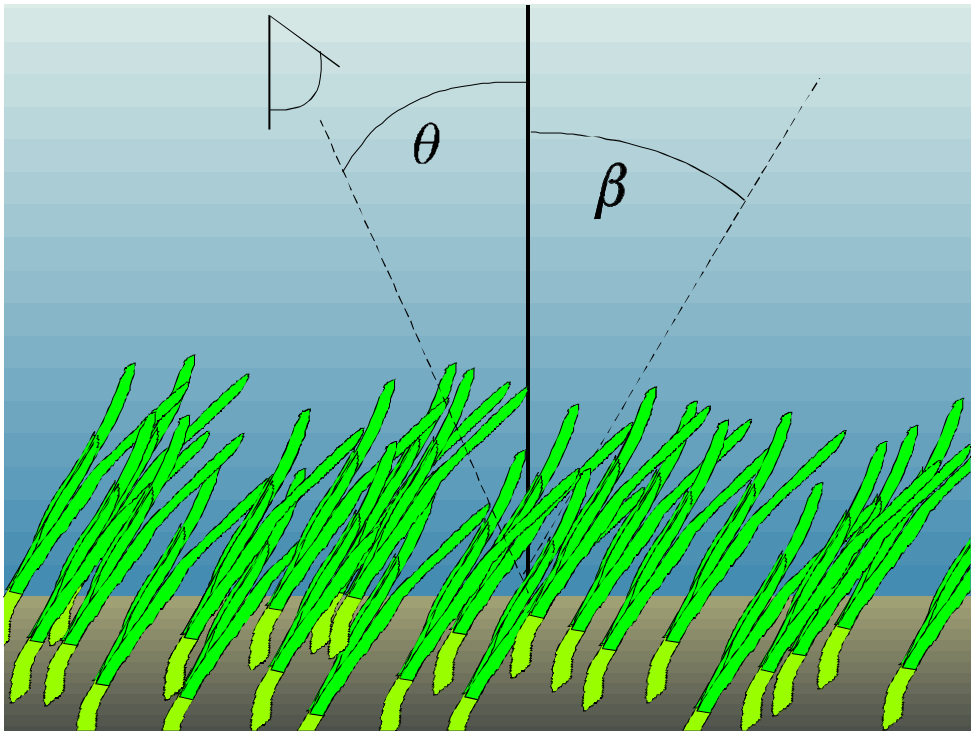
GrassLight 3.2 User's Guide

A Simulation Model of Radiative Transfer and Photosynthesis in Submerged Plant Canopies



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Richard C. Zimmerman reserves the right to revise *GrassLight* software, User's Guide, Technical Documentation, or other publications or products without obligation to notify any person or organization of such revision.

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Technical Support

Limited technical support for program execution, operation and modification may be provided by Richard C. Zimmerman (rzimmerm@odu.edu) at my discretion. However, the author reserves the right to refuse to provide technical support, at my discretion, without providing any reason whatsoever for such refusal.

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1. INTRODUCTION

This User's Guide is intended for new users of the *GrassLight* software package. It explains essential computer requirements, how to install the software and perform basic operations through the graphical user interface (GUI). The information provided here should be adequate run the software as a " black box" model, and assumes the user is familiar with the basic principles and terminology of radiative transfer theory, aquatic optics and plant physiology, particularly photosynthesis. More detailed information about the general theory of radiative transfer and the field of aquatic optics can be found in Mobley (1994) and Kirk (1994). Those seeking a deeper understanding of photosynthesis in aquatic environments should consult Falkowski and Raven (2007). See Lee et al. (2005) for information about the specific implementations of transfer functions used to derive spectral diffuse attenuation coefficients from water quality parameters and inherent optical properties. See Zimmerman (2003a, 2006) and Zimmerman et al. (2015) for more information on the development of the seagrass canopy radiative transfer model.

GrassLight is a coupled model of 2-flow radiative transfer and photosynthesis in submerged plant canopies. The model computes the spectral diffuse attenuation coefficient $K_d(\lambda)$, an apparent optical property (AOP), for an optically homogeneous water column beneath a clear (cloudless) sky from user-provided estimates of sun angle (geographic position and date), Chl *a* concentration (a proxy for phytoplankton abundance), total suspended matter (TSM) concentration, and absorption by colored dissolved organic matter (CDOM). No other direct user knowledge of water column inherent optical properties (IOPs include absorption, scattering and beam attenuation coefficients, volume scattering functions, etc.) is required . *GrassLight* computes light absorption by the submerged plant canopy from user-supplied information on vertical canopy architecture and leaf optical properties. The diffuse attenuation coefficients for the optically homogeneous water column and vertically defined plant canopy are then used to solve the time independent, unpolarized 2-flow radiative transfer equations to obtain the vertical distribution of upwelling and downwelling irradiance within a plant canopy submerged in plane parallel body of water, and the photosynthesis resulting from light absorption by the geometrically -oriented plant canopy.

GrassLight 3.2 is provided as an executable application with associated input files required for its execution. The source code, consisting of the app design and all required

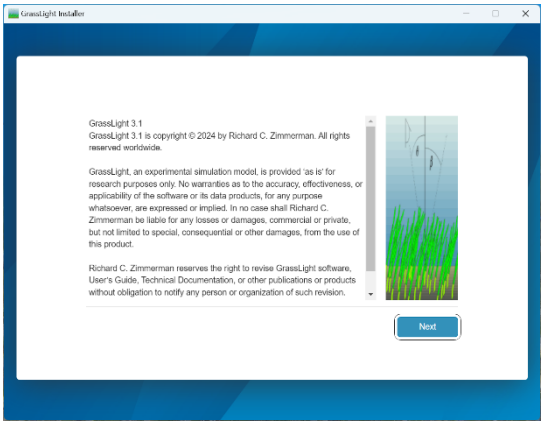
functions written entirely in Matlab R2024b are also available for users wishing to compile their own version, or wishing to modify and help improve the model.

I support the concept of open-source software development and will consider incorporating user revisions and suggestions in future releases of *GrassLight* providing no copyright restrictions are placed on my ability to freely distribute the updated version. Please notify me of any publication incorporating *GrassLight,* and include the following statement in the *Acknowledgements* section of any publication:

***GrassLight* Ver 3.2 was provided free of charge by Richard C. Zimmerman.**

2. INSTALLING *GrassLight* 3.2

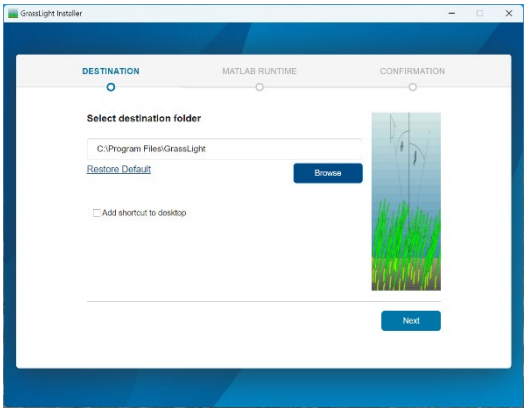
2.1 Computer Requirements



An executable version of *GrassLight* is available for Windows 10 and 11 and MacOS 15 Sequoia computer systems. It does not require Matlab. However, Matlab users can download the original script files (see next section) and run the app in any Matlab environment.

2.2 Installing *GrassLight*

Download the contents of the folder **GrassLight_3_2_Distribution** from GitHub. To begin the installation for Windows machines, click on **GL_3_2_Windows_Installer_web.exe**. In about 30 seconds, it will display the Copyright window (upper right). Click the Next button to bring up the DESTINATION window (lower right). and select the destination folder where the app will be installed. The default location will be c:\Program Files\GrassLight. **If that folder does not exist, you must create it before continuing.** You can also install *GrassLight* into any other folder you like by selecting the Browse button. To add a shortcut to the desktop, click that box on this window. After you have selected the folder, click the Next button.



If it does not already exist on your computer, you will then be directed to install the MATLAB Runtime library from the following MathWorks website: https://www.mathworks.com/products/compiler/mcr/index.html. The default location for this library will be C:\Program Files\MATLAB\MATLAB Runtime\. You can change the default location to any existing folder. If MATLAB is not installed on your computer and *GrassLight* is the only MATLAB-based app you have installed, you can place it in the same folder where you are installing *GrassLight*. If MATLAB is installed on your computer or you want to install other MATLAB-based apps, you should put the runtime library in the default folder suggested by the installer. Then click Begin Install. When the installation is complete, you can run *GrassLight* by clicking on the GrassLight.exe file located inside your destination folder or on the shortcut icon placed on your desktop. If you launch *GrassLight* from the desktop icon and want to access the *GrassLight* User's Guide from the **File** drop-down menu on the top ribbon of the app, a window will appear asking you to locate the User's Guide pdf. You can avoid this step by placing a copy of the User's Guide pdf on your desktop.

For more information about the MATLAB Runtime and the MATLAB Runtime installer, see "Distribute Applications" in the MATLAB Compiler documentation in the MathWorks Documentation Center.

2.3 Modifying *GrassLight*

The folder **GrassLight 3.2 Source Code** provides all the scripts, including the main app, and required functions that can be modified within the MATLAB Editor environment or with a stand-alone text editor such as Notepad++. To modify the app within the Matlab environment, point the **Current Folder** to the one containing the scripts and click on **GL3_11_GUI.mlapp** to open the GUI in the **Matlab App Designer** window. **Design View** allows you to modify the GUI display by moving or adding more buttons. **Code View** gives you access to the code behind the GUI. You can launch the app by pushing the Run button located on the **Editor** tab. Users wishing to create a stand-alone desktop app from their modified scripts will have to re-compile the app using the **Share** feature on the **Designer** tab.

2.4 Uninstalling *GrassLight*

GrassLight can be removed from your computer using the **Uninstall** feature available in the list of installed apps.

3. OVERVIEW OF *GrassLight*

This section provides brief descriptions of the ways *GrassLight* can be used to understand the interaction of submerged plant canopies with the submarine light environment.

3.1 Application of GrassLight

To date, *GrassLight* has been used to determine:

- the effect of canopy architecture (shoot density, leaf morphology and leaf orientation) on light absorption and photosynthesis by seagrass canopies
- whole plant carbon balance (daily ratios of photosynthesis:respiration, *P*:*R*) for a given light environment (date/time, water transparency, depth).
- the effect of water quality (Chl *a*, TSM, CDOM) on seagrass canopy productivity and light-limited depth distribution of seagrasses across the submarine landscape.
- the fraction of the day that canopy photosynthesis is light-saturated or light-limited, with subsequent effects on stable carbon isotope composition ($\delta^{13}C$)
- the total reflectance of spectral irradiance from the submerged plant canopy as a function of canopy architecture
- the influence of epiphyte load on seagrass canopy productivity and light limited depth distribution across the submarine landscape
- the influence of climate change (temperature and CO_2 availability) on seagrass canopy productivity and light limited depth distribution across the submarine landscape
- the influence of seagrass canopy productivity on ocean acidification.

3.2 The Physical Model

GrassLight simulates the propagation of photons through a vertically defined plant canopy submerged in an optically homogeneous water column using a 2-flow approach. The water column is divided into 1000 discrete layers of finite thickness (Δz) containing separately defined optical properties for the water and the submerged plant canopy. The 1-dimensional nature of the *GrassLight* model assumes a horizontally (but not vertically) homogeneous distribution of leaf and water column optical properties. Exact solutions to the radiance transfer equations have been developed for natural waters in which the optical medium is a continuous material composed of randomly arranged scattering elements separated by large distances relative to the wavelength of

light (Mobley 1994). Plant leaves, however, represent a dense packaging of optically active material, which violates the single-scattering assumptions of these exact solutions. Consequently, models of irradiance distribution in plant canopies often rely on more empirical relationships between leaf optical properties and light attenuation by the bulk canopy (Goudriaan 1988, Shultis and Myneni 1988, Ganapol and Myneni 1992). Although less precise mathematically than global illumination models for aquatic radiative transfer (Hedley and Enríquez 2010), the 2-flow simulation of irradiance transfer provides a computationally efficient, quasi-mechanistic framework for understanding the relationship between water column optical properties, submerged plant canopies and their metabolism, and irradiance distribution in shallow waters. Detailed descriptions of the model and underlying equations, along with some applications, can be found in (Zimmerman 2003b, Zimmerman and Dekker 2006, McPherson et al. 2015, Zimmerman et al. 2015)

3.2.1 The Water Column. The light environment above and within the submerged plant canopy is defined by the time-independent, depth dependent (one dimensional) downwelling and upwelling spectral plane irradiances:

$$E_d(\lambda, z) = \int_{2\pi} L(\lambda, z, \theta, \phi)\, cos\, \theta\, d\omega \quad (1)$$

$$E_u(\lambda, z) = \int_{-2\pi} L(\lambda, z, \theta, \phi)\, cos\, \theta\, d\omega \quad (2)$$

which represent the upper and lower hemispheric integrals of the spectral radiance [$L(\lambda,z,\theta,\phi)$] passing through a horizontal plane at a specified depth (z). The zenith and azimuthal directions of the solid angle dΩ are defined by θ and ϕ, respectively.

GrassLight partitions the absorption coefficient into contributions due to different substances:

$$a_{\text{t-w}}(\lambda) = a_g(\lambda) + a_\varphi(\lambda) + a_{\text{p-}\varphi}(\lambda) \quad (3)$$

where $a_{\text{t-w}}$ is the total absorption coefficient for all dissolved and suspended components except for water, and $a_g(\lambda)$, $a_\phi(\lambda)$, and $a_{\text{p-}\phi}(\lambda)$ are the spectral absorption coefficients due to CDOM, phytoplankton, and non-algal particulates (NAP), respectively (Gallegos 2001, Biber et al. 2008). *GL* uses the absorption spectrum of pure water from (Pope and Fry 1997). The water column

IOPs are calculated from user provided concentrations of water quality constituents using mass-specific absorption and scattering coefficients, with the exception of CDOM, which is calculated directly from absorption coefficients. *GrassLight* represents absorption by CDOM as a negative exponential scaled by the absorption at 440 nm (Bricaud et al. 1981, Roesler et al. 1989):

$$a_g(\lambda) = a_g(440)\, exp\left[-s_g(\lambda - 440)\right] \quad (4)$$

where s_g is the spectral slopes for absorption by CDOM. Absorption by NAP is represented as the product of a specific-absorption spectrum, $a^*_{\text{p-}\phi}(\lambda)$, multiplied by a measure of the concentration of NAP, which may be turbidity (NTU), or, for illustration here, total suspended matter, *TSM*:

$$a^*_{\text{p-}\varphi}(\lambda) = c_1 + c_2\, exp[-s_{\text{NAP}}(\lambda - 440)] \quad (5)$$

$$a_{\text{p-}\varphi}(440) = a^*_{\text{p-}\varphi}(440)[TSM]^{\nu_{sa}} \quad (6)$$

where c_2 scales the absorption by NAP at 440 nm, c_1 allows for some small amount (typically $\leq$2% of value at 440 nm, Bowers and Binding 2006) of absorption at long wavelengths, s_{NAP} is the spectral slope of absorption by NAP, and ν_{sa} allows for non-linearity in the relationship with *TSS*. The chlorophyll specific-absorption spectrum, $a_\phi^*(\lambda)$, was determined by regression of measured phytoplankton absorption against Chl *a* for various sites around Chesapeake Bay (Gallegos and Neale 2002, Magnusen et al. 2004):

$$a_\varphi(\lambda) = a^*_\varphi(\lambda)[\text{Chl}a]^{\nu_\varphi} \quad (7)$$

where the exponent, v_ϕ, allows the possibility of a non-linear relationship (Bricaud et al. 1995).

The particulate scattering spectrum, $b_p(\lambda)$, is a power function of wavelength (Snyder et al. 2008)):

$$b_p(\lambda) = b_p(555)\left(\frac{555}{\lambda}\right)^{\eta} \quad (8)$$

where b_p = particulate scattering coefficient, and η is a spectral exponent. As with absorption by NAP, we scale the magnitude of scattering at the reference wavelength by a specific-scattering and TSM:

$$b_p(555) = b_p^*(555)[TSM]^{\nu_{sb}} \quad (9)$$

where $b_p^*(555)$ is the specific-scattering coefficient for TSM (or turbidity) at 555 nm and the exponent, v_{sb} allows for non-linearity. We calculate backscattering by multiplying the particulate scattering spectrum by a constant backscattering ratio, b_{bp}:b_p, with a default value of 0.0159 measured in lower Chesapeake Bay (Zimmerman et al., unpubl). Presently there is no basis for generalizing the spectral shape of the backscattering ratio (Snyder et al. 2008). By scaling the overall magnitude near the center of the visible spectrum (555 nm), errors in calculated $K_d(\lambda)$ due to spectral variability of b_{bp}:b_p are minimized (Snyder et al. 2008). The wavelength-dependent IOPs are $a_t(\lambda)$, the total absorption coefficient and $b_b(\lambda)$, the backscattering coefficient, both of which are dimensionalized as m^{-1}.

3.2.2. The Submerged Plant Canopy. The next step in developing a robust theory of seagrass-light interactions requires a mathematical description of the distribution of leaf biomass within the canopy. Most seagrass species bear leaves that emerge more-or-less vertically from the base of a vertical shoot. The basal origin of the leaves allows the vertical distribution of canopy biomass to be represented as a sigmoid function of height above the substrate. The relative amount of biomass [$B(z)$] at any depth (z) depends on four separate parameters: (i) the percentage of biomass at the base of the canopy (ψ), (ii) the height of that point above the seafloor [$h(z)$],(iii) an intermediate point within the canopy (I), and (iv) a shape factor (s):

$$B(z) = \frac{\psi}{1+\left[\frac{h(z)}{I}\right]^s} \tag{10}$$

Specific values of ψ, I and s can be provided by the user from measurements of leaf length and width data for a given population, or more easily approximated from knowledge of canopy height (h_c). The absolute amount of leaf biomass (or area) in any depth layer (z) is then determined by the product of total leaf area index of the canopy (L) and shoot density:

$$l(z) = L \cdot B(z) \tag{11}$$

In this case, $l(z)$ represents the leaf area index at depth z within the canopy.

After defining the vertical biomass distribution, *GrassLight* next accounts for the geometric orientation of the leaves because the light absorbed by a flat seagrass leaf is strongly dependent on the angular relationship between the leaf and the submarine light field. Consequently, interception of the downwelling irradiance by the canopy depends on the horizontally projected leaf area [$l_p(z)$] , which is a function of the total leaf area in that layer [$l(z)$] and nadir bending angle (β) of the leaf:

$$l_p(z) = l(z)\, sin\, \beta \qquad (12)$$

Light absorption or reflection by the horizontally projected leaf area requires further correction for the angular distribution of irradiance incident on the leaf. The Cosine Law defines this correction as $\frac{l_p(z)}{cos\,\theta}$, where θ represents the zenith angle of a collimated beam incident on $l_p(z)$. The angular distribution of diffuse downwelling irradiance in natural waters can be very complex, but the *average* distribution is usefully approximated by the average cosine, denoted as $\overline{\mu}$. Thus, the ratio $\frac{l_p(z)}{\overline{\mu}_d}$ approximates the average geometric relationship between seagrass leaves and downwelling plane irradiance. In contrast, phytoplankton respond to the submarine light field as scalar irradiance collectors, as the amount of light absorbed (or shadow cast) by a phytoplankton cell is more-or-less independent of its orientation with respect to the illuminating beam.

The *GrassLight* 2-flow approach computes the downwelling plane irradiance emerging from each layer (z) within the water column as:

$$E_d(\lambda,z) = E_d(\lambda,z-1) \cdot [1-\rho_d(\lambda,z)] \cdot exp\left[-\{a_L(\lambda)\cdot t_L + a_{\text{epi}}\}\cdot \frac{l_p(z)}{\overline{\mu}_d(z)} - K_d(\lambda,z)\cdot \Delta z\right] \qquad (13)$$

where $E_d(\lambda,z\text{-}1)$ represents the spectral downwelling plane irradiance emerging from layer above (z-1). The term [1-$\rho_d(\lambda,z)$] accounts for the loss of downwelling spectral irradiance by upward reflection back into layer (z-1), which depends on the reflectance spectrum of pure leaves [$\rho_L(\lambda)$] normalized to the horizontal silhouette of leaf area and the average cosine for downwelling irradiance:

$$\rho_d(\lambda,z) = \rho_L(\lambda)\frac{l_p(z)}{\overline{\mu}_d(z)} \qquad (14)$$

The amount of light transmitted through each layer (z) is controlled by the exponential loss term$\left[-\{a_L(\lambda)\cdot t_L + a_{\text{epi}}\}\cdot \frac{l_p(z)}{\overline{\mu}_d(z)} - K_d(\lambda,z)\cdot \Delta z\right]$ that includes (canopy + epiphyte) and water column effects (absorption and backscattering). Light absorption by epiphytes (a_{epi}) is determined by epiphyte mass density (mg DW cm^{-2}) and optical density, which can be specified from the user menu. If there is no leaf biomass in layer (z) [i.e., if $l_p(z) = 0$], $\rho_d(\lambda,z) = 0$ and the exponential attenuation of light is determined by the attenuation coefficient of the water and the thickness of each layer [i.e., $-K_d(\lambda,z)\cdot \Delta z$]. Spectral diffuse attenuation coefficients are calculated from water column IOPs by the equation of (Lee et al. 2005), which was developed

using extensive simulations with the mechanistic radiative transfer model *Hydrolight* (Mobley 1994):

$$K_{\mathrm{d}}(\lambda) = (1 + 0.005\theta_0)a_{\mathrm{t}}(\lambda) + 4.18[1 - 0.52\,exp(-10.8a_t)]b_{\mathrm{b}}(\lambda) \quad (15)$$

where θ_0 is the above-water solar angle of incidence (degrees), a_{t}. The total backscattering coefficient [$b_{\mathrm{b\text{-}t}}(\lambda)$] is calculated as the sum of the backscattering from pure water (assumed to be isotropic) and that from particles:

$$b_{b-t} = 0.5b_w + \frac{b_{b-p}}{b_p} \quad (16)$$

Attenuation of downwelling irradiance by the plant canopy is defined by the product of the leaf absorption coefficient [$a_{\mathrm{L}}(\lambda)$], the thickness of the leaf (t_{L}), and the geometric correction factor defined as $\frac{l_p(z)}{\overline{\mu}_d(z)}$. The value of the average cosine $\left[\overline{\mu}_d(z)\right]$ can be approximated assuming that scattering is hemispherically isotropic (bi-lambertian) about the leaf surface (Shultis and Myneni 1988). This means that forward scattering by the leaf canopy will cause the average cosine for downwelling irradiance to become increasingly isotropic [i.e., $\overline{\mu}_d(z) \rightarrow 0.5$] in proportion to the horizontally projected leaf area in each layer through which the light passes. It also means that the light attenuation coefficient for the water column [$K_{\mathrm{d}}(\lambda,z)$] will increase with depth in proportion to $\overline{\mu}_d$ (Zimmerman 2003a). Mathematically, this effect is implemented in *GrassLight* as:

$$\overline{\mu}_d(z) = \overline{\mu}_d(z-1) - \left\{\left[\overline{\mu}_d(z-1) - 0.5\right] \cdot l_p(z)\right\} \quad (17)$$

where the notation (z-1) refers to the value of $\overline{\mu}_d$ for light entering layer (z). Upon reaching the sea floor, a portion of the light is reflected back in the upward direction. The downwelling irradiance reflected by the canopy and backscattered by the water column is then attenuated by the plant canopy and water column along its path back to the sea surface in a process symmetrical to that for downwelling irradiance:

$$E_u(\lambda,z) = \{[E_d(\lambda,z) \cdot \rho_d(\lambda,z+1)] + E_u(\lambda,z+1)\} \cdot [1 - \rho_u(\lambda,z)] \cdot exp\left[-a_L(\lambda) \cdot t_L \cdot \frac{l_p(z)}{\overline{\mu}_u} - K_u(\lambda) \cdot \Delta z\right]$$

(3)

The total upward irradiance incident on layer z, $\{[E_d(\lambda,z) \cdot \rho_d(\lambda,z)] + E_u(\lambda,z+1)\}$, represents the sum of the downward irradiance reflected from, and the upward irradiance propagated through the layer (z +1) below. In reality, the downwelling irradiance incident on layer z also includes

some upwelling light reflected downward by upper layers of the canopy. This two-flow approach, however, ignores the secondary reflection, which is so low [$E_u(\lambda, z) \cdot \rho_u(\lambda, z-1) < 0.005 \cdot E_d(\lambda, z)$] that its contribution to $E_d(\lambda,z)$ is extremely difficult to measure practically, and its contribution to photosynthesis is insignificant.

The two-flow approach described by Eqs. (11) and (14) provides a mechanistic density-dependence to the determination of in-canopy light fields because it links absorption and reflection to leaf area [$l(z)$] in each layer, and, therefore, the total leaf area index (L) of the canopy. Self-shading within the canopy, however, is ultimately determined by the projected leaf area [$l_p(z)$], which is a function of leaf orientation as well as shoot density.

3.2.3 Photosynthesis and Carbon Assimilation by the Submerged Plant Canopy.

The photosynthetically used radiation [$PUR(z)$] represents the amount of light absorbed by the seagrass canopy for photosynthesis. PUR is less than the total irradiance attenuated by the canopy [$E_d(\lambda,z\text{-}1)$-$E_d(\lambda,z)$], which includes losses due to reflection from, and non-specific absorption by, the leaves. The calculation of $PUR(z)$ requires spectral integration of the total plane irradiance normalized by the photosynthetic absorptance [$A_p(\lambda)$] of the leaf and the horizontally projected leaf area [$l_p(z)$]:

$$PUR(z) = \sum_\lambda A_p(\lambda) \cdot l_p(z) \cdot \left[\frac{E_d(\lambda,z\text{-}1)\cdot(1-\rho_d)}{\overline{\mu}_d(z-1)} + \frac{E_u(\lambda,z+1)\cdot(1-\rho_u)}{\overline{\mu}_u(z+1)}\right] \quad (4)$$

Although the 2 flow equations are equally valid whether irradiance is expressed in terms of energy or quanta, the stoichiometry of photosynthesis requires that we express $PUR(z)$ in quantum units, where:

$$\text{quanta } s^{-1} = \text{Watts} \cdot \lambda \cdot 5.03 \times 10^{15} \quad (5)$$

Knowledge of $PUR(z)$ allows the instantaneous photosynthetic rate of the leaf tissue in layer (z) to be calculated using the cumulative one-hit Poisson function, which provides a quasi-mechanistic relationship between photosynthetic yield and the amount of light absorbed by the leaf (Falkowski and Raven 2007):

$$P(z) = l(z) \cdot P_E \left\{1 - exp\left[-\frac{\varphi_p \cdot PUR(z)}{P_E}\right]\right\} \quad (6)$$

In this relation, ϕ_p is the theoretical quantum yield of photosynthesis (1/8 mol C mol^{-1} PUR) which should not be confused with the more commonly reported (and more vaguely defined) α, which represents the slope of photosynthesis vs. incident light ($E_d + E_u$), not the absorbed light (PUR). Most production models treat P_E as the physiological maximum rate of photosynthesis

(often denoted as P_m), at least with respect to external environmental influences. However, because light-saturated photosynthesis of eelgrass (and most seagrasses) can be carbon-limited in natural seawater, P_E is actually a variable term that depends on the concentration of CO_2 at the reaction site of carbon fixation, the control of which can be expressed as a square root quadratic (hyperbolic) function of substrate concentration and flow-dependent permeability (Hill and Whittingham 1955, Smith and Walker 1980, McPherson et al. 2015):

$$P_E = \frac{1}{2}\left\{\left(K_s U_p + cU_p + P_F\right) - \left[\left(K_s U_p + cU_p + P_F\right)^2 - 4cU_p P_F\right]^{\frac{1}{2}}\right\} \quad (22)$$

Here, c represents the inorganic carbon concentration of the mainstream water and P_F represents the rate of carbon limited photosynthesis under light and flow saturation empirically described by the Michaelis-Menten equation for CO_2 and HCO_3^-:

$$P_F = P_{m(CO_2)}\frac{[CO_2]}{K_{s(CO_2)}} + P_{m(HCO_3^-)}\frac{[HCO_3^-]}{K_{s(HCO_3^-)}} \quad (23)$$

U_p controls the permeability of DIC through an unstirred fluid boundary of variable thickness controlled by flow, plus all the structural leaf elements (cell membranes, etc.) that resist the diffusion from the leaf surface to the reaction site in the chloroplast. For given concentrations of CO_2 and HCO_3^- in the bulk fluid, flow exerts a saturation type response on Up than can be expressed using a negative exponential function similar in form to Eq. 21:

$$U_p = U_{pF}\left[1 - \exp\left(-\frac{\beta u}{U_{pF}}\right)\right] + U_{p0} \quad (24)$$

Determination of the instantaneous photosynthesis rate in layer (z) allows *GrassLight* to calculate whole canopy production (P_c) by summation of $P(z)$ over all layers (z):

$$P_c = \sum_z P(z) \quad (25)$$

Daily production (P_d) of the canopy is approximated by numerical integration of P_c over the photoperiod, using a time step of 10 minutes. This integration makes two important assumptions:

(i) The top-of-canopy irradiance used to initiate the radiative transfer calculations and determine P_c represents local solar noon.

(ii) The daily variation in $[E_d(\lambda,0)]$ is sinusoidal function of photoperiod.

The resulting photosynthesis rates are used to determine whole plant carbon balance by normalizing P_d to the daily respiratory demand:

$$\text{Daily}P{:}R = \frac{P_d}{(R_{Leaf}+R_{Root}+R_{Rhizome})} \quad (26)$$

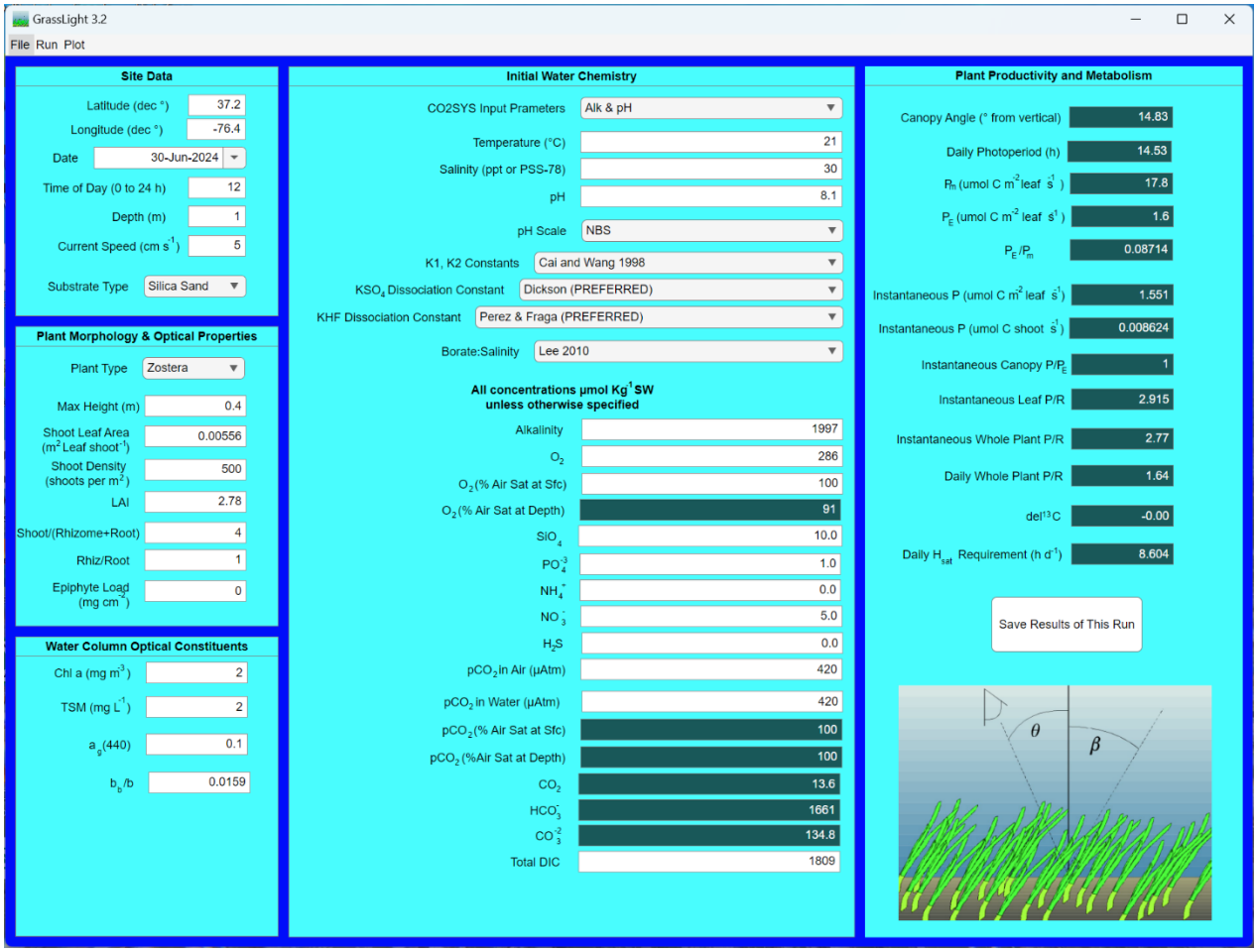
The ratio of Daily P:R provides a convenient index of whole plant or canopy production. Carbon accumulates and growth is possible under light-replete conditions that produce Daily P:$R > 1$. Conversely, the canopy is light limited if the Daily P:$R < 1$. Growth and survival under light limitation require mobilization of stored internal reserves, reducing the total carbon density of individual shoots and the seagrass meadow. If internal reserves are insufficient to provide for growth and survival, shoots will die and the meadow will thin. The daily respiratory carbon demand, defined by ($R_{Leaf} + R_{Root} + R_{Rhizome}$), accounts for the combined metabolic consumption by above- and below-ground tissues. Leaf respiration is constant day and night and he anaerobic rate of metabolic carbon consumption by roots slows to about 65% of the aerobic rate (Smith et al. 1984, Smith et al. 1988, Smith 1989).

The $\delta^{13}C$ signature is modeled as a negative linear relationship between the degree of isotopic fractionation by RUBISCO, and the ratio of P_E/P_m derived from Eqs. 22–24 that quantify the degree to which light-saturated photosynthesis is carbon-limited by external conditions (i.e., [DIC] and/or flow). When light is limiting or P_E is carbon- and flow-saturated (i.e., $P < P_E$ or $P_E/P_m = 1$), assimilation fractionates against $^{13}CO_2$ at $-28‰$ relative to the DIC source, based on the inherent fraction capacity of RUBISCO(Falkowski and Raven 2007). When P is light-saturated (i.e., $P = P_E$), but limited by flow or DIC concentration (i.e., $P_E/P_m < 1$), leaf d13C is isotopically heavier, or less negative, because RUBISCO discriminates less against $^{13}CO_2$. The absolute capacity for RUBISCO to discriminate against $^{13}CO_2$ is also influenced by $\delta^{13}C$ of the DIC source, which was derived from the combined $\delta^{13}C$ signatures of HCO_3^{-2} ($\delta^{13}C = 0‰$) and CO_2 ($\delta^{13}C = -29-28‰$; Kroopnick 1985) available to the plant, based on source water alkalinity and pH.

4.0 The GrassLight App

4.1 The Graphical User Interface

Clicking on the installed icon or running the app from the **Matlab App Designer** window will display the user-interface (below) and initialize the model using **GL3_Setup_Defalut.xlsx.** This Excel file contains all the initialization parameters required to run the model. You can re-size the window by clicking on the icons in the upper right corner of the app or by dragging the edges or corners to fit your screen.



The GUI consists of several panels in which various parameters are grouped. Values displayed in the white boxes can be altered by clicking into those boxes and entering new numeric value or selecting options from the drop-down menus. *GrassLight* will automatically update the impact of

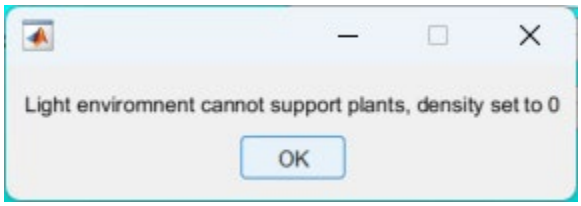
those change on all other boxes displayed. Values displayed in black boxes are calculated by the app, and will be updated when changes are made, but cannot be modified directly by the user.

The **File** tab located in the menu ribbon at the top of the GUI window allows the user to

- **Load new setup file** that can be different from the default file (**GL3_Setup_Defalut.xlsx)** used at startup. It can also be used to re-load **GL3_Setup_Defalut.xlsx** at any point if the user decides to revert all settings to the default condition.
- **Save new setup file** allows the user to create a new setup file after modifying parameters in the white boxes. All data required to initialize the model will be saved to a new **.xlsx** file defined by the user. The parameters in this file can then be used to initialize the model by selecting the **Load new setup file** option at any time, thereby avoiding the need to repeatedly make manual changes to the run conditions. However the default file (**GL3_Setup_Defalut.xlsx)** will always be loaded with the app is started. Over-writing this file will permanently change the default conditions on startup
- **About GL** displays the contents of this user manual in a PDF window. The Table of Contents is indexed to facilitate access to specific sections without scrolling through the whole document.
- **Exit** closes the program, including all plots, without saving any results or settings.

The **Run** tab options include:

- **Optimize density**, which iteratively adjusts the plant density & LAI to values where daily whole plant P/R = 1, which creates the maximum sustainable plant density for a given physical environment. This optimization will automatically adjust the time of day to local noon if it is set at another time. If the light environment is insufficient for plants to maintain a positive carbon balance, a message will be displayed and density/productivity estimates will be set to 0 or Inf:



Clicking the 'OK' button will close this window and allow you to perform another task. However it has set the Shoot Density and LAI boxes, as well as several of the black boxes in the **Plant Productivity and Metabolism** area to 0 or "Inf".

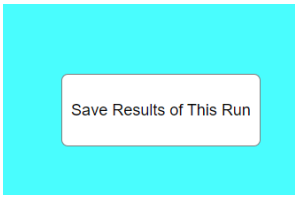
- **Time Series** will eventually perform time series calculations using input from another data file to drive plant performance over time. **It is not yet implemented in GL 3.0 Alpha.**

The **Plot** tab enables the user to generate plots of:

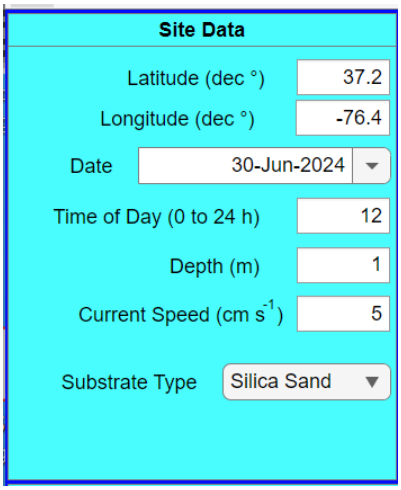
- **Surface Irradiance and Reflectance Spectra** above the water surface.
- **Submarine Irradiance and Reflectance Spectra** throughout the water column.
- **Water Column Optical Properties**, which are vertically homogeneous throughout the water column.
- **Leaf Optical Properties**, which are vertically homogeneous throughout the water column.
- **Substrate Reflectance Spectrum**, which depends on the substrate type selected.
- **Vertical Biomass Distribution**, which depends on the maximum height of the plant canopy, water depth, current speed, and plant density.
- **Canopy Production** throughout the water column, which depends on all the parameters required to run *GL*.
- **CIE Color Simulations of Canopy R and Rrs**

Users can explore impacts of different parameters on model results by successively changing values in the white boxes and re-selecting the different plots. New plots will be generated in new windows without destroying the old plots. Once generated, the plot windows can be saved, printed or edited using the command ribbons at the top of each plot window.

Detailed results of each model state can be saved to a **.xlsx** file by clicking on the Save Results button in the lower right corner of the GUI . The user will be asked to select a folder and file name for the saved information, which includes all the irradiance, reflectance and productivity values for each of the 1000 model layers. The button will then turn red and a notice will appear on the screen indicating the writing of each page of data to the file. Once the file is completed, the color of the button will return to white.



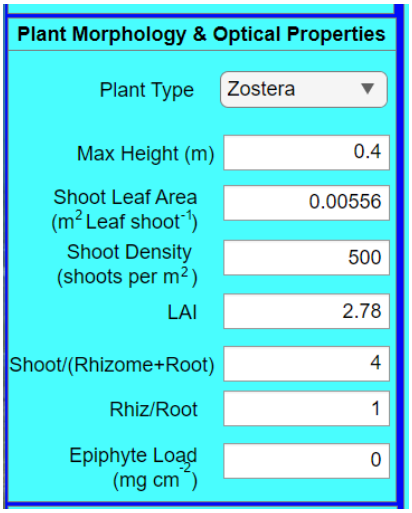
4.2 Site Data



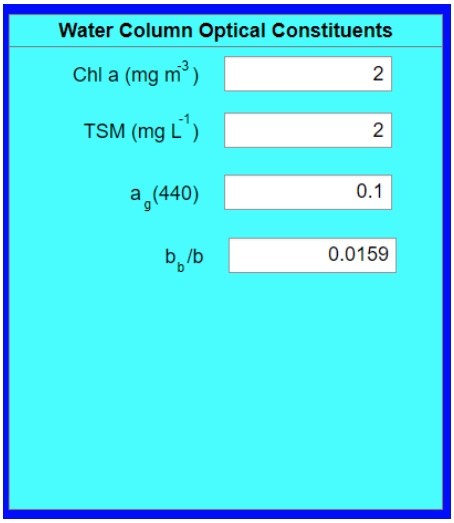
The **Site Data** panel (right) allows the geographic position, date and time, water depth, current speed, substrate type and plant type to be modified. **Latitude** and **longitude** are expressed in decimal degrees. Latitude values (-90 to 90) are negative south and positive north of the equator. Longitude values (-180 to 180) are negative to the west of the prime meridian and positive to the east. **Date** can be selected from a drop-down menu that allows the user to select the day, month and year. **Time of day** is expressed as a decimal value between 0 and 24 h, with 12 representing local solar noon. **Water depth** is expressed as a decimal value ranging from 0.1 to 100 m. **Current Speed** is represented as decimal value that affects the vertical height distribution and leaf orientation. **Substrate Type** controls the reflectance at the base of the plant canopy. Choices in the drop-down menu are arranged by strength of the reflectance value, with Bright Carbonate sand reflecting ~ 50% of the incident light and Silica Mud reflecting ~ 10%.

4.3 Plant Morphology & Optical Properties

The **Plant Morphology & Optical Properties** panel (right) allows the user to select the plant type and various properties for each run. The selection of **Plant Type** allows the user to select among 6 genera of SAV characterized by distinct optical and metabolic properties detailed in the **GL3_Setup_Defalut.xlsx file.** For any **Plant Type** selected, users can modify **Max Height** of the plant canopy, the **Shoot Leaf Area** of the plants, **Shoot Density, Leaf Area Index,** the above/below ground biomass ratio, and the ratio of rhizomes to roots, all of which have impacts on overall plant metabolic rates. Default values for these parameters are provided in the setup file, depending on the species selected. **Epiphyte load** can be used to explore the effects of light attenuation by leaf biofilms, which acts as a neutral density absorption filter.

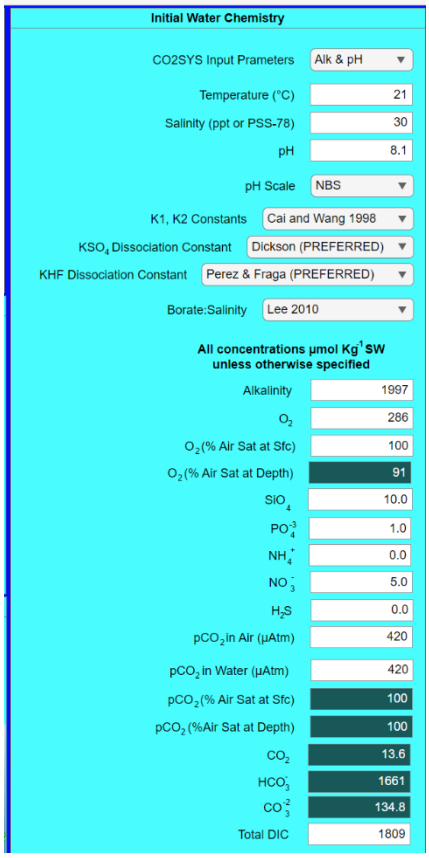


4.4 Water Column Optical Constituents



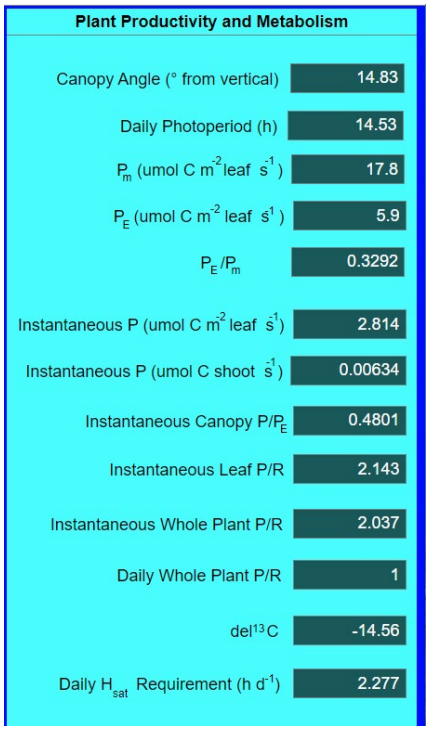
The **Water Column Optical Constituents** panel control the rate of light attenuation and backscattering by the water column. Concentrations of phytoplankton, suspended matter and colored dissolved organic matter (CDOM) are expressed using mass concentrations of Chl *a* and suspended matter and the absorption coefficient for CDOM absorption at 440 nm (m^{-1}). Only single values are allowed for each parameter as the water column is assumed to be optically homogenous throughout its vertical extent, except for the presence of the submerged plant canopy. The value of b_b/b can be any positive number between 0 and 1. Typical values are ~ 0.004 for clear ocean water, 0.015 for coastal water and 0.02 (or greater) for turbid estuarine and harbor water.

4.5 Initial Water Chemistry



The **Initial Water Chemistry** panel controls the dissolved chemical environment that affects photosynthesis and growth. The carbonate system parameters are calculated using a modification of the CO2SYS Matlab function Ver 3.1.1 created by Denis Pierot at CIMAS, University of Miami, Florida. Dropdown menus allow the user to select the pair of input parameters used to calculate the DIC distribution, the pH scale, the dissociation constants and the borate:salinity relationship. Numerical values in the white boxes can be changed by the user. Saturation values for O_2 and CO_2 are calculated using a model developed using equations from (García and Grodon 1992) as corrected and reported by (Pilson 1998). Black boxes represent derived values calculated from the inputs but they cannot be changed directly by the user.

4.6 Plant Productivity and Metabolism



The **Plant Productivity and Metabolism** panel displays the results of the current simulation based on all the driving parameters used in the previous sections. None of these values can be modified directly by the user, but they are updated every time a change is made to any of the driving parameters. **Canopy Angle** provides the canopy orientation in degrees from the vertical. It is affected primarily by current speed. A nearly vertical canopy will have the greatest height and the lowest horizontally projected leaf area. As the canopy bends in flow (increased angle), its vertical extent will decrease and the horizontally projected leaf area will increase, potentially increasing the degree of self-shading in the canopy. The **Daily Photoperiod** represents the time from sunrise to sunset and is calculated from the **Latitude** and **Date** values in the **Site Data** section. **P_m** lists the maximum rate of light, flow and CO_2 – saturated gross photosynthesis *per unit leaf area*, which is a property of the **Plant Type** selected in the **Site Data** section and the temperature specified in the **Initial Water Chemistry** section. **P_E** lists the maximum rate of light and flow-saturated gross photosynthesis *per unit leaf area* for the temperature and CO_2 environment specified in the **Initial Water Chemistry** section. **P_E/P_m** provides the ratio of light-saturated photosynthesis to the physiological maximum rate. **Instantaneous P** *per unit leaf area* provides the current rate of gross photosynthesis for the current light and water chemistry environment, and is affected by many of the parameters in the other sections. **Instantaneous P** per shoot provides the current rate of gross photosynthesis for a whole shoot. **Instantaneous Canopy P/P_E** ranges from 0 to 1 and provides a measure of the degree to which photosynthesis of the entire canopy is light-saturated under the current conditions. **Instantaneous Whole Plant P/R** provides the ratio of instantaneous gross photosynthesis to respiration for the current light and chemical environment. **Daily Whole Plant P/R** provides the same ratio, but is integrated over the whole photoperiod assuming the **Time of Day** is set to 12 (local solar noon). If the **Time of Day** is not 12, the value of **Daily Whole Plant P/R** becomes undefined and the display is set to "Inf". **del^{13}C** provides the isotopic ratio of the

carbon fixed in this instantaneous step simulated by the model, based on the degree to which photosynthesis is light saturated and carbon-limited. **Daily H_{sat} Requirement** indicates the number of hours per day that photosynthesis must be light-saturated to meet the daily respiratory demand of the plants.

5.0 The Setup File

GrassLight requires numerous parameters to be specified for each run. A default set of parameter value parameters is read from the excel file **GL3_Setup_Default.xlsx** upon execution of the app. Users can change parameter values by entering values. This excel file can be opened and examined/modified directly by the user as long as you **DO NOT** change the names of any tabs or insert or delete rows from the pages. Altering the file layout or spreadsheet position of any of the data values will destroy the format structure of the file and cause the app to crash. For most parameters of interest, the safest way to modify this file is to change the parameter value within the GUI and save a new setup file with a different name. You can even over-write the original **GL3_Setup_Default.xlsx** file if you want, but you will lose the original settings that came with this distribution.

5.1 Site Data

The **Site Data** page contains information regarding the physical environment for this run, including latitude, longitude, date, time, water depth, current velocity, sediment type, and plant type. The first 9 lines provide some parameter definitions and the data read in are on line 12.

5.2 IOP Spectra

The **IOP Spectra** page provides the absorption and scattering coefficients for pure water (Pope and Fry 1997). The absorption spectrum for phytoplankton is provided as a dimensionless relative value [$a^*(\lambda)$] normalized to $a(675)$ and scaled to [Chl *a*] according to Eq. (7). Users wishing to employ different $a^*(\lambda)$ spectra than the one provided in the default file can replace the data in this column with a new relative spectrum of their own creation.

5.3 IOP Constants

The **IOP Constants** tab provides values and definitions for the IOP constants used in Eqs. (4) through (9) to define the absorption, scattering and attenuation spectra used to calculate the irradiance distribution throughout the water. Originally derived from values provided by (Lee et al. 2005), these parameters can be tuned to improve model performance for different water bodies or phytoplankton community types. Examples are provided to adjust the backscattering ratio $\left(\frac{b_b}{b}\right)$ for clear ocean waters, the coastal ocean and turbid harbors.

5.4 Water Quality Parameters

The **Water Quality Parameters** tab lists the concentrations of phytoplankton (as Chl *a*), suspended matter required to scale the light attenuation parameters, as well as temperature, salinity, dissolved gases and nutrients required to calculate the DIC speciation values using the CO2SYS function.

5.5 Atmospheric Optical Properties

The **Atmospheric Optical Properties** tab lists the atmospheric absorption spectra for ozone, water and oxygen, based on (Gregg and Carder 1990).

5.6 Atmospheric Constants

The **Atmospheric Constants** tab provides atmospheric constants for determining downwelling plane irradiance at the surface of the earth:

(i) Air mass type, 1-10 as defined by (Gregg and Carder 1990). The air mass type is one of three parameters used to estimate the aerosol particle size distribution. A value of 1 represents marine aerosols far from land, and 10 is for continental air masses. Marine aerosols have larger particles that attenuate light less efficiently than continental aerosols. The determination of air-mass type is not always straightforward. In the open ocean a value of 1 is reliable, but in coastal areas the value depends on the origin of the prevailing air mass which can be defined by the wind direction. Use a value of 1 if the prevailing wind originates from the ocean and 10 if from land. Use intermediate values if mixtures of continental and marine air sources can be determined.

(ii) Windspeed averaged over previous 24 h, 1-10 m/s

(iii) Instantaneous windspeed, 1-20 m/s

(iv) Relative humidity

(v) Atmospheric pressure, mb

(vi) Precipitable water vapor, cm

(vii) Aerosol scale height

(viii) Visibility, 5-25 km

5.7 Leaf Optical Properties

The **Leaf Optical Properties** tab provides the absorption and reflectance spectra for each of the seagrass species available in the model. Absorption coefficients are provided as *Napierian (i.e., natural) log* values (=2.303*spectrophotometric absorbance) per unit leaf thickness. Reflectance values represent the fraction of the incident irradiance backscattered from the leaf.

5.8 Metabolic Parameters

The **Metabolic Parameters** tab provides the maximum rates of leaf photosynthesis at 21 °C based on CO_2 and HCO_3^-, half saturation constants for DIC uptake, permeability and effects of flow, and leaf respiration at 21 °C. Temperature effects on these processes are computed within the model using a Q_{10} temperature coefficient of 3, defined on line 126 in the function **produce_v301_for_app.m** called by the app.

5.9 Plant Architecture

The **Plant Architecture** tab provides shape parameters for vertically distributing the plant biomass through the water column using the sigmoid function presented in Eq.(10). Zero values for parameters in columns H to M will cause *GrassLight* to calculate the vertical distribution based on canopy height. Non-zero values can be inserted into these columns if the user does not wish to use the biomass distribution derived from the height estimate. See (Zimmerman 2003a) for details on calculating these parameters and their impact on the vertical distribution of plant biomass.

5.10 Sediment Reflectance

The **Sediment Reflectance** tab lists the reflectance spectra for various sediment types placed at the base of the plant canopy. Wavelength is denominated in nanometers (nm) and reflectance in relative units such that a value of 1 is equivalent to 100% reflectance.

6.0 The Results File

The Results file saved by the user contains all the data generated by a specific run in a single Excel containing multiple tabs.

6.1 Site Data

The **Site Data** tab contains the location, date, depth, water speed, sediment type and plant type, as modified by the user for each run.

6.2 Biomass Distribution

The **Biomass Distribution** tab contains the realized canopy height, accounting for current speed, bending and water depth, the shoot density, shoot size, LAI and horizontally projected LAI (LAP). It also provides a matrix containing the vertical distribution of LAI and LAP for each of the 1000 layers in the model.

6.3. Plant Productivity

The **Plant Productivity** tab contains plant biomass, carbon, and metabolic rate data for this run expressed as canopy integrals. It also provides a matrix of the incident irradiance (PAR), photosynthetically absorbed irradiance, instantaneous photosynthesis per leaf, daily photosynthesis per leaf and daily photosynthesis per shoot.

6.4. Surface Irradiance Spectra

The **Surface Irradiance Spectra** tab provides a matrix of the spectral direct (EDD), sky (EDS) and total downwelling irradiance reaching the water surface (ED0_air) and just below the water surface (ED0_water)

6.5 IOP and AOP spectra

This tab provides the absorption and scattering coefficients for CDOM (AG), phytoplankton (ACHL), and non-algal particles (ANAP), total absorption (AT), the total scattering (BB) and backscattering (BBP) coefficients, and the contribution of each of these components to the diffuse attenuation coefficient for downwelling irradiance (various Kds) calculated from IOP properties provided in the setup file and concentrations of Chl *a*, suspended matter and CDOM absorption read from the setup file or provided by the user.

6.6 Rrs and R_canopy Spectra

This tab provides the remote sensing reflectance spectrum above the water surface and the top-of-canopy reflectance spectrum in the water calculated by *GrassLight*. It also provides the depth from which the top-of-canopy reflectance spectrum was determined.

6.7. Ed Spectra

This tab provides a matrix of the downwelling irradiance spectra calculated by *GrassLight* as a function of depth in the water.

6.8 Eu Spectra

This tab provides a matrix of the upwelling irradiance spectra calculated by *GrassLight* as a function of depth in the water.

7.0 Example Plots

This section provides a brief description of the plots generated directly by *GrassLight* from the **Plot** ribbon at the top of the GUI. All plots can be re-sized, edited, printed and saved using the functions and icons shown on the top ribbons of each figure.

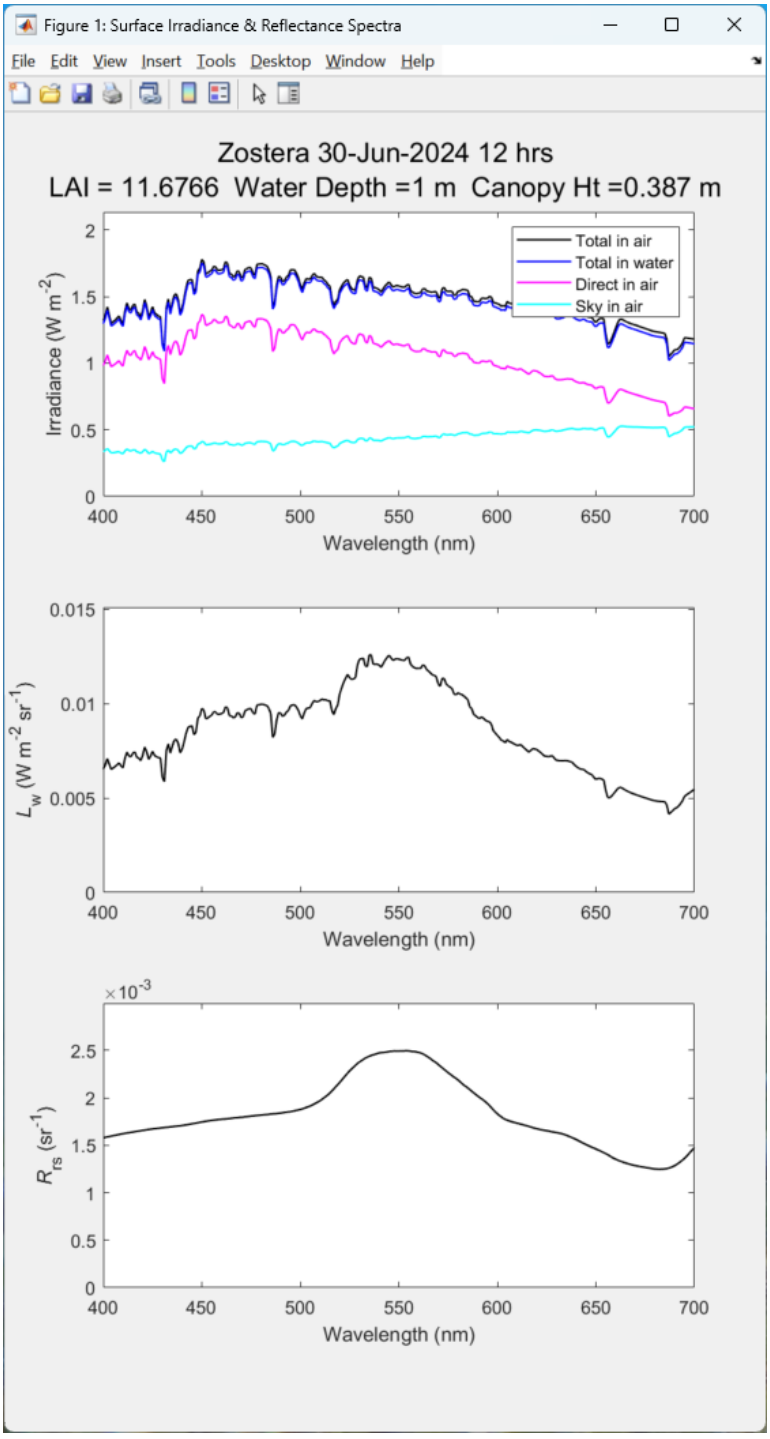


Figure 1. The plots of surface irradiance and reflectance spectra are generated from data provided in the setup file. The figure title indicates the plant type (*Zostera*), date and time of the simulation, plant LAI, water depth and canopy height. The top panel shows the instantaneous downwelling total irradiance in air and in water, as well as the direct and sky components of the downwelling irradiance in air. Difference between Total Irradiance in air and in water represents the loss of radiation across the air-water interface. The middle panel provides the spectrum of water leaving radiance (L_w) generated by water column backscattering and canopy reflectance. The bottom panel shows the remote sensing reflectance $\left(R_{rs} = {L_w}/{E_{d-air}}\right)$. The downwelling irradiances (top panel) are sensitive to position, date and time values shown in the GUI. L_w and R_{rs} are also sensitive to water depth, values displayed in the **Plant Morphology & Optical Properties** and **Water Column Optical Constituents** panels.

Figure 2. The plots of Submarine Irradiance & Reflectance Spectra reveal the light distribution throughout the simulated water column. Spectra of downwelling (E_d) irradiance, upwelling (E_u) irradiance and reflectance $\left(R = \frac{E_u}{E_d}\right)$ are plotted on the vertical axes with depth and wavelength plotted on the two horizontal axes. The fourth panel illustrate the depth distribution of wavelength-integrated quantum irradiance $\left(\mathrm{PAR(z)} = \int_{400\ \mathrm{nm}}^{700\ \mathrm{nm}} E_d(\lambda) + E_u(\lambda)\, d\lambda\right)$ throughout the water column. Above the plant canopy (z < 0.387 m), PAR is attenuated by the water column. Within the canopy (z ≥ 0.387) PAR is attenuated by the water column and the submerged plant canopy, as evidenced by the increased rate of PAR decline. The bottom panel shows a plot of photosynthetically utilized irradiance (Π) absorbed by the plant canopy that extends to 0.387 m in this example.

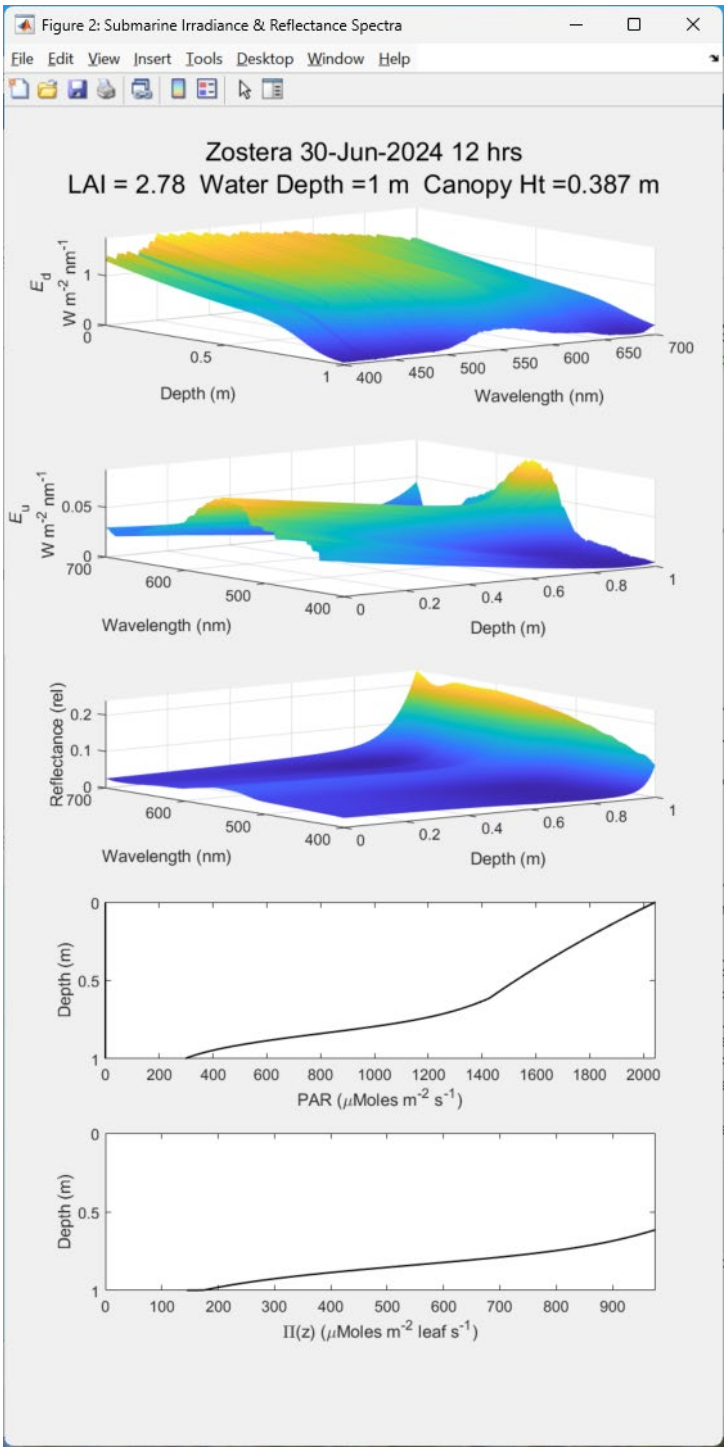
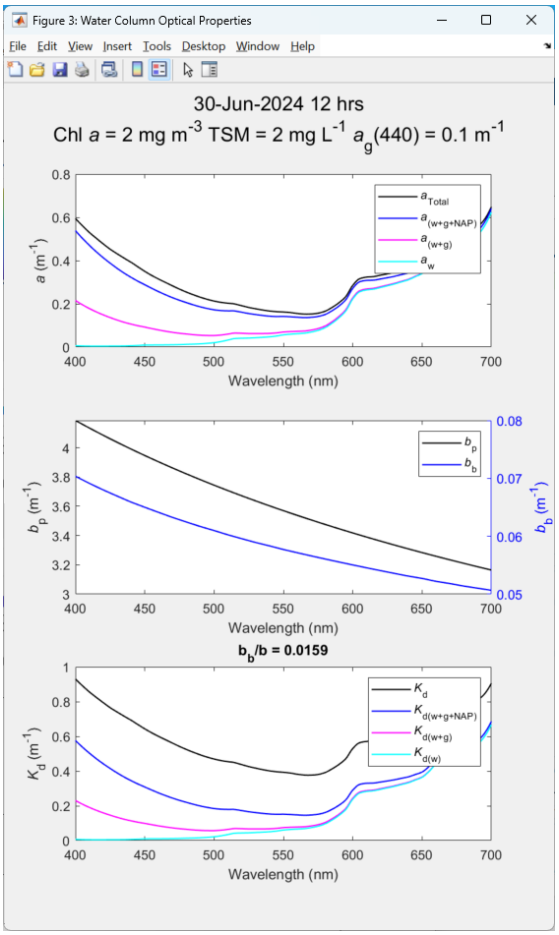


Figure 3. The plot of Water Column Optical Properties illustrates the spectra of inherent (a's and b's) and apparent (K_d's) optical properties using the values provided in the **Water Column Optical Constituents** panel and the coefficients provided in the excel setup file.



Absorption coefficients (a's) are partitioned into their component spectra. a_{Total} represents all optically active components. $a_{(w+g+NAP)}$ is the absorption spectrum for (water + CDOM + non-algal particles). $a_{(w+g)}$ represents the spectrum for water + CDOM (the "g" is for gilvin) and a_w is the absorption spectrum for pure water.

Particulate scattering coefficients (b's) are partitioned into total particulate scattering (b_p) and the backscattering component (b_b). Although not plotted, scattering by pure water is included in the total scattering coefficient, and is assumed to be isotropic in the forward and backward directions.

The diffuse attenuation coefficient for downwelling irradiance (K_d) is plotted as partitioned as for absorption.

Figure 4. The plot of Leaf Optical Properties displays the absorption and reflectance spectra for the chosen plant type. These optical properties are used to drive the values of R_{rs} canopy light attenuation shown in **Figs. 1 & 2.**

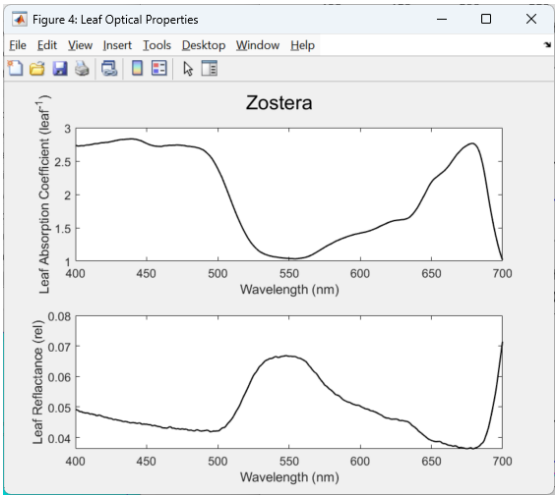
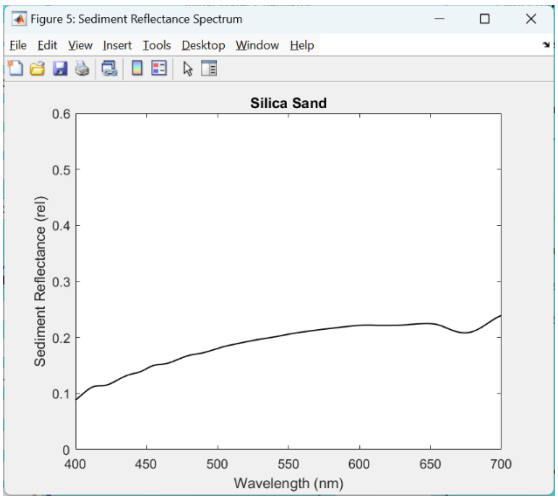
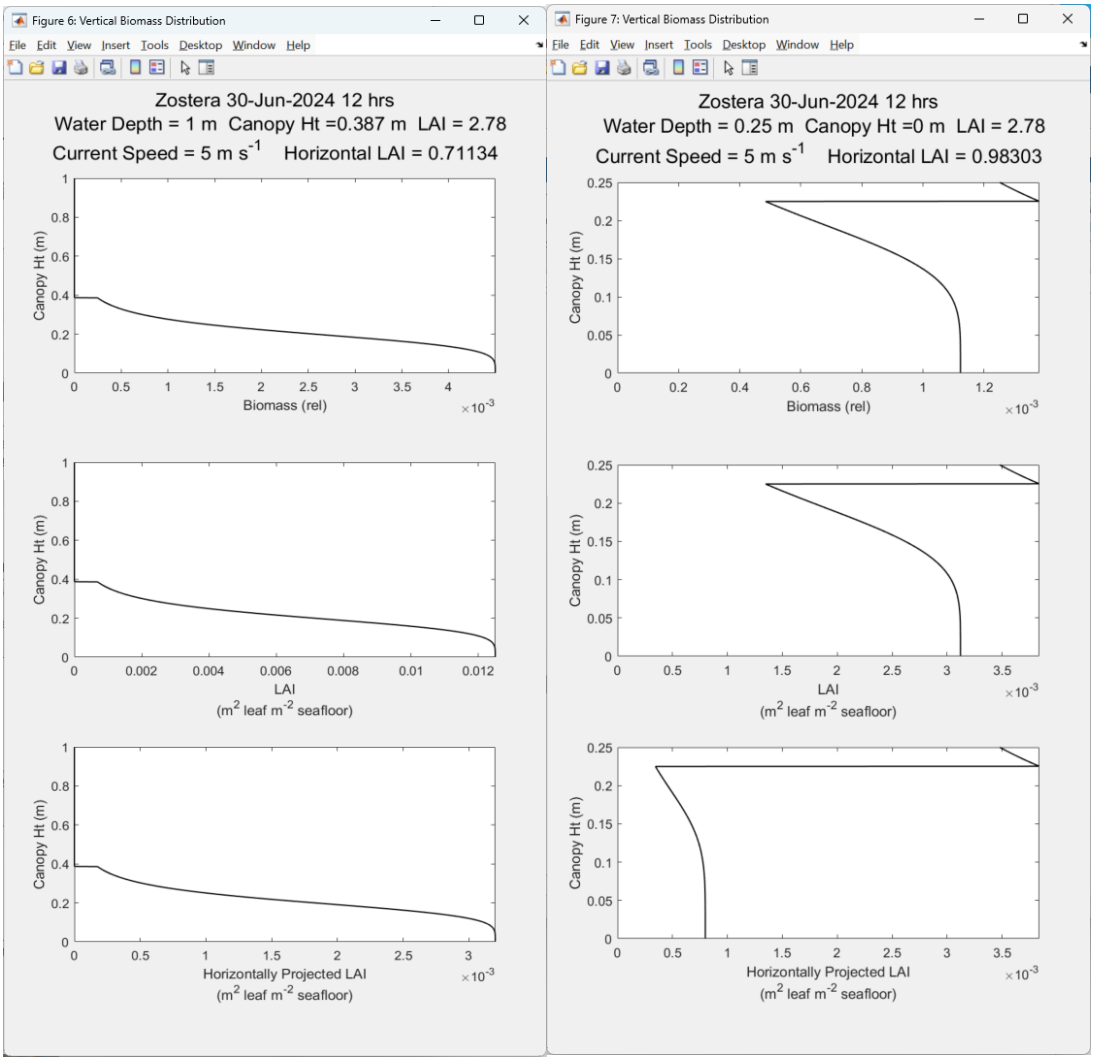


Figure 5. The plot of sediment reflectance reveals the optical property of the bottom boundary layer in the model for the substrate type listed in the **Site Data** panel of the GUI.

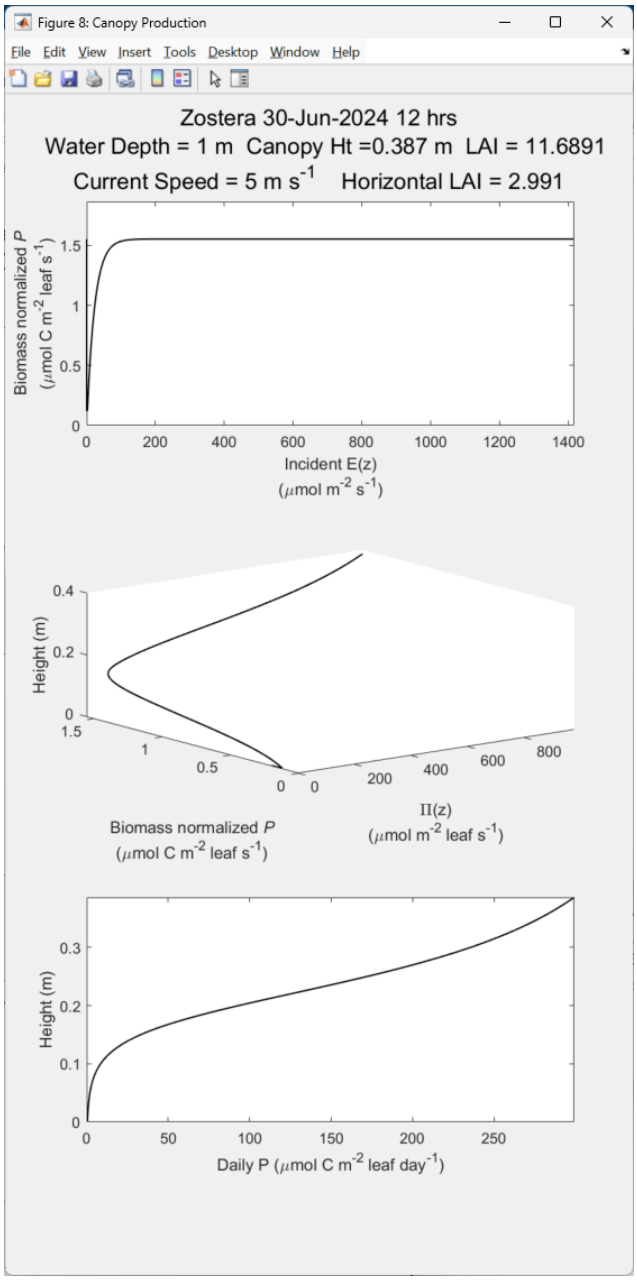


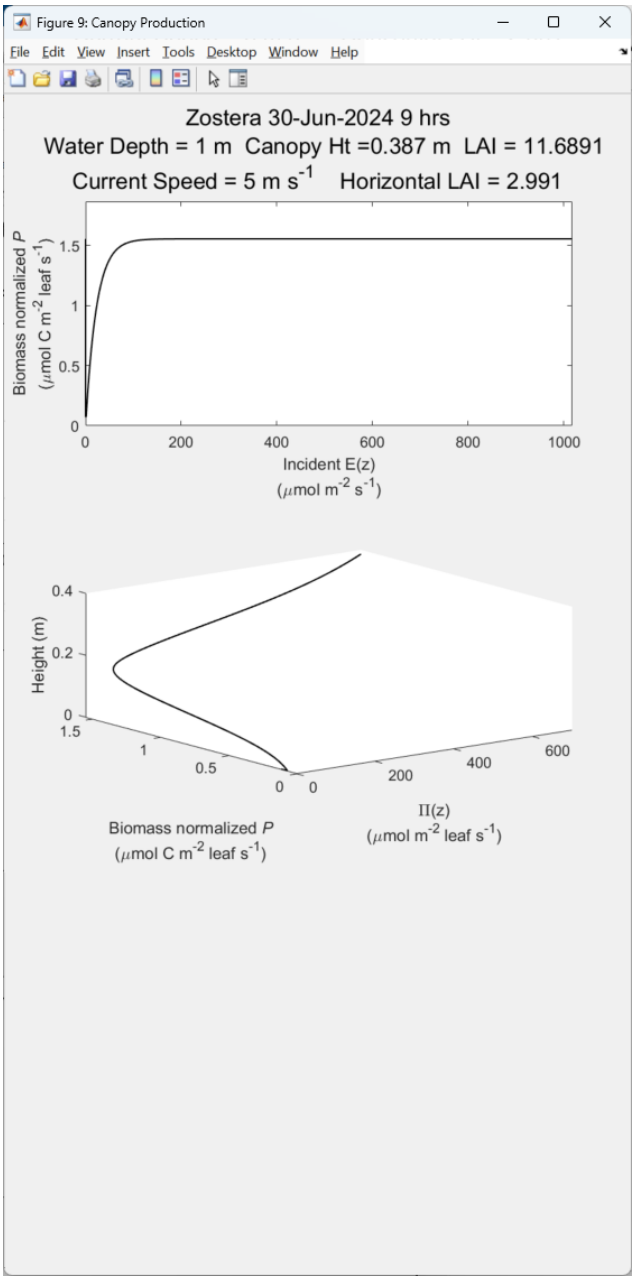
Figures 6 & 7. The vertical biomass distribution illustrates how biomass and leaf are area are distributed throughout the water column. The upper plot shows the relatve amount of biomass in each of the layers containing plant biomass, and the area under this curve sums to 1. The middle panel transforms the relative biomass distribution into an LAI distribution that sums to the total LAI indicated in the **Plant Morphology and Optical Properties** panel of the GUI. The bottom panel transforms the LAI distribution into the horizontally projected LAI used to calculate the fraction of light intercepted by the plant canopy. If the the realized canopy height is taller than the water column, the fraction of the canopy that exceeds the height of the water column is redistributed into the upper 10% of



the water column and the leavcs are assumed to be horizontal (Fig. 7).

Figures 8 & 9. The Canopy Production plots reveal rates of gross instantaneous leaf photosynthesis versus incident quantum irradiance (*E*, upper plot), gross instantaneous leaf photosynthesis vs. photosynthetically absorbed irradiance (Π) and height above the seafloor (middle plot) and gross daily leaf photosynthesis vs. height above the seafloor, assuming the simulation time was set to local solar noon (Fig. 8). If Time of Day < or > 12, the bottom plot will not be displayed (Fig.9).





Figures 10 to 13. The CIE color simulation plots provide a visual approximation of the color of the water using the 3-vector color matrix corresponding to reflectance spectra above the water as viewed at the surface (R_{rs}) and at the top of the SAV canopy (Canopy R) using the Commission Internationale de l'Êclairage (CIE) 1964 colorimetric standard for an idealized observer whose color matching properties correspond to the CIE color matching functions for the 10º field size and converting to the standard colors used in a computer monitor. The following examples demonstrate how the water colors at the sea surface (Rrs) and at the top of the canopy (Canopy R) are affected by water column transparency and canopy density.

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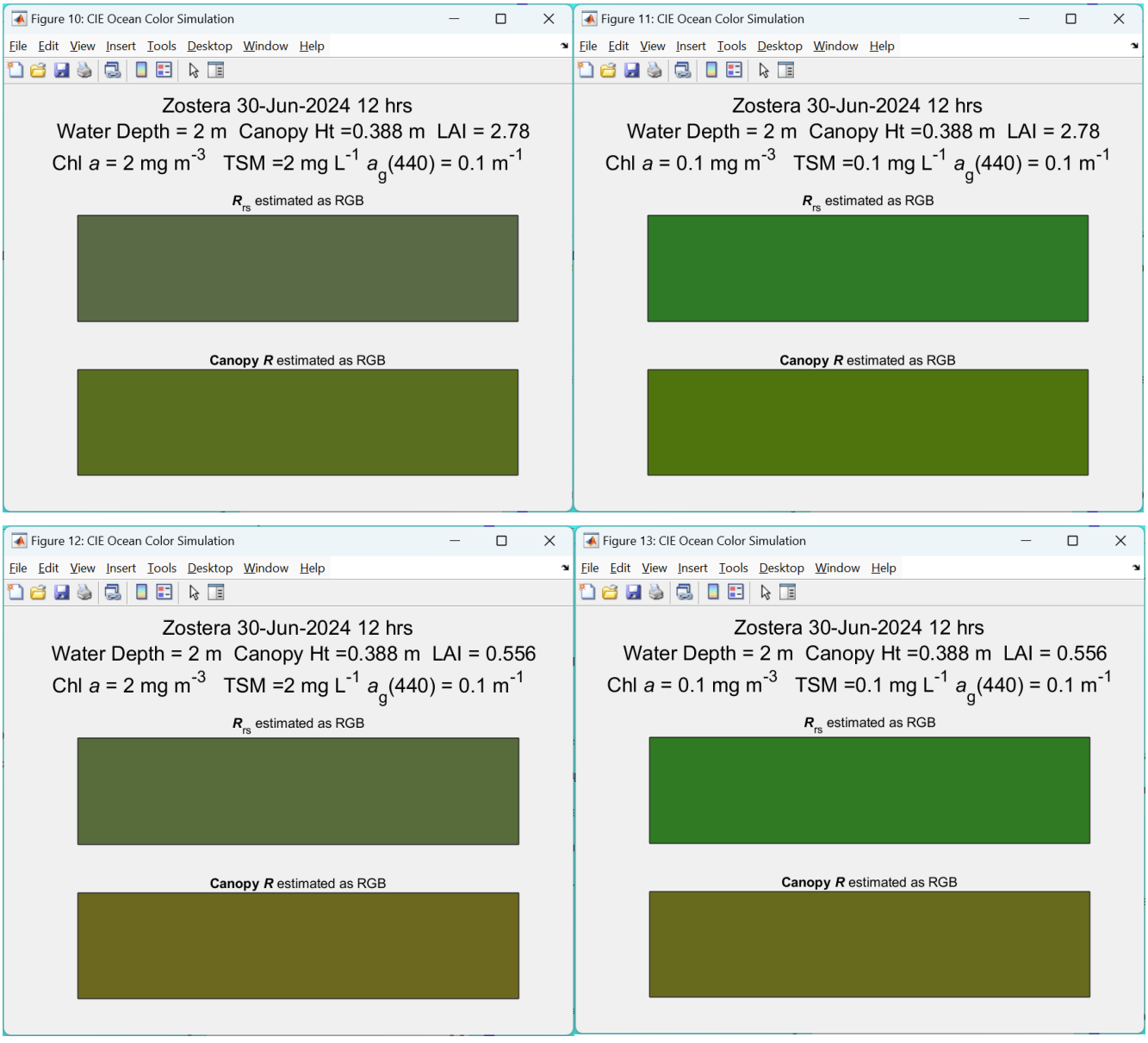

8.0 Literature Cited

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