APPLICATION

PhycoCanopy: An R Shiny tool for exploring primary production in macroalgal canopies

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Abstract

1. Macroalgal canopies are considered important for coastal food webs and may have a role in carbon sequestration. Until recently, measures of canopy photosynthesis have been relatively rare, and simulations have sometimes omitted key aspects (e.g. self-shading, photosynthesis in air). PhycoCanopy offers a way of exploring how different algal parameters and environmental settings can affect net canopy photosynthesis.

2. The model uses the approach of dividing the canopy into vertical layers, calculating the available light for photosynthesis in each layer with respect to attenuation by the water column and the canopy. A total of 23 parameters can be varied to investigate the consequences of changes in key processes such as the tidal cycle, position of algae relative to the low tide mark and photosynthesis in air.

3. Predicted net photosynthesis can vary within a day as the timing of tides interacts with the light level at different times. The model offers a means of exploring the sensitivity of different parameters and building a fuller understanding of canopy photosynthesis.

4. PhycoCanopy allows users to visualize net canopy photosynthesis and to make predictions in situations where parameters are well characterized. The results give an integrated insight into net photosynthesis, particularly as intertidal observations cannot be maintained continuously over the tidal cycle. The model also demonstrates important covariates, such as the area of algal thallus m⁻² (thallus area index, $T_{AI}$), that should be measured to interpret observed variation in canopy photosynthesis.

KEYWORDS
canopy, desiccation, interactive, macroalgae, net primary production, R Shiny, self-shading, simulation
1 | INTRODUCTION

Canopies formed by macroalgae are a widespread feature of marine ecosystems. Estimates of canopy photosynthesis form an important part of the debate around the contribution of macroalgae to local and global carbon budgets and the potential associated value of algae as Blue Carbon (Macreadie et al., 2019). Direct measurements of canopy production are possible using chambers (e.g. Migné et al., 2015) or eddy covariance measures (e.g. Attard et al., 2019). However, macroalgal canopies are heterogeneous (Johnson, 2020) and are found along strong environmental gradients, particularly those associated with height on the shore. The dynamic nature of the environment, coupled with the physical structure of macroalgal canopies, makes it difficult to scale up estimates of photosynthetic production. A simulation tool would be useful to researchers seeking to interpret field measurements and develop hypotheses about canopy production. An R Shiny tool, PhycoCanopy, was therefore developed to make estimates of algal production, including the effects of tides and height on shore on net photosynthesis.

The net photosynthesis of macroalgal canopies reflects many different processes. The photosynthesis–irradiance (P–I) response may vary between species, with environmental conditions, or different time-scales (Ní Longphuirt et al., 2013). For tidal waters, the light climate varies on time-scales superimposed on the daylight cycle (e.g. Migné et al., 2004). This can cause amplification of photosynthesis, depending on the interaction between the non-linear decline of light with depth and the nonlinear P–I response (Roberts et al., 2018). Areal photosynthesis will increase with biomass of algae, up to the point where competition, including canopy self-shading, limits net production (Binzer & Sand-Jensen, 2002). Periodic exposure of intertidal species to the air has multiple effects on photosynthesis. While macroalgae remain hydrated, photosynthesis continues, and may even be enhanced (Madsen & Maberly, 1990). Prolonged exposure to the air will, however, dry out algal tissues, resulting in reduced photosynthesis. Intertidal algal species vary in the extent to which they can tolerate desiccation (Dring & Brown, 1982).

The consequences of complex interacting processes affecting algal photosynthesis can be explored using simulation models. Maberly and Madsen (1990) simulated the growth of Fucus spiralis tips under various conditions, demonstrating the importance of the height on the shore and the rate at which fronds desiccate. The fraction of net photosynthesis in air was predicted to vary between 23% and 84%, depending on desiccation rate and other environmental conditions (Maberly & Madsen, 1990). Johnson et al. (1998) added canopy interactions and multiple species to investigate the influences of algal growth on the size and dominance of separate species at different heights on the shore. This model highlighted the importance of the number of algal fronds and the related shading effects for net photosynthesis and growth. Where the relationship between photosynthesis, respiration and temperature is known, these can be used to simulate algal photosynthesis in the context of climate change. For example, Colvard et al. (2014) modelled the photosynthesis of Fucus gardneri tips at different temperatures and at sites where the timing of low water springs varies.

While models are useful for integrating various influences on macroalgal photosynthesis, no widely available tool exists. PhycoCanopy is intended to fill this gap: providing an accessible means to visualize changes in net photosynthesis over different time periods under different conditions. The interactive nature of R Shiny (Chang et al., 2021) facilitates sensitivity tests for individual parameters and allows the user to tune simulations to particular environmental conditions.

2 | MODEL

The model represents 1 m² of seabed, with the user able to choose the number of algal fronds, their length and the standard deviation of lengths (based on a log-normal distribution, as frond lengths generally have a skewed distribution). Morphological traits are included, using the length–area relationship (based on logged variables), and a measure of frond thickness (thallus specific mass: g dry mass m⁻², one sided area).

Environmental conditions are based on specifying the midday irradiance and daylength, with changes in daytime irradiance modelled using a cosine curve. A simple representation of tides is used. Diurnal and spring tide heights are specified using the amplitude of the principal lunar semi-diurnal constituent (M2) and the principal solar semi-diurnal constituent (S2). An adjustable phase lag for S2 means that the timing of spring tides relative to midday is under user control. M2 and S2 amplitudes define the tidal range, with the height of simulated algae above the lowest possible tide controlling the timing and durations of aerial exposure during simulations. On natural shores, the lowest possible tide excluding short-term weather effects is known as the lowest astronomical tide (LAT). The height of the modelled 1 m² of seabed relative to LAT determines the pattern of submersion and emersion. Although algae can be simulated in conditions below LAT, the maximum depth of water above the point where algae are attached is currently limited to 10 m.

Simulations of net photosynthesis follow the approach of Johnson et al. (1998) by dividing the water into 1 cm vertical layers. Algal fronds are assumed to be buoyant or to have sufficient stiffness to maintain a vertical orientation when submerged. If the water level is less than the fond height, the excess frond length is assumed to float in the surface 1 cm layer. When fronds are submerged, light is attenuated by the water column and by the canopy such that:

$$I_s = I_0 e^{(-\kappa z + \alpha T_{AI})},$$

where $I_0$ (mmol photon m⁻² s⁻¹) is the irradiance at depth z (m), $I_s$ is the surface irradiance, $\kappa$ is the attenuation coefficient of sea water (m⁻¹), $\alpha$ (T_{AI}⁻¹) is the attenuation from the area of algal canopy above z ($T_{AI}$ is the thallus area index: m² algal frond m⁻² seabed). Thallus and frond have similar meanings. In this context, however, thallus refers to algal tissue in general, covering both depth segments of a single frond and
the biomass of more than one frond in one or more depth layers. In contrast, ‘frond’ means a single branched or unbranched blade of algal tissue rising from a holdfast. Several fronds may come from the same algal holdfast.

The photosynthesis–irradiance (P-I) relationship is modelled in each 1 cm depth layer using the equation of Smith (1936):

\[
P = \frac{P_{\text{max}}aI}{\sqrt{P_{\text{max}}^2 + (aI)^2}},
\]

where \( P \) is the instantaneous gross photosynthesis rate (\( \mu \text{mol C m}^{-2} \text{ frond s}^{-1} \)), \( P_{\text{max}} \) is the maximum gross photosynthetic rate (\( \mu \text{mol C m}^{-2} \text{ frond s}^{-1} \)) and \( a \) is the initial slope of P-I curve (\( \mu \text{mol C} [\mu \text{mol photon}]^{-1} \)). The net photosynthesis rate in each 1 cm segment of frond is calculated as:

\[
P_{\text{net}} = PA - rt_{\text{run}}A,
\]

where \( P_{\text{net}} \) is the net photosynthesis (\( \mu \text{mol C s}^{-1} \)) in each segment, \( A \) is the frond area in each segment (m\(^2\)), \( r \) is the respiration rate (\( \mu \text{mol C g}^{-1} \text{ s}^{-1} \)) and \( t_{\text{run}} \) is the thallus specific mass (g m\(^{-2}\)).

When the depth of water above fronds is 0, fronds are considered to be exposed to the air. Frond photosynthesis is initially increased when algae are in air (Maberly & Madsen, 1990). Photosynthesis declines as the fronds desiccate during prolonged exposure. Madsen and Maberly (1990) established a linear relationship to describe the initial stimulation and then decline of net photosynthesis in air. PhycoCanopy uses a similar approach, linking the maximum photosynthetic rate to the water content \( (W_c) \) of fronds:

\[
P_{\text{max}} = P_{\text{max}}(c + dW_c),
\]

\[W_c = 100e^{-dk}.
\]

Desiccation of fronds is therefore an exponential decline in water content, dependent on the time (s) that fronds are exposed in air (\( E \)) and a desiccation rate \( (d, \text{s}^{-1}) \). The constants \( c \) and \( d \) together define whether there is any stimulation of photosynthesis in air and the rate of decline in photosynthesis with water content. The appropriate desiccation rate and relationships of photosynthesis to water content are not extensively documented for macroalgae. In PhycoCanopy, users can enter their own values, including the option to remove any enhancement of photosynthesis in air and to have no photosynthesis in air. For simplicity, model respiration does not alter in air or with desiccation (e.g. Bordeyne et al., 2017); however, it is possible to use model output water depth and water content to add variable respiration by post-processing results. If fronds are resubmerged, the default hydration rate is 1% of water content every minute, consistent with statements of full photosynthetic recovery within 1–2 hr (Dring & Brown, 1982).

Dring and Brown (1982) compared water loss rates in six species of brown algae, concluding that relationships of photosynthesis to water content were similar, but the extent of recovery from more severe dehydration differed between species. This extent of recovery was modelled using a threshold. The extent of recovery below the threshold was a linear function of minimum water content, with no recovery if water content was zero, rising to 100% recovery if minimum water content remains at or above the threshold value.

On a shore with a full algal canopy, fronds tend to lie on each other at low tide. While this self-shading will reduce photosynthesis (and is accounted for in the model), the layering of fronds will also slow the drying of fronds (Schonbeck & Norton, 1979). This is another process that is not particularly well characterized. As a first approximation, the desiccation rate is unaffected when the thallus area index \( (T_{\text{AI}}) \) is below 1. With canopy coverage \( (T_{\text{CB}}) \) above one, the desiccation rate is divided by the \( T_{\text{AI}} \), so that fronds dry out more slowly as the number of layers increases.

Sliders are used in the R Shiny implementation to allow users to select 23 parameters affecting algal traits, photosynthesis rates and environmental conditions. Simulations can be run for periods ranging from 1 to 14 days; the latter time allowing spring-neap tidal influences to be observed. Model output is summarized by plots of frond water content, surface irradiance, instantaneous net photosynthetic rate and the height of water above the shore level where the algae are attached. To aid interpretation, the \( T_{\text{AI}} \) generated by the chosen frond parameters is given, along with the estimated net photosynthesis over the chosen time period of simulations (g C m\(^{-2}\)). The final value of \( P_{\text{max}} \) used in simulations is also shown. Comparison to the original \( P_{\text{max}} \) illustrates whether desiccation losses have been sufficient to reduce photosynthetic capacity of the algae. Initial parameter values and variables are given in \( \text{Table 1} \).

### 3 | USAGE

The photosynthesis parameters values initially specified when using PhycoCanopy are from Johnson et al. (1998), with length–area and thallus specific mass values representative of \( \text{Fucus serratus} \) (Johnson et al., 1998). A wider range of species can be covered using morphological parameters drawn from the literature (e.g. Mauffrey et al., 2020; Scrosati et al., 2020).

The initial environmental parameter set up has no tides and the fronds are exposed to the air. As a consequence, the water content declines and there is a brief pulse of photosynthesis after dawn and before the algae are too dehydrated to function. Setting the M2 tidal amplitude to 1.5 m (a range of 3 m) and the fronds at 1 m above the low tide point reveals the potential complexity of intertidal photosynthesis (Figure 1). With a midday high tide, the water content in fronds is low at dawn, but net photosynthesis initially increases as irradiance rises. With continued drying out, photosynthesis starts to decline, even as irradiance continues to increase. The space between the vertical dotted lines is the period of daylight where tide covers algae attached 1 m above the low tide point. Within this immersion period, net photosynthesis rises as the algae rehydrate and light levels continue to increase. Photosynthesis does not, however, peak at midday. Although light is at a maximum, attenuation of light by the water above the submerged algae reduces net photosynthesis. The
second period of drying out does not have much time to influence photosynthesis as the falling levels of irradiance rapidly limit any net production.

A moment’s reflection suggests how critical the balance of rates and timing is for the daily pattern of net photosynthesis. A major aim of PhycoCanopy is to allow users to investigate the consequences of such changes on net photosynthesis. Simulation results reflect the importance of canopy light absorption for areal net photosynthetic rates (Middelboe et al., 2006). Increases in the $T_{AI}$ capture more photons, raising net photosynthesis until biomass-related increases in areal respiration overtake light absorption (Figure 2). The influence of $T_{AI}$ on net photosynthesis was demonstrated by Binzer and Sand-Jensen (2002), although their experimentally defined peak of net photosynthesis was estimated at a marginally higher $T_{AI}$ of 8–10 (comparison in supplementary material). Values of $T_{AI}$ in the intertidal certainly span the range of 0–14, based on the weights in Johnson (2020).

Simulated photosynthesis of intertidal canopies at low values of $T_{AI}$ is less than submerged fronds due to desiccation (Figure 2). The modelled effect of canopy sheltering reduces the effect of desiccation above $T_{AI} = 1$. Net photosynthesis in some intertidal canopies may exceed that of submerged canopies in some cases (Figure 2). This reflects photosynthesis in air with reduced desiccation due to canopy sheltering, and the period of time that biomass is in the surface layers when the water depth is less than frond height. $T_{AI}$ can increase due to increases in frond density and/or frond height.

| TABLE 1 | Initial parameter values and state variables used in PhycoCanopy |
|---------|-------------------------------------------------------------|
| **Parameter** | **Symbol if in text** | **Initial value** | **Units** |
| Allometry intercept | — | 0.21 | m² |
| Allometry slope | — | 2.85 | m |
| Canopy attenuation coefficient | $\kappa$ | 0.5 | $T_{AI}^{-1}$ |
| Daylength | — | 12 | hours |
| Days simulated | — | 1 | days |
| Density of fronds | — | 100 | m² |
| Desiccation rate | $d$ | $1.17 \times 10^{-4}$ | s⁻¹ |
| Frond height SD | — | 0 | m |
| Height of algae on shore relative to LAT | — | 0 | m |
| Hydration rate | — | 1 | %water min⁻¹ |
| Initial slope P-I curve | $\alpha$ | 0.05 | $\mu$mol C ($\mu$mol photon)⁻¹ |
| Intercept for aerial $P_{max}$ with water content | $c$ | -0.236 | $\mu$mol C m⁻² frond s⁻¹ |
| M2 tidal amplitude | — | 0 | m |
| Maximum gross photosynthetic rate | $P_{max}$ | 7 | $\mu$mol C m⁻² frond s⁻¹ |
| Mean frond height | — | 0.25 | m |
| Midday irradiance | — | 1600 | mmol photon m⁻² s⁻¹ |
| Rate of change in aerial $P_{max}$ with water content | $d$ | 0.015 | $\mu$mol C m⁻² s⁻¹%⁻¹ |
| Recovery threshold | — | 40 | % |
| Respiration rate | $r$ | 0.002 | $\mu$mol C g⁻¹ s⁻¹ |
| S2 tidal amplitude | — | 0 | m |
| S2 tidal phase lag | — | 0 | ° |
| Thallus specific mass | $t_{sm}$ | 168 | g (dry mass) m⁻² |
| Water attenuation coefficient | $\lambda$ | 0.7 | m⁻¹ |

| **Variables** | **Symbol if in text** | **Initial value** | **Units** |
|---------------|----------------------|------------------|-----------|
| Depth | $z$ | — | m |
| Frond area | $A$ | — | m² |
| Frond water content | $W_c$ | 100 | % |
| Gross photosynthesis rate | $P$ | — | $\mu$mol C m⁻² frond s⁻¹ |
| Irradiance at depth $z$ | $I_z$ | — | mmol photon m⁻² s⁻¹ |
| Irradiance at sea surface | $I_s$ | — | mmol photon m⁻² s⁻¹ |
| Net photosynthesis rate | $P_{net}$ | — | $\mu$mol C s⁻¹ |
| Thallus area index | $T_{AI}$ | 2.37 | Ratio, m² area m⁻² seabed |
| Time fronds exposed to air | $E$ | — | s |
Differences between the intertidal simulations suggest that the separate components of $T_{AI}$ will not always have equivalent effects on net photosynthesis: canopy structure may have a role.

The variable parameters of PhycoCanopy facilitate sensitivity testing in isolation or in combination. For example, both respiration and $P_{\text{max}}$ may vary with temperature (Colvard et al., 2014). Where the associations with variables like temperature are known (e.g. Tait & Schiel, 2013), sensitivity tests can make predictions for climate change effects on photosynthesis. Colvard et al. (2014) made such predictions but did not include variable effects of aerial exposure or canopy interactions. Similarly, if environmental conditions like pH levels, nutrient availability or pollution can be linked to the PhycoCanopy parameters, then evaluations of the effects of these factors on canopy photosynthesis can be made.

Phycocanopy differs from other macroalgal models (e.g. Bordeyne et al., 2020; Rogers & Shears, 2016) by including explicit processes of canopy shading and desiccation mitigation. Miller et al. (2012) found that canopy shading was not important for predictions of kelp understory production in respirometry chambers but suggested that canopy effects may be important in other contexts. These other contexts can be explored with PhycoCanopy to help define when canopy interactions are necessary for models of productivity.

PhycoCanopy offers an integrated view of algal photosynthesis incorporating the particular role of fluctuating water depths. The model can be used to demonstrate the action of factors affecting net photosynthesis. Comparing simulations can help interpret observed production measurements and highlights variables that should be measured when comparing field measurements (e.g. $T_{AI}$). Photosynthesis rates in PhycoCanopy are based on generalized parameters for fucoid algae. The model could be twinned with experimental work to develop more specific production estimates for particular conditions.

CONFLICT OF INTEREST
No conflict of interest to declare.

AUTHORS’ CONTRIBUTIONS
M.P.J.: conceptualization, methodology, software and writing.

PEER REVIEW
The peer review history for this article is available at https://publons.com/publon/10.1111/2041-210X.13843.
DATA AVAILABILITY STATEMENT
The PhycoCanopy model (mar-env, 2022, https://doi.org/10.5281/zenodo.6327096) is available at Github, with code that can be run using Rstudio or R. The libraries for Shiny and REDaS should be loaded first (library(Shiny), library(REDaS)). The following R code will load the PhycoCanopy app < runGitHub("PhycoCanopy","mar-env",ref = "main"). The GitHub repository with a copy of the Shiny app code is https://github.com/mar-env/PhycoCanopy.

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SUPPORTING INFORMATION
Additional supporting information may be found in the online version of the article at the publisher’s website.

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