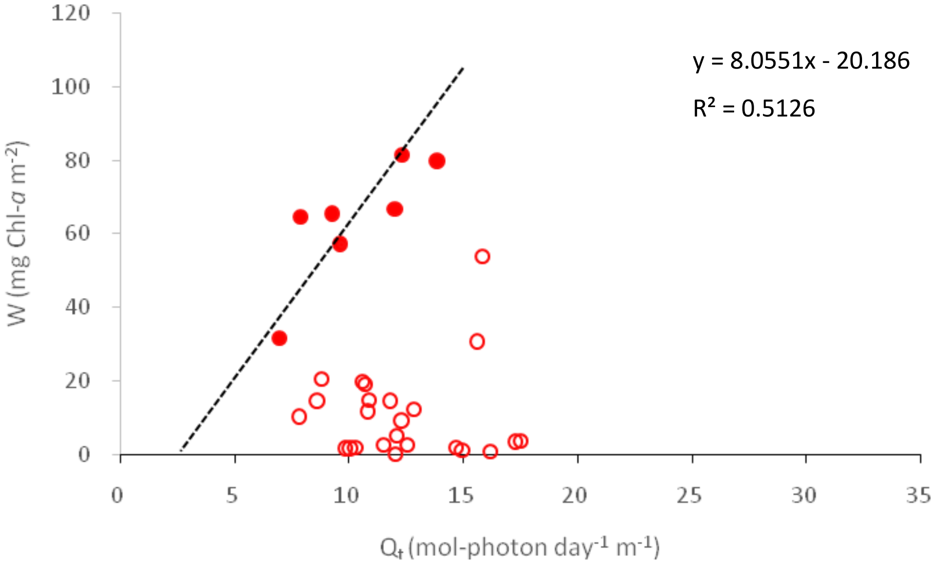

Figure 4. Relationships between depth-integrated irradiance (Q_t) and phytoplankton biomass (*W*) – tidal wetlands (closed circles are light-limited data points) .

圖 4. 混合層光照量(Q_t)與藻類生物量(*W*)之關係—潮汐濕地 (實心圓爲光限制數據點)。

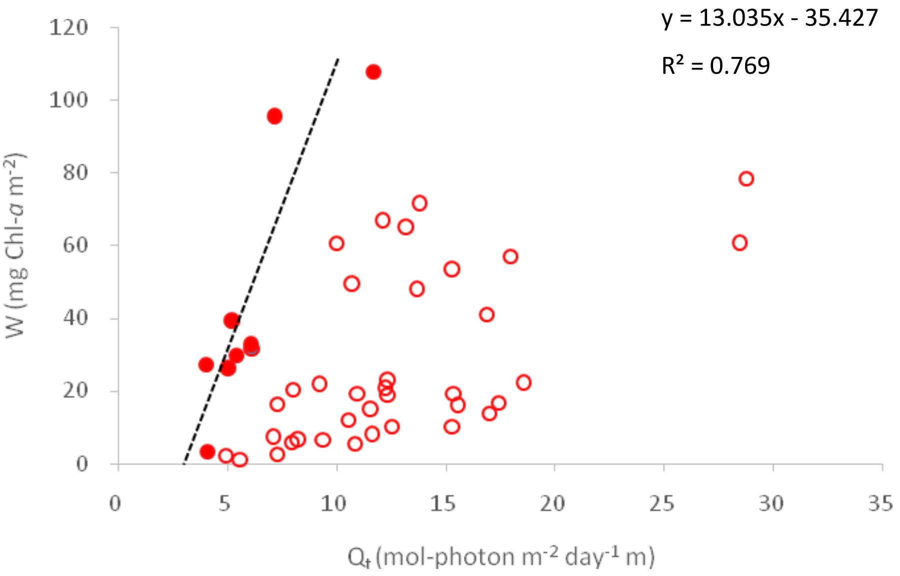

Figure 5. Relationships between depth-integrated irradiance (Q_t) and phytoplankton biomass (*W*) –closed impoundments (closed circles are light-limited data points).

圖 5. 混合層光照量(Q_t)與藻類生物量(*W*)之關係—封閉池塘 (實心圓爲光限制數據點)。

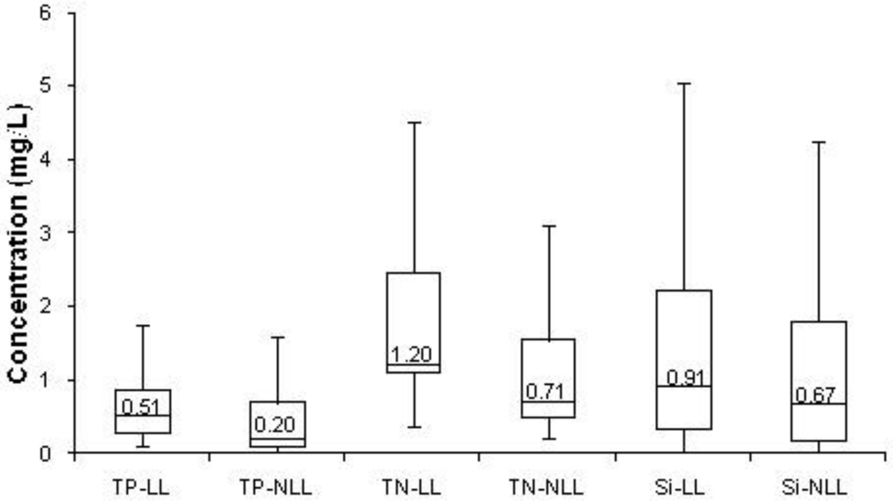

Figure 6. Box plot comparing nutrient levels (TP, mg-P/L; TN, mg-N/L; Si, mg-SiO_2/L) between light-limiting (LL) and non-light-limiting (NLL) waterbodies (max-Q3-median-Q1-min, numerical numbers shown are medians).

圖 6. 光限制水體(LL)與非光限制水體(NLL)營養鹽濃度(TP, mg-P/L; TN, mg-N/L; Si, mg-SiO_2/L)盒鬚圖(max-Q3-median-Q1-min, 數字所示爲中位數)。

Conclusions

Phytoplankton biomass in natural waterbodies is highly unpredictable due its dependence with the complicated environmental and biological factors. The methodology proposed by Loiselle *et al.* (2007) presents a practicable procedure for the determination of algal biomass under light limitation. The saline coastal impoundments of this study exhibited similar critical light requirements but very different minimum light requirements as those of the freshwater Lake Victoria. The observations suggest that light utilization efficiency between algal communities of different species composition may not differ as much as the compensation irradiance. However, a closer examination is warranted for such a presumption.

Light-limitation is less likely under certain hydraulic conditions, such as the case of the well-flushed Spoonbill Reserve. Care must be taken to ensure that a light-limited model of algal biomass is developed exclusively using light-limiting data. Consistent with the observations of other studies, algal self-shading is a major contributor to light attenuation in coastal wetlands and impoundments. The negative feedback form self-shading presents a regulating mechanism for algal biomass of the highly productive aquatic ecosystems.

Primary productivity is vital for sustaining an aquatic food chain and maintaining the integrity of an aquatic ecosystem. However, deterioration of ecosystems can occur in over-productive water bodies due to negative effects such as intense diurnal oxygen swing, oxygen depletion of the bottom water, and the blockage of sunlight. Therefore, a moderate productivity is beneficial for the health of an aquatic ecosystem. Coastal wetlands receive nutrients from upland watersheds, therefore are usually highly nutrient-enriched. Lowering wetland productivity through nutrient control is generally infeasible. Knowing that light limitation occur commonly in coastal wetlands, favorable algal productivity can be achieved by manipulating the availability of light through measures such as surface shading using wetland plants, and increasing water depth through hydrological modifications. Wetland productivity can also be controlled by enhanced water circulation, such as the case of the Spoonbill Reserve in this study.

Acknowledgements

This research is funded in part by the Taiwanese Ministry of the Interior, Grant No. PG10101-0394.

Literature Cited

Boyd, P. W, T. A. Rynearson, E. A. Armstrong, F. Fu, K. Hayashi, Z. Hu, D. A. Hutchins, R. M. Kudela, E. Litchman, M. R. Mulholland, U. Passow, R. F. Strzepek, K. A. Whittaker, E. Yu and M. K. Thomas. 2013. Marine phytoplankton temperature versus growth responses from polar to tropical waters- Outcome of a scientific community-wide study. PLOS ONE 8(5), e63091. doi:10.1371 / journal.pone.0063091.

Cloern, J. E. 1987. Turbidity as a control on phytoplankton biomass and productivity in estuaries. Continental Shelf Research 7: 1367-1381.

Cornelissen, I. J. M., G. M. Silsbe, J. A. J. Verreth, E. van Donk and L. A. J. Nagelkerke. 2014. Dynamics and limitations of phytoplankton biomass along a gradient in Mwanza Gulf, southern Lake Victoria (Tanzania). Freshwater Biology 59(1):127–141.

Diehl, S., S. A. Berger, Q. Soissons, D. P. Giling and H. Stibor. 2015. An experimental demonstration of the critical depth principle. ICES Journal of Marine Science, doi:10. 1093/ icesjms/fsv032

Diehl, S., S. Berger, R. Ptacnik and A. Wild. 2002. Phytoplankton, light, and nutrients in a gradient of mixing depths: field experiments. Ecology 83(2): 399-411.

Domingues, R. B., A. Barbosa and H. Galvao. 2005. Nutrients, light and phytoplankton succession in a temperate estuary (the Guadiana, south-western Iberia). Estuarine, Coastal and Shelf Science 64:249-260.

Dortch, Q. and T. E. Whitledge. 1992. Does nitrogen or silicon limit phytoplankton production in the Mississippi River plume and nearby regions? Continental Shelf Research 12(11): 1293-1309.

Gameiro, C., J. Zwolinski and V. Brotas.2011. Light control on phytoplankton production in a shallow and turbid estuarine system. Hydrobiologia 669: 249-263.

Gikuma-Njuru, P. and R. E. Hecky. 2005. Nutrient concentrations in Nyanza Gulf, Lake Victoria, Kenya: light limits algal demand and abundance. Hydrobiologia 534: 131-140.

Gobler, C. J., N. J. Buck and S. A. Sañudo-Wilhelmy. 2006. Nitrogen and silicon limitation of phytoplankton communities across an urban estuary: The East River-Long Island Sound system. Estuarine, Coastal and Shelf Science 68(1-2):127-138.

Grover, J. P. 1990. Resource competition in a variable environment: phytoplankton growing according to Monod’s model. The American Naturalist 136: 771-789.

Heckey, R. E. and P. Kilham.1988. Nutrient limitation of phytoplankton in freshwater and marine environments: A review of recent evidence on the effects of enrichment. Limnology and Oceanography 33: 796-822.

Huisman, J. 1999. Population dynamics of light-limited phytoplankton: microcosm experiments. Ecology 80(1):202-210.

Huisman, J., J. Sharples, J. M. Stroom, P. M. Visser, W. E. A. Kardinaal, J. M. H. Verspagen and B. Sommeijer. 2004. Changes in turbulent mixing shift competition for light between phytoplankton species. Ecology 85: 2960-2970.

Iachetti, C. M. and M. E. Llames. 2015. Light limitation helps stabilize the phytoplankton assemblage steady-state in a temperate and highly turbid, hypertrophic shallow lake (Laguna Chascomús, Argentina).

Hydrobiologia 752(1): 33-46.

Kirk, J. T. O. 1976. Yellow substance (Gelbstoff) and its contribution to the attenuation of photosynthesis active radiation in some island and coastal South-Eastern Australian waters. Australian Journal of Marine and Freshwater Research 27:61-71.

Kirk, J. T. O. 1994. Light and photosynthesis in aquatic ecosystems, 2nd ed. Cambridge University Press.

Lee, R. W. and W. Rast. 1997. Light attenuation in a shallow, turbid reservoir, Lake Houston, Texas. U. S. G. S. Water Resources Investigations Report 97-4064.

Lin, S., T. Zou, H. Gao and X. Guo. 2009. The vertical attenuation of irradiance as a function of turbidity: a case of the Huanghai (Yellow) Sea in spring. Acta Oceanologica Sinica 28(5): 66-75.

Loiselle S.A., N. Azza, A. Cozar, L. Bracchini, A. Tognazzi, A. Dattilo and C. Rossi. 2008. Variability in factors causing light attenuation in Lake Victoria. Freshwater Biology 53: 535– 545.

Loiselle, S.A., A. Cozar, A. Dattilo, L. Bracchini and J.A. Galvei. 2007. Light limitations to algal growth in tropical ecosystems. Freshwater Biology 52: 305–312.

Marra, J. 2004. The compensation irradiance for phytoplankton in nature. Geophysics Research Letters 31:L06305, doi:10.1029/2003GL018881.

Nicolausi, S., S. R. Erga, B. Hamre, J. J. Stamnes and Ø. Frette. 2013. Light conditions and photosynthetic efficiency of phytoplankton in Murchison Bay, Lake Victoria, Uganda. Limnologica 43:185-193.

Ou, W. S., M. C. Ho, J. L. Chen, J. F. Chen and S. C. Lo. 2008. The study on the typical radiation for solar architecture design of Taiwan (in Chinese). Journal of Architec. Science 64: 103-118.

Padial, A. A. and S. M. Thomaz. 2008. Prediction of the light attenuation coefficient through the Secchi disk depth: empirical modeling in two large Neotropical ecosystems. Limnology 9(2): 143-151.

Pan, C. W., Y. L. Chuang, L. S. Chou, M. H. Chen and H. J. Lin. 2016. Factors governing phytoplankton biomass and production in tropical estuaries of western Taiwan. Continental Shelf Research 118: 88-99.

Papaioannou, G., N. Papanikolaou and D. Retails. 1993. Relationships of photosynthetically active radiation and shortwave irradiance. Theor. and Appl. Climato. 48: 23–27.

Priscu, J. C. 1983. In situ quantum yield of phytoplankton in a subalpine lake. Journal Plankton Research 6: 53l-542.

Regaudie-de-Gioux, A. and C. M. Duarte. 2010. Compensation irradiance for planktonic community metabolism in the ocean. Global Biogeochemical Cycles 24(4): GB4013, doi: 10.1029/2009GB003639

Reynolds, C. S. and S. C. Maberly. 2002. A simple method for approximating the supportive capacities and metabolic constraints in lakes and reservoirs. Freshwater Biology 47: 1183-1188.

Roelke, D. L., P. M. Eldridge and L. A.

Cifuentes. 1999. A model of phytoplankton competition for limiting and non-limiting nutrients: implications for development of estuarine and nearshore management schemes. Estuaries 22: 92-104.

Siegel, D. A., S. C. Doney and J. A. Yoder. 2002. The North Atlantic spring phytoplankton bloom and Sverdrup's critical depth hypothesis. Science 296: 730-733.

Sommer, U., K. Lengfellner and A. M. Lewandowska. 2011. Experimental induction of a coastal spring bloom early in the year by intermittent high-light episodes. Marine Ecology Progress Series 446: 61 -71.

Sudhakar, K., T. Srivastava, G. Satpathy and M. Premalatha. 2013. Modelling and estimation of photosynthetically active incident radiation based on global irradiance in Indian latitudes.Int. Joural Energy and Enviroment Engineering 4: 21.

Vollenweider R. A. 1976. Advances in defining critical loading levels for phosphorous in lake eutrophication. Memorie dell' Instituto Italiano di Idrobiologia 33: 53-83.