**Using digital camera and Landsat imagery with eddy covariance data to model gross
primary production in restored wetlands**

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Abstract

Wetlands have the ability to accumulate large amounts of carbon (C), and therefore wetland restoration has been proposed as a means of sequestering atmospheric carbon dioxide (CO₂) to help mitigate climate change. There is a growing interest in using the C services of wetlands to help reduce habitat loss and finance restoration projects. However, including wetlands in C markets worldwide requires a better mechanistic understanding of CO₂ and methane exchange and instruments and models that can accurately and inexpensively monitor and predict these fluxes across global wetlands. Remote sensing technology, including near-surface and satellite instruments/approaches, is an effective tool for modeling C fluxes including gross primary productivity (GPP) from the site to global scale. In this study, we evaluate the potential of using digital cameras as a simple, cost-effective means of estimating GPP in restored wetlands, and assess the suitability of using Landsat data to model GPP in these environments for regional upscaling. Our research focused on restored temperate freshwater marshes due to their high C sequestration potential.

As observed in other ecosystems, daily GPP was strongly correlated with site greenness derived from camera imagery (GCC_{cam}). Based on this, we show the potential of using GCC_{cam} and eddy covariance data to adapt and parameterize a light use efficiency (LUE) model to predict daily GPP. The LUE model combining GCC_{cam} and meteorological data was able to explain up to 91 % of the variation in daily GPP at the restored marshes, and predict annual GPP budgets within 0 % to 20 % of observed budgets. However, model performance decreased with increasing site complexity, highlighting the need to explicitly consider spatial heterogeneity in LUE models. We also tested a similar model using Landsat-derived indices, and found that although model performance was high at a homogeneous wetland dominated by emergent

vegetation, data-model agreement decreased at a site comprised of a mixture of open water and vegetation, reflecting limitations of Landsat data. Nonetheless, we show that digital camera and Landsat imagery can be used to model photosynthesis in restored wetlands, providing low-cost methods for monitoring C capture that can be used in C market-funded wetland conservation and restoration.

Keywords: PhenoCam; Landsat; eddy covariance; photosynthesis; light use efficiency model; wetlands

1. Introduction

Wetlands play an important role in global carbon (C) dynamics due to their large soil C pools, high methane (CH₄) fluxes, and potential for C sequestration in soils and biomass (Bridgham et al., 2006; Mitra et al., 2005). Although wetlands cover only 2 to 6 % of the earth's land surface, they store a considerable proportion of the C in terrestrial soil reservoirs ($\sim 15 \times 10^2$ Pg) (Kayranli et al., 2009). Much of this C resides in peatlands, defined as wetland environments with > 40 cm of surface organic matter, which contain 16-33 % of the global soil C pool (Bridgham et al., 2006).

Due to their ability to accumulate large amounts of C as a result of limited decomposition rates in anaerobic soils and potential for high productivity, there has been a growing interest in the greenhouse gas (GHG) mitigation potential of wetland restoration (Crooks et al., 2011; Duarte et al., 2013; Hiraishi et al., 2014; Mack et al., 2012; Merrill et al., 2010). Wetland restoration and conservation projects can play an important role in managing atmospheric C (Pendleton et al., 2012), provided conditions are optimized to minimize CH₄ emissions. Freshwater marshes are especially productive ecosystems with a large capacity to sequester carbon dioxide (CO₂), as rates of net primary productivity can be comparable to that of tropical forests and intensive agricultural ecosystems (Miller and Fujii, 2010; Rocha and Goulden, 2009). In addition to C sequestration, wetlands offer numerous environmental co-benefits and ecosystem services, including wildlife habitat, improved water quality, and flood protection (Costanza et al., 1997; Zedler and Kercher, 2005). Wetland destruction and degradation is widespread, with over 50 % lost globally (Zedler and Kercher, 2005). Consequently, there is broad interest in using GHG offset programs and markets to help reduce habitat loss and finance restoration projects (Emmett-Mattox et al., 2011; McLeod et al., 2011). However, including

wetlands in C markets worldwide requires a better understanding of wetland C cycling and robust, yet inexpensive instruments and models that can accurately and cheaply monitor and predict C fluxes.

Remote sensing methods are effective tools for modeling C fluxes including gross primary productivity (GPP) and net primary productivity (NPP) from site to global scales (Hilker et al., 2008; Ruimy et al., 1999; Running et al., 2004; Xiao et al., 2004). Greenness indices from digital repeat photography, a form of near-surface remote sensing, has recently been shown to be strongly correlated with canopy-scale photosynthesis in deciduous broadleaf forests, evergreen needleleaf forests, grasslands, and croplands (Ahrends et al., 2009; Keenan et al., 2014; Migliavacca et al., 2011; Rossini et al., 2010; Toomey et al., 2015). However, whether camera-derived greenness can predict canopy-scale photosynthesis in wetland ecosystems is largely unexplored (e.g. Westergaard-Nielsen et al., 2013). Spaceborne remote sensing has traditionally been used to provide regional and global estimates of GPP (Heinsch et al., 2006; Kalfas et al., 2011; Running et al., 2000; Ryu et al., 2011). Current satellite remote sensing-based GPP models have largely been developed and validated for forest, crop, and grassland ecosystems (e.g. Gitelson et al., 2012; Heinsch et al., 2006; Sims et al., 2008; Sjöström et al., 2011), with a limited number of studies focused on wetland ecosystems (Kang et al., 2014; Wu et al., 2015). Most of these satellite-based studies have used the light use efficiency (LUE) approach to estimate GPP (Xiao et al., 2004), which is based on the work by Monteith (1972) and Monteith and Moss (1977) relating GPP to the amount of photosynthetically active radiation absorbed by photosynthetic biomass and the radiation use conversion efficiency of the vegetation (Heinsch et al., 2006).

Since 1999, the National Aeronautics and Space Administration (NASA) has provided GPP estimates for the entire globe based on the Moderate Resolution Imaging Spectroradiometer (MODIS) 1 km products (i.e., the MOD17A2 data product) (e.g. Running et al., 2004; Running et al., 2000). While the MODIS GPP algorithm provides reasonable spatio-temporal patterns and variability across a diverse range of biomes and climate types (Heinsch et al., 2006), it has been shown to underestimate GPP in natural wetlands (Kang et al., 2014) and flooded rice agriculture (Xin et al., 2017), which has been attributed to the climate data, pixel heterogeneity, and the light use efficiency parameter used in the MODIS GPP model. The coarse spatial resolution (1 km) of MODIS can also be problematic for estimating wetland GPP as these ecosystems can be small in size, and highly distributed, fragmented or disconnected from other habitat types (Byrd et al., 2014). Furthermore, for some wetland types, the deciduousness of these systems and the presence of standing litter can complicate estimation of the fraction of radiation absorbed by photosynthetically active elements of plants (Rocha et al., 2008). Possible alternatives to MODIS are the Landsat Thematic Mapper (TM), Landsat Enhanced Thematic Mapper (ETM), and Landsat Operational Land Imager (OLI) products, which have considerably finer spatial resolution (30 m pixel), spectral sensitivity in electromagnetic regions characteristic of vegetation function, and are available at no cost. Landsat data may therefore provide useful information to facilitate the analysis of CO₂ fluxes in wetland ecosystems. With the opening of Landsat archives to free and web-based access, the use of the sensor data with much greater spatial resolution may be well suited to accurately estimating GPP in natural and restored wetland ecosystems.

Based on the broad interest of including wetlands in GHG offset programs and markets, our aim is to provide accurate and inexpensive means of modeling wetland GPP that is relevant

to C market-funded wetland restoration. Specifically, the objectives of this study were to: 1) Evaluate the potential use of digital cameras as a simple and low-cost means of estimating GPP in wetland ecosystems, and 2) Assess the suitability of using Landsat data to model GPP in these environments. We combine eddy covariance CO₂ flux measurements, flux footprint analysis, and near-surface or satellite remote sensing data to investigate the potential of using the light use efficiency approach to accurately and cost-effectively estimate GPP in wetland systems.

2. Methods

2.1. Study sites

We focus on two freshwater marshes in the Sacramento-San Joaquin River Delta, California, USA (hereafter, the Delta). This study was designed to help inform methodologies to quantify GHG emission reductions from wetland restoration, including the methodology currently being developed specifically for the Delta (Deverel et al., 2016; Oikawa et al., 2017). Wetland restoration in the Delta offers large C removal potential. Since drainage of the wetlands in this region for agriculture around 1850, islands in the Delta have subsided between 3 and 8 m below sea level due largely to peat soil oxidation (Deverel and Leighton, 2010; Rojstaczer and Deverel, 1993). This peat soil oxidation corresponds to roughly 200×10^{12} g of C lost since drainage, making it a large atmospheric C source (Oikawa et al., 2017). Restoring drained and degraded peatlands in the Delta back to wetlands can help recover soil C and reverse soil subsidence as these ecosystems can sequester over $350 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Knox et al., 2015). Previous studies in the Delta have shown that converting a corn field to a wetland can have a GHG benefit up to $2100 \text{ g CO}_2\text{eq m}^{-2} \text{ yr}^{-1}$ after accounting for CH₄ emissions with a global warming potential of 32-45 times greater than CO₂ over a 100 year time horizon (Knox et al., 2015; Neubauer and Megonigal, 2015).

Field measurements were collected at two restored wetland sites in the Delta: West Pond wetland and Mayberry wetland (Figure 1). The West Pond site (38.0498°N, 121.7650°W) is a 0.03 km² wetland that was built in 1997 (Miller et al., 2008; Miller and Fujii, 2010). The site is permanently flooded to a depth of ~25 cm, and contains virtually no areas of open water. The wetland is narrow, only about 75 m wide, and characterized by a high intermixing of emergent marsh species, including *Schoenoplectus acutus* and *Typha* species. A dense layer of dead *S. acutus* stems 1 to 3 m tall mixed with other plant litter has accumulated at this site. We began eddy covariance measurements of CO₂, water and energy at this location in July 2012. Measurements from July 2012 through December 2015 were considered in this study.

The Mayberry site is a considerably larger restored wetland (1.2 km²) that was constructed in 2010. Flux measurements at this site were initiated shortly after construction (October 2010), and, again we considered measurements up until December 2015. Unlike the West Pond wetland, a heterogeneous bathymetry was excavated to generate regions of shallow water (a few centimeters) and adjoining areas of deeper water (1 – 2 m deep). As a result, this wetland is spatially heterogeneous, consisting of a mix of open water and vegetation patches (Figure 1), also comprised of *Typha* sp. and *Schoenoplectus acutus*. Vegetation dynamics at the site are controlled by in-filling of vegetation following flooding in 2010, with percent cover of emergent vegetation increasing from 0 to 63 % from 2010 to 2012, and changing very little thereafter (Matthes et al., 2014). Plant litter only began accumulating at the site following the 2012 growing season. Similar to the West Pond site, this wetland is permanently flooded to maximize peat accretion and C sequestration.

2.2. Eddy covariance flux measurements and micrometeorological data

Biosphere-atmosphere exchange of CO₂ (net ecosystem exchange; NEE), water (H₂O)

and energy were measured using the eddy covariance technique (Baldocchi et al., 1988) as described in Knox et al. (2015). A suite of meteorological measurements including air temperature (T_a), relative humidity, water table depth, incoming and outgoing shortwave and longwave radiation, incoming and reflected photosynthetically active radiation (PAR), and soil and water temperature accompanied flux measurements, with details given in Knox et al. (2015). Micrometeorological measurements were recorded as 30-minute averages. High-frequency 3-D wind speed components and virtual temperature were measured with a sonic anemometer (Windmaster, Gill Instruments Ltd., Lymington, Hampshire, UK) at 4.6 m, and between 3.7 and 5.7 m above the typical water surface at the West Pond and Mayberry wetlands, respectively. The variable sensor height at Mayberry reflects the fact that the tower was raised as the vegetation increased in height over time. At all sites, open-path gas analyzers measured molar concentrations of CO_2 , H_2O (LI-7500A, LI-COR Biosciences Inc., Lincoln, NE, USA), and CH_4 (LI-7700, LI-COR Biosciences Inc., Lincoln, NE, USA). Raw flux measurements were recorded at 10 Hz and eventually at 20 Hz on an analyzer interface unit (LI-7550, LI-COR Biosciences Inc., Lincoln, NE, USA) since it slightly reduced high-frequency attenuation (Knox et al., 2016). Half hourly fluxes were calculated using in-house MATLAB software (Mathworks Inc., Natick, MA, USA) (Detto et al., 2011; Hatala et al., 2012; Knox et al., 2015). The details of the flux processing routine are outlined in Knox et al. (2015). Briefly, this included despiking high-frequency data, applying coordinate rotations, correcting for effects of air density fluctuations, filtering fluxes with low friction velocity (<0.2 m/s), large vertical rotation angles ($> \pm 7^\circ$), and spikes in half hourly mean densities, variances, and covariances, and rejecting winds between $290 - 250^\circ$ for West Pond.

As outlined in other studies at these sites (Knox et al., 2015; Sturtevant et al., 2016), flux

measurements were gap-filled and partitioned using an artificial neural network (ANN) approach, as this approach has shown strong performance across a range of ecosystems types (Baldocchi and Sturtevant, 2015; Knox et al., 2016; Knox et al., 2015; Moffat et al., 2007). NEE was gap-filled with two separate ANNs, with one for daytime and another for nighttime conditions. Ecosystem respiration (ER) was then estimated by extrapolating the ANN trained for nighttime NEE to the entire day, and GPP was subsequently calculated by subtracting gap-filled NEE from modeled respiration (i.e. $NEE = ER - GPP$).

2.3. Flux footprint modeling

We used an analytical two-dimensional footprint model to model the spatial origin of the flux measurements (Detto et al., 2006; Hsieh et al., 2000). The eddy covariance flux footprint indicates the spatial portion of the landscape represented by each half hourly eddy covariance flux measurement. The footprint model uses wind speed and direction, roughness length (z_0 ; m), displacement height (d ; m), turbulence data and boundary layer stability to trace the probability that a certain air parcel measured by the eddy covariance sensors originated from any particular point within the landscape. This model has been tested against several data sets, and overall has been shown to succeed at reproducing the source region for flux measurements at eddy covariance towers in spatially heterogeneous ecosystems (Matthes et al., 2014). Continuous estimates of canopy height, z_0 and d were derived using surface layer theory and turbulence measurements (Pennypacker and Baldocchi, 2015). For the climatological footprints, data were separated by year at the Mayberry wetland since vegetation height and percent cover along with tower height changed throughout the study, resulting in considerable year-to-year differences in the integrated cumulative flux footprint (Figure 1). Data were not separated by year at the West Pond wetland since the tower height remained the same throughout the study and vegetation

cover and height were roughly the same between years. In Figure 1, we show the 85 % analytical footprint (i.e. the areal extent from which 85 % of the measured flux originated), because as the analytical footprint approaches 100 %, the area of the footprint expands rapidly, although there is only a small contribution to the measured flux from this extensive area (Matthes et al., 2014).

2.4. Digital camera set-up and image analysis

On both eddy covariance towers, a digital camera (i.e. ‘PhenoCam’) was installed in a fixed position, leveled with the horizon, with a view across the top of the canopy. Cameras were pointed toward the West, which corresponds to the dominant wind direction matching the eddy covariance tower footprint (Figure 1), and enclosed in waterproof housings. At both sites, Canon Powershot Series A (model A480 at Mayberry and A800 at West Pond) provided JPEG images (image resolution of 10 MP, with three color channels of 8-bit RGB color information, i.e. digital numbers (DN) ranging from 0 to 255) at 30-minute intervals for 12 hours per day. A Canon Hack Development Kit (CHDK; <http://chdk.wikia.com/wiki/CHDK>) was used with a custom script to take photos every 30 minutes. Cameras were operated in the automatic aperture and exposure mode.

Time series were first visually inspected for camera shifts and changes in field of view (FOV). The FOV remained largely unchanged at the West Pond wetland, however, larger shifts in the FOV were observed at the Mayberry wetland as the positioning of the camera changed a few times throughout the study, with the largest shift in FOV after March 2014 (Figure 2). Noting these changes, images were processed to extract regions of interest (ROI) encompassing all portions of the wetland within the foreground (Figure 2). As illustrated in Figure 3b, the changes in the FOV at Mayberry had a relatively small influence on the greenness indices described below.

To quantify canopy greenness, we calculated the green chromatic coordinate (GCC_{cam}), which is widely used to monitor canopy development and is strongly related to GPP (Ahrends et al., 2009; Migliavacca et al., 2011; Richardson et al., 2007; Sonnentag et al., 2012; Toomey et al., 2015)

$$GCC_{cam} = \frac{DN_G}{DN_R + DN_G + DN_B} \quad (1)$$

where the subscripts R, G, and B indicate the red, green, and blue channels, respectively. We also computed another color index, the excess green (ExG_{cam}) index

$$ExG_{cam} = 2DN_G - (DN_R + DN_B) \quad (2)$$

which can be less noisy than GCC_{cam} in some ecosystems, notably in conifer canopies (Toomey et al., 2015), although GCC_{cam} is generally more effective than ExG_{cam} in suppressing the effects of changes in scene illumination (Sonnentag et al., 2012).

Color indices were calculated for the selected ROI for each image, and computed for images recorded between 1300 to 1500 hours, although images with underexposed ROIs (defined as <15 % color saturation) were excluded. Daily GCC_{cam} and ExG_{cam} values were calculated using a three-day running median filter. This reduced some of the unwanted variability in the GCC_{cam} and ExG_{cam} due to changes in scene illumination compared to simply calculating a daily mean or median value. Sonnentag et al. (2012) suggest using a moving window approach that assigns the 90th percentile of all daytime values (0600 to 1800) within a three-day window to the centered day, resulting in three-day ExG_{cam} and GCC_{cam} . We also tested this method using a full year of measurements at West Pond, but found that this approach did not increase correlations between camera-derived indices and daily GPP.

Although we used the camera's automatic white balance setting and our sites weren't equipped with a reference panel (Richardson et al., 2007), we assessed the overall quality of the

retrieved signal and the day-to-day stability of the imagery color balance by extracting a ROI from the white CH₄ analyzer (LI-7700) at the Mayberry wetland. The coefficient of variation of the GCC_{cam} calculated for this ROI was 0.23 % during the 2013 growing season, which is over an order of magnitude smaller than the GCC_{cam} calculated for the primary ROI, giving us confidence in the quality of the retrieved signal (Migliavacca et al., 2011).

2.5. Landsat data and vegetation indices

Spectral vegetation indices (VIs) were quantified from the archive of Landsat satellite imagery: Landsat 5 TM for 2010-2011, Landsat 7 ETM+ for 2012 and Landsat 8 OLI for 2013-2015. For each year, the images representing cloud-free conditions over the study area were selected as geo-registered, terrain-corrected Level 1T product converted to surface reflectance with Landsat Ecosystem Disturbance Adaptive Processing System (LEDAPS; Masek et al. 2006). Five of the Landsat spectral bands with 30 m spatial resolution were used in this study: blue, green, red, near-infrared, and shortwave-infrared (Table A1). Using Google Earth Engine, a cloud-based geospatial data processing platform (<https://earthengine.google.com/>), Landsat pixels falling within the 85 % climatological footprint of the eddy covariance towers (Figure 1) were selected for subsequent analysis. For West Pond, where the footprint size did not vary significantly between years (Figure 1), the number of Landsat pixels falling within the footprint was consistently 12. The only partial exception was in 2012 when the only Landsat data source (Landsat 7 ETM+) had gaps, however, this only reduced the number of pixels for 4 of the 18 total data points that year. For Mayberry, where the size of the footprint differed between years (Figure 1), the number of Landsat pixels within the flux footprint was 24 in 2010 and 2011; predominantly 10 in 2012 (only 3 dates were influenced by gaps in the Landsat data); 9 in 2013; and 21 in 2014 and 2015. Overall, the spatial positions of the Landsat pixels from different-

mission surface reflectance products (Landsat 5, Landsat 7 and Landsat 8) were extremely consistent among years when compared in the Google Earth Engine interface. Using pixel band reflectance values, seven VIs were quantified (Table 1) and summarized as footprint averages for GPP estimation.

In addition to the Landsat-retrieved normalized difference vegetation index (NDVI_L), we also calculated broadband NDVI from radiometric measurements at West Pond (NDVI_{tower}) as described in Richardson et al. (2007) since this site was equipped with both a four-component net radiometer (NR01, Hukseflux, Delft, The Netherlands) and quantum sensors (PQS 1, Kipp and Zonen). Although broadband NDVI could not be estimated at the Mayberry wetland since this site only had a double-sided net radiometer, unlike West Pond, this tower was equipped with a spectral reflectance sensor, built in-house with light emitting diodes, allowing us to compute narrowband NDVI (NDVI_{tower}) as outlined in Ryu et al. (2010).

2.6. Light use efficiency models

We used a light use efficiency (LUE) approach to estimate GPP

$$GPP = \varepsilon \times fAPAR \times PAR \quad (3)$$

where PAR is incident photosynthetically active radiation (μmol photosynthetic photon flux density, PPFD), ε is light use efficiency ($\mu\text{mol CO}_2/\mu\text{mol PPFD}$), and fAPAR is the fraction of PAR absorbed by the canopy, which was estimated as (Rossini et al., 2010; Xiao et al., 2004)

$$fAPAR = a_0 + a_1 VI \quad (4)$$

where a_0 and a_1 are the coefficients relating VI, retrieved from either tower measurements (i.e. GCC_{cam}, ExG_{cam}, NDVI_{tower}) or Landsat data (Table 1) and fAPAR, and were estimated by fitting the LUE model against observed GPP.

Light use efficiency (ε) is affected by temperature and water stress (Kang et al., 2014;

298 Xiao et al., 2004)

$$\varepsilon = \varepsilon_0 \times T_{\text{scalar}} \times W_{\text{scalar}} \quad (5)$$

299 where ε_0 is the apparent quantum yield or maximum LUE ($\mu\text{mol CO}_2/\mu\text{mol PPFD}$) and T_{scalar} and
300 W_{scalar} are the scalars for the effects of temperature and water on canopy light use efficiency.

301 ε_0 values vary with vegetation type, and in this study ε_0 was estimated from eddy
302 covariance measurements by fitting a non-linear (i.e. rectangular hyperbola) model to the
303 relationship between NEE and PAR, based on data collected during peak growing season (mid-
304 July to mid-August) (Frolking et al., 1998; Kang et al., 2014; Xiao et al., 2004)

$$\text{NEE} = \frac{\varepsilon_0 \times \text{PAR} \times \text{GPP}_{\text{max}}}{\varepsilon_0 \times \text{PAR} + \text{GPP}_{\text{max}}} + \text{ER} \quad (6)$$

305 where GPP_{max} is the maximum gross productivity ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). We used nonlinear least
306 squares regression to fit the light response curves with a rectangular hyperbola (MATLAB,
307 version 8.6.0, Mathworks Inc., Natick, MA, USA). This gave ε_0 values of $0.035 \mu\text{mol CO}_2/\mu\text{mol}$
308 PPFD ($0.42 \text{ g C/mol PPFD}$) and $0.020 \mu\text{mol CO}_2/\mu\text{mol PPFD}$ ($0.24 \text{ g C/mol PPFD}$) for the West
309 Pond and Mayberry wetlands, respectively. Lower ecosystem-scale ε_0 at the Mayberry wetland
310 reflects the fact that this is a heterogeneous canopy, and therefore at the canopy level ε_0 is
311 influenced by the presence of both vegetation and open water.

312 In this study, we used the down-regulation scalars from the satellite-based Vegetation
313 Photosynthesis Model (VPM) (Xiao et al., 2004). As in the VPM model, T_{scalar} was estimated at
314 each time step using the equation developed for the Terrestrial Ecosystem Model (Raich et al.,
315 1991)

$$T_{\text{scalar}} = \frac{(T - T_{\text{min}})(T - T_{\text{max}})}{[(T - T_{\text{min}})(T - T_{\text{max}})] - (T - T_{\text{opt}})^2} \quad (7)$$

316 where T_{min} , T_{max} , and T_{opt} are minimum, maximum, and optimal temperature for photosynthesis,

respectively. As wetland plants can photosynthesize across a broad range, $T_{\min}$ and $T_{\max}$ were set to 0 °C and 50 °C (Larcher, 2003), and we used a value of 22 °C for T_{opt} based on the relationship between GPP and air temperature (Xin et al., 2016). For Landsat-retrieved VIs only, W_{scalar} was calculated using a simple approach utilizing a water-sensitive vegetation index (Oikawa et al., 2017; Xiao et al., 2004)

$$W_{\text{scalar}} = \frac{1 + \text{LSWI}}{1 + \text{LSWI}_{\max}} \quad (8)$$

where $\text{LSWI}_{\max}$ is the maximum land surface water index (LSWI; Table 1) within the growing season, and was estimated separately for each year (Kang et al., 2014).

2.7. Model parameter estimates and evaluation of model performance

Best-fit model parameters were estimated using linear least square regression implemented in MATLAB (version 8.6.0, Mathworks Inc., Natick, MA, USA). At West Pond, model parameterization was conducted with data from 2012, 2013 and 2015, while data from 2014 were used for validation. Similarly, at Mayberry, all data excluding measurements from 2014 were used for model parameterization and data from 2014 were again used in validation. We selected 2014 as the validation period since there were minimal gaps in model drivers that year. Model performance was evaluated using the linear relationship between modeled and observed daily GPP (slope and intercept), the coefficient of determination (R^2), and the root mean square error (RMSE). We also explored the model's ability to predict annual and multi-year GPP budgets. When estimating modeled GPP sums, gaps in PAR and T_a were estimated using data from a nearby weather station. Continuous daily time series for both Landsat-derived and tower-based VIs were obtained by piecewise cubic interpolation (MATLAB).

3. Results

3.1. Seasonal dynamics of photosynthesis and vegetation indices

3.1.1. Tower-based indices

Both wetland sites exhibited clear seasonality in both daily GPP and GCC_{cam} , with high values during the primary growing season and low values during the inactive period (Figure 3). Both sites also showed considerable interannual variability in GPP, particularly at the recently restored Mayberry wetland (Figure 3). GCC_{cam} closely paralleled year-to-year differences in GPP at both sites (Figure 3a,b). At Mayberry, with the exception of the first two growing seasons characterized by rapid vegetation growth and expansion, GCC_{cam} tracked daily GPP nearly synchronously, and was able to capture the decrease in GPP in the middle of the 2014 growing season caused by a caterpillar infestation at the site. At the West Pond wetland, daily GPP increased somewhat more slowly than GCC_{cam} , reaching maximum values up to ~4 weeks after GCC_{cam} reached peak values, and then tended to decline before the decrease in GCC_{cam} . Correlations between daily GPP and GCC_{cam} were high at both sites, ranging between 0.65 and 0.89 (Table 2). Lower correlations were observed at the Mayberry wetland in part due to the more heterogeneous nature of this site; as a result of the flux footprint moving over the mosaic of open water and vegetation, there was considerable day-to-day variability in GPP, however, this was not detected by GCC_{cam} (Figure 3b).

Across all years, the relationship between daily GPP and GCC_{cam} was essentially linear at both wetland sites (Table 2; Figure 4), although at Mayberry this relationship was influenced by the time since restoration. At this recently restored site, in the first two years following restoration (2011 and 2012), when emergent marsh vegetation colonization and spread was rapid and there was very little accumulation of standing leaf litter, there was a non-linear relationship between daily GPP and GCC_{cam} , with higher GCC_{cam} values for a given daily GPP value than in subsequent years (Figure 4b). After 2012, daily GPP scaled linearly with GCC_{cam} and the

relationship between daily GPP and GCC_{cam} showed little variation between years, similar to the older West Pond wetland (Figure 4a,b).

At West Pond, the relationship between daily GPP and ExG_{cam} was similar to that observed for GCC_{cam} (Table 2), however, at Mayberry GCC_{cam} somewhat outperformed ExG_{cam} since GCC_{cam} was better able to capture interannual variability in GPP. Since GCC_{cam} was better correlated with daily GPP than ExG_{cam} , we focus on GCC_{cam} in the subsequent results.

Broadband NDVI measured at West Pond using radiometric measurements and narrowband NDVI estimated at Mayberry using an in-house built LED-sensor (both $NDVI_{tower}$) also showed clear seasonality, however, at both wetland sites $NDVI_{tower}$ showed poorer agreement with daily GPP compared with camera-derived indices (Table 2). Furthermore, $NDVI_{tower}$ at West Pond (and to a lesser extent at Mayberry) appeared to saturate at high GPP values (Figure 4c,d), making GCC_{cam} a better predictor of interannual variability in GPP (Table 2; Figure 3).

3.1.2. Landsat-based indices

All VIs retrieved from Landsat data showed strong seasonality, although some indices tracked GPP better than others (Table 2; Figure 5). Comparisons between VIs and daily GPP showed that at both wetland sites EVI_L and $SAVI_L$ had the strongest relationship with GPP (Table 2), as the seasonal dynamics of these indices followed the phase and amplitude of GPP better than the other VIs (Figure 5). Conversely, at both wetlands, GCC_L and $GNDVI_L$ had the weakest relationship with GPP (Table 2). While VIs generally paralleled GPP relatively well across years, there were two notable discrepancies; all VIs at West Pond reached peaked values in 2015 although GPP was lowest during that growing season, and VIs at Mayberry remained high in 2013 despite a considerable drop in GPP that year. The regression of $LSWI_L$ against

observed GPP also showed that land surface water content was significantly ($p < 0.001$) correlated with photosynthesis at both wetlands (Table 2). Again, GPP was better correlated with VIs at West Pond ($R^2 = 0.49$ to 0.72) than Mayberry ($R^2 = 0.23$ to 0.52) due to the more homogenous and less dynamic nature of the West Pond wetland.

3.2. Model performance

3.2.1. Tower-based indices

Performance of the LUE model using GCC_{cam} as a proxy for fAPAR was strong, with high data-model agreement, particularly at the older, more homogeneous West Pond site (slope = 0.90 , intercept = 0.68 ; $R^2 = 0.91$; $RMSE = 1.27 \text{ g C m}^{-2} \text{ d}^{-1}$ calculated during the validation period) (Table 3; Figure 6). Nonetheless, despite higher variability in GPP, model performance at the Mayberry wetland was also strong (slope = 0.75 , intercept = 0.15 ; $R^2 = 0.91$; $RMSE = 1.47 \text{ g C m}^{-2} \text{ d}^{-1}$ calculated during the validation period). At West Pond, the model overestimated GPP by only 6 % during the validation period (2014) and underestimated GPP by less than 1 % across the entire observation period (2013-2015) (Table 4). At Mayberry, discrepancies between measured and modeled annual GPP sums were larger, again due to the more dynamic nature of GPP within and across years, with the model overestimating GPP by 20 % during the validation period (2014), but underestimating GPP by only 4 % for the whole record (2011-2014) (Table 4). While modeled and observed daily GPP at Mayberry varied nearly in phase, at West Pond modeled GPP tended to peak a few weeks before observed GPP (Figure 6), largely as a result of daily GPP increasing somewhat more slowly than GCC_{cam} as described above (Figure 3). In addition, at both sites, the LUE model tended to underestimate GPP during less sunny conditions.

For both West Pond and Mayberry, model performance metrics indicated that data-model agreement tended to be slightly better when GCC_{cam} rather than $NDVI_{tower}$ was included in the

LUE model (Table 3). Furthermore, when comparing observed and modeled GPP sums, the relative error was consistently lower when GCC_{cam} rather than $NDVI_{tower}$ was used as a proxy for fAPAR (Table 4). As noted previously, interannual dynamics of GCC_{cam} followed those of GPP better than $NDVI_{tower}$ since GCC_{cam} , unlike $NDVI_{tower}$, tended not to saturate.

3.2.2. Landsat-derived indices

All VIs resulted in overall reasonable agreement between predicted and observed GPP at the West Pond wetland (slope = 0.65 to 0.77, intercept = 1.09 to 2.59; $R^2 = 0.86$ to 0.97; RMSE = 1.11 to 1.89 g C m⁻² d⁻¹ calculated during the validation period). When considering individual vegetation indices, EVI_L and $SAVI_L$ tended to slightly outperform the other indices while GCC_L and ExG_L resulted in the poorest agreement between predicted and observed GPP (Table 3). Despite the limited temporal frequency of Landsat, data were acquired at sufficient intervals to reasonably capture seasonal dynamics of GPP (Figure 7). Interpolation of VIs between sampling dates resulted in overall good agreement between observed and modeled GPP sums when integrated across years (Table 4), with relative errors across the three full years of measurements (2013-2015) as low as 2 % and 3 % when EVI_L and $SAVI_L$ were included in the LUE model, respectively. Although relative errors across years were small, they were larger for individual years (Table 4). For instance, when considering EVI_L , the Landsat-derived vegetation index resulting in best model performance, modeled GPP was underestimated by 13 % in 2013 and overestimated by 26 % in 2015 (Table 4; Figure 7). The greater overestimation in 2015 relative to the underestimation in 2013 was largely due to the earlier and somewhat more rapid increase in EVI_L compared to GPP in 2015 (Figure 5).

Model performance across all vegetation indices was lower at Mayberry, although again EVI_L resulted in best model performance (slope = 0.69, intercept = 1.48; $R^2 = 0.88$; RMSE =

1.42 g C m⁻² d⁻¹ calculated during the validation period), while GCC_L resulted in the lowest fit between predicted and observed GPP (Table 3). Similar to West Pond, the relative error across years was low (between -6 % and 1 %), although within years modeled GPP could be strongly over or underestimated (Table 4).

3.2.3. Tower-based vs. Landsat-derived VIs

Comparisons between vegetation indices and GPP showed that GCC_{cam} followed the seasonal and interannual dynamics of GPP better than other VIs (Figure 3 and Figure 5). As such, GCC_{cam} resulted in the best agreement between observed and predicted GPP when compared to the other VIs explored in this study (Table 3). Although this is in part related to the greater temporal frequency of GCC_{cam} relative to the VIs obtained from Landsat, even when GCC_{cam} was temporally downsampled to correspond to the same dates as the Landsat imagery (GCC_{cam_L}), camera-derived GCC was still better correlated with daily GPP and resulted in stronger model performance compared with all Landsat-based VIs (Table 2; Table 3).

4. Discussion

4.1. Digital camera imagery for GPP modeling – strengths and limitations

As observed in other ecosystems, including forests, grasslands, and crops (Keenan et al., 2014; Migliavacca et al., 2011; Richardson et al., 2009; Toomey et al., 2015), GPP was highly correlated with greenness derived from camera imagery at both wetlands. At both sites, GCC_{cam} also strongly tracked interannual variability in GPP, better than tower-based NDVI measurements, highlighting that interannual variation in annual GPP can be estimated using camera-derived color indices (Toomey et al., 2015). This in part reflects the ability of GCC_{cam} at both Delta sites to capture year-to-year differences in litter accumulation, with lower GCC_{cam} values reflecting years with higher standing litter, which shades the green leaves resulting in a

reduction in GPP (Rocha and Goulden, 2008; Rocha et al., 2008).

We show that camera-based color indices combined with eddy covariance measurements are highly valuable for developing and testing LUE models to predict daily photosynthesis. Analysis of the LUE model highlighted that GPP can be accurately predicted by combining GCC_{cam} and meteorological data, similar to the results obtained by Migliavacca et al. (2011) for a subalpine grassland. We were able to explain up to 91 % of the variation in GPP, and predict annual GPP budgets within 0 % to 20 % of observed budgets, and cumulative GPP across years to within 0 % to 4 % of observed values. However, as a result of the considerable differences between the wetlands, model parameters differed between sites ($\epsilon_0 = 0.42$ g C/mol PPFD and 0.24 g C/mol PPFD, $a_0 = -1.5$ and -2.6 and $a_1 = 4.8$ and 8.4 for West Pond and Mayberry, respectively). The ϵ_0 values reported in this study fall within the range of growing season values reported for a temperate freshwater marsh (0.23 to 0.56 g C/mol PPFD) (Strachan et al., 2015), and within the range of values reported for northern peatlands (0.08 to 0.46 g C/mol PPFD) (Frolking et al., 1998). Differences in model parameters between sites reflect one of the drawbacks of using empirical approaches for estimating fAPAR (Hilker et al., 2008). Although re-parameterization of the model is required when applying it to other wetlands types (or when large differences are observed within wetland types), once the model has been developed for a representative site, it can be applied to other similar environments at minimal costs (i.e. the cost of a digital camera or webcam which runs from around \$100 to \$5000 USD; Brown et al. (2016)), with meteorological data obtained from nearby weather stations.

Since consumer-grade cameras are not calibrated scientific instruments, it is important to understand the strengths and limitations of the information they produce (Brown et al., 2016; Ide and Oguma, 2010; Richardson et al., 2013; Sonnentag et al., 2012). Camera hardware and

settings, and image format have considerable impact on image quality (Brown et al., 2016; Richardson et al., 2009; Sonnentag et al., 2012), and GCC_{cam} and ExG_{cam} calculated for the same site and ROI using different camera types and models are not directly comparable (Figure 8 in Sonnentag et al., 2012). As such, consistency in camera hardware and image format, or the development of calibration protocols and standards is important when developing and applying LUE models across sites, particularly with a growing global digital camera – “PhenoCam” – network (Brown et al., 2016; Richardson et al., 2013). These limitations and uncertainties need to be addressed in order to improve the reliability of camera-based color indices for monitoring and modeling canopy phenology and photosynthesis.

Furthermore, studies should be designed to minimize changes in camera positioning and location to maintain a continuous image record of a consistent FOV to ensure long-term data continuity and facilitate automated processing (Brown et al., 2016). While this was achieved at West Pond, the FOV and ROI at Mayberry changed several times during the study due to the changes in tower set-up and camera location. Despite these changes, GCC_{cam} and GPP remained strongly correlated and high data-model agreement was observed, indicating that this approach is relatively robust to changes in FOV so long as the FOV is representative of wetland conditions. However, the relationship between GCC_{cam} and GPP could have potentially been improved by minimizing changes in the FOV.

Our analysis also revealed a number of other limitations of using GCC_{cam} to model GPP. Similar to other studies, we observed that GCC_{cam} did not always vary synchronously with daily GPP (Keenan et al., 2014; Toomey et al., 2015), but rather daily GPP tended to lag behind increases in canopy greenness in spring and lead decreases in greenness in fall, particularly at the West Pond wetland. This was reflected in modeled daily GPP reaching peak values before daily

GPP estimated from eddy covariance measurements. This is likely caused by seasonal variation in foliage pigments, and accentuated by the viewing angle of the camera (Keenan et al., 2014; Toomey et al., 2015). Although in this study we did not explicitly consider the spatial heterogeneity at Mayberry, the greater complexity of this site notably influenced the reliability of using camera-based indices for the development and parameterization of the LUE model. The lower model performance at the Mayberry wetland can in part be explained by the fact that GCC_{cam} is a saturating, nonlinear function that is influenced by developmental changes in leaf color and the influence leaf area index, and in this case the percent cover of emergent vegetation, on the mixing of leaf color with background color (Keenan et al., 2014). Furthermore, as a result of the flux footprint moving over the complex mosaic of open water and vegetation, greater day-to-day variability in GPP was also observed at this site (as indicated by the higher variance in the daily difference in GPP; data not shown). The fact that the camera-based indices do not detect this short-term variability in GPP also contributes to poorer ability of GCC_{cam} to predict daily GPP at Mayberry compared to West Pond.

4.2. Landsat-derived indices for GPP modeling – strengths and limitations

We chose Landsat data over MODIS imagery since despite the lower frequency of data acquisition, greater spatial resolution is needed when considering wetlands in the Sacramento-San Joaquin Delta and elsewhere since these ecosystems are often heterogeneous, small and fragmented within the landscape (Byrd et al., 2014). For example, in the Delta the area of remaining wetlands represents only 3 % of its historical extent. We also only selected Landsat pixels falling within the climatological footprints since considering the flux footprint is important when comparing remote sensing indices with eddy covariance flux measurements.

Although GCC_{cam} resulted in better data-model agreement relative to the other vegetation

indices explored in this study, Landsat-derived VIs also resulted in overall good agreement between predicted and observed GPP at the homogeneous and established West Pond wetland. As observed in other studies (Hilker et al., 2008; Huete et al., 2002), EVI_L outperformed the other Landsat indices we investigated, since EVI is designed to enhance the vegetation signal with improved sensitivity to high biomass thus de-coupling canopy background signals and reducing atmospheric influences (Hilker et al., 2008; Huete et al., 2002). This index is also a good estimate of the amount of PAR absorbed by photosynthetically active vegetation (Kalfas et al., 2011; Kang et al., 2014; Rocha et al., 2008; Xiao et al., 2004).

Although EVI_L typically followed seasonal and interannual dynamics in GPP at West Pond, EVI_L reached peak values in 2015, while GPP remained lower relative to other years. This reflects the influence of a newly restored wetland built in 2013 surrounding the West Pond wetland, where emergent vegetation at this recently restored site expanded rapidly at the end of 2014 and in 2015. The lack of litter (Byrd et al., 2014) coupled with the high reflectance of the young canopy (Ustin and Trabucco, 2000) likely influenced band reflectance values in some of the Landsat pixels falling within the flux footprint, contributing to the decoupling in the dynamics of Landsat-based VIs and GPP in 2015. Nonetheless, despite the limited temporal frequency of Landsat data, we show that LUE models using EVI_L can adequately predict daily and annual GPP in small, homogeneous wetland ecosystems, allowing for regional upscaling of wetland photosynthesis and representing an improvement over MODIS GPP. However, as with any empirical determination of absorbed PAR, a direct conversion of satellite spectral reflectance of surface fAPAR over large areas is difficult, since empirical relationships are site and sensor specific, can vary in time and space, and may be unsuitable for application to large areas (Hilker et al., 2008).

Again the greater spatial and temporal variability at Mayberry resulted in poorer agreement between observed and modeled GPP when compared with West Pond. The divergence in the dynamics of Landsat-based VIs and GPP at Mayberry was particularly pronounced in the first few years following restoration, as vegetation began to emerge and the fraction of vegetation and water changed rapidly. This can be attributed to issues of patch size, vegetation dynamics, data saturation and water inundation that are important to consider in these heterogeneous wetland sites (Byrd et al., 2014). In particular, field spectra of emergent wetland vegetation are strongly influenced by water depth, which can highly influence VI-based estimates of wetland productivity (Byrd et al., 2014; Kearney et al., 2009). This represents a drawback of estimating GPP using Landsat data and explains in part why GCC_{cam} , which is less influenced by background effects due to the viewing angle of the camera, is a better predictor of GPP in these heterogeneous environments. However, the horizontal camera-viewing angle that emphasizes vegetation and reduces the background effect from water can ‘over-emphasize’ the role of vegetation, thus also contributing to potential model error.

4.3. Implications and future work

In this study, we show the potential of using a simple LUE approach combining camera-derived greenness indices or Landsat-based vegetation indices and meteorological data to inexpensively and accurately predict canopy-scale photosynthesis, thereby providing a valuable tool for C market-funded wetland conservation and restoration. While initial model development requires near-continuous, ecosystem scale CO_2 flux measurements, once the model is parameterized and validated for a representative wetland site, it can be applied to other similar environments, allowing for cost-effective, long-term monitoring and/or spatial upscaling of wetland photosynthesis. This is relevant to a growing number of wetland restoration and

conservation projects worldwide (Mitsch and Gosselink, 2007). In the Delta alone, over 12 km² of freshwater marshes have been restored since 2013, with more wetland restoration projects anticipated in the near future. While we showed the potential of using this approach in non-tidal, temperate freshwater marshes, additional studies are needed to investigate the potential of applying this LUE method across the broad range of wetland types.

This study, however, also highlights some limitations of this modeling approach, notably the influence of spatial heterogeneity on model performance. While directly addressing spatial heterogeneity is beyond the scope of this paper, future efforts should explicitly consider spatial heterogeneity when modeling photosynthesis using LUE models. This can potentially be done by considering vegetation patches and open water separately (rather than treating the canopy as a single entity as we did in this study, and is typically done by others), similar to the two-layer LUE model proposed by Huemmrich et al. (2010). However, for satellite-remote sensing VIs, this may require higher spatial resolution imagery that currently may be cost prohibitive and/or of limited temporal frequency. In addition, time since restoration appears to influence the relationship between VIs and GPP, and the reliability of using these indices to predict photosynthesis in the early years following restoration. Additional research is needed to more thoroughly investigate how time since restoration influences model performance and reliability. Furthermore, due to different viewing angles, background effects may more strongly influence Landsat-based indices compared with camera-derived indices, reflecting potential limitations of using Landsat data. However, Landsat imagery offers promising potential for regional upscaling of wetland photosynthesis, particularly in more homogeneous and established systems. Although model performance was highest using camera-based indices, digital cameras are not calibrated scientific instruments, and therefore further work is needed to develop calibration protocols and

standards to ensure congruence of long-term datasets across sites.

5. Conclusion

This study demonstrates that camera-based and Landsat-derived indices can be used to model photosynthesis in wetland ecosystems. Although some limitations still need to be addressed, the LUE approach presented in this paper provides a simple and cost-effective means of monitoring C capture that can be used in C market-funded wetland conservation and restoration. Although in this study we focus only on modeling C uptake, the model we present can be integrated into full biogeochemical models designed for C market and Cap-and-Trade systems (e.g. Oikawa et al., 2017) to accurately estimate both CO₂ and CH₄ exchange. This is critical for evaluating the full C benefits and GHG mitigation potential of wetland restoration, thereby providing opportunities to counteract the widespread degradation of wetlands worldwide.

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615 **7. Appendix**

616 This appendix provides additional details on the Landsat spectral bands used in this study.

617 Table A1. Landsat spectral bands used in this study.

Spectral band	Landsat 5	Landsat 7	Landsat 8
Blue	Band 1: 450 – 520 nm	Band 1: 450 – 520 nm	Band 2: 450 – 510 nm
Green	Band 2: 520 – 600 nm	Band 2: 520 – 600 nm	Band 3: 530 – 590 nm
Red	Band 3: 630-690 nm	Band 3: 630-690 nm	Band 4: 640 – 670 nm
Near-infrared	Band 4: 760 – 900 nm	Band 4: 770 – 900 nm	Band 5: 850 – 880
Shortwave-infrared	Band 5: 1550 – 1750 nm	Band 5: 1550 – 1750 nm	Band 6: 1570 – 1650 nm

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893 **9. Tables**

894 Table 1. Landsat-derived vegetation indices used in this study.

Landsat vegetation index	Formula	Reference
Enhanced vegetation index (EVI _L)	$G \times (\rho_{NIR} - \rho_{red}) / (\rho_{NIR} + C1 \times \rho_{red} - C2 \times \rho_{blue} + L)$	Huete et al. (2002)
Normalized difference vegetation index (NDVI _L)	$(\rho_{NIR} - \rho_{red}) / (\rho_{NIR} + \rho_{red})$	Kriegler et al. (1969), Rouse et al. (1974)
Green NDVI (GNDVI _L)	$(\rho_{NIR} - \rho_{green}) / (\rho_{NIR} + \rho_{green})$	Gitelson and Merzlyak (1997)
Soil enhanced vegetation index (SAVI _L)	$(\rho_{NIR} - \rho_{red} + L) / (\rho_{NIR} + \rho_{red}) \times (1 + L)$	Huete (1988)
Land surface water index (LSWI _L)	$(\rho_{NIR} - \rho_{SWIR}) / (\rho_{NIR} + \rho_{SWIR})$	Xiao et al. (2004)
Green chromatic coordinate (GCC _L)	$\rho_{green} / (\rho_{green} + \rho_{red} + \rho_{blue})$	Woebbecke et al. (1995)
Excess green index (ExG _L)	$2 \times \rho_{green} - (\rho_{red} + \rho_{blue})$	Woebbecke et al. (1995), Meyer et al. (1998)

895

896

897 Table 2. Coefficients of determination for linear (R^2) and quadratic regression (R^2_{quad}) of camera-derived greenness indices (GCC_{cam} ,
898 ExG_{cam}), tower-based NDVI ($\text{NDVI}_{\text{tower}}$), and Landsat-derived vegetation indices (EVI_L , SAVI_L , NDVI_L , GNDVI_L , ExG_L , GCC_L ,
899 LSWI_L) with daily GPP, and number of daily samples (n) corresponding to each vegetation index.

	West Pond			Mayberry		
	R^2	R^2_{quad}	n	R^2	R^2_{quad}	n
GCC_{cam}	0.88	0.89	1193	0.65	0.65	1650
$\text{GCC}_{\text{cam}_L}^a$	0.93	0.92	41	0.85	0.71	59
ExG_{cam}	0.85	0.87	1193	0.55	0.55	1650
$\text{NDVI}_{\text{tower}}$	0.64	0.67	1307	0.58	0.59	1305
EVI_L	0.72	0.71	44	0.50	0.52	65
SAVI_L	0.71	0.70	44	0.47	0.49	65
NDVI_L	0.61	0.59	44	0.40	0.41	65
GNDVI_L	0.51	0.49	44	0.24	0.23	65
ExG_L	0.63	0.68	44	0.38	0.36	65
GCC_L	0.57	0.56	44	0.28	0.27	65
LSWI_L	0.64	0.62	44	0.40	0.39	65

900 ^a $\text{GCC}_{\text{cam}_L}$ indicates GCC_{cam} measurements corresponding to the same dates as the Landsat imagery. Note that in 2015 there were
901 three days when Landsat imagery was available but there were no available camera images, which explains the lower number of
902 samples for $\text{GCC}_{\text{cam}_L}$ (n = 41) compared with the Landsat VIs (n = 44).

903

904 Table 3. Comparison of observed and simulated daily GPP at the West Pond (WP) and Mayberry (MB) wetlands during the
 905 parameterization (all years excluding 2014) and validation (2014) periods.

		R^2		Slope (g C m ⁻² d ⁻¹)		Intercept (g C m ⁻² d ⁻¹)		RMSE (g C m ⁻² d ⁻¹)		n
		Param	Val	Param	Val	Param	Val	Param	Val	
WP	GCC _{cam}	0.91	0.91	0.94	0.90	0.16	0.68	1.30	1.27	1193
	GCC _{cam_L}	0.93	0.92	0.95	0.91	0.18	0.56	1.17	1.15	41
	NDVI _{tower}	0.86	0.94	0.81	0.83	1.04	1.37	1.65	1.34	1307
	EVI _L	0.79	0.97	0.77	0.75	1.39	1.10	1.95	1.21	44
	SAVI _L	0.78	0.97	0.77	0.77	1.44	1.09	1.97	1.11	44
	NDVI _L	0.78	0.96	0.75	0.75	1.57	1.32	1.98	1.20	44
	GNDVI _L	0.78	0.96	0.72	0.77	1.79	1.30	2.02	1.14	44
	ExG _L	0.74	0.87	0.71	0.68	1.83	2.28	2.16	1.76	44
	GCC _L	0.73	0.86	0.67	0.65	2.14	2.59	2.21	1.89	44
MB	GCC _{cam}	0.84	0.91	0.87	0.75	0.40	0.15	1.55	1.47	1650
	GCC _{cam_L}	0.83	0.90	0.86	0.63	0.60	0.90	1.55	1.75	59
	NDVI _{tower}	0.76	0.93	0.77	1.26	1.07	0.34	2.02	2.00	1305
	EVI _L	0.69	0.88	0.70	0.69	1.55	1.48	2.04	1.42	65
	SAVI _L	0.66	0.87	0.67	0.70	1.73	1.60	2.14	1.43	65
	NDVI _L	0.66	0.85	0.66	0.63	1.80	1.52	2.13	1.59	65
	GNDVI _L	0.62	0.80	0.59	0.63	2.19	2.33	2.26	1.81	65
	ExG _L	0.44	0.87	0.44	0.60	2.92	1.99	2.74	1.61	65
	GCC _L	0.42	0.80	0.40	0.56	3.21	2.56	2.78	1.90	65

Table 4. Cumulative eddy covariance estimated gross primary production (GPP_{obs} ; g C/m²) and modeled GPP (GPP_{pred} ; g C/m²) for a range of vegetation indices, and comparison between observed and predicted GPP (relative error^a; RE (%)) at both wetland sites.

		GCC _{cam}			NDVI _{tower}		EVI _L		SAVI _L		NDVI _L		GNDVI _L		ExG _L		GCC _L	
		GPP_{obs}	GPP_{pred}	RE	GPP_{pred}	RE	GPP_{pred}	RE	GPP_{pred}	RE	GPP_{pred}	RE	GPP_{pred}	RE	GPP_{pred}	RE	GPP_{pred}	RE
WP	2013	1780	1716	-4	1740	-2	1542	-13	1568	-12	1610	-10	1647	-7	1722	-3	1769	-1
	2014	1513	1598	6	1757	16	1464	-3	1490	-2	1541	2	1574	4	1721	14	1773	17
	2015	1411	1381	-2	1827	30	1782	26	1798	27	1828	30	1838	30	1852	31	1896	34
	2013-2015	4704	4696	0	5324	13	4788	2	4856	3	4979	6	5059	8	5295	13	5438	16
MB	2011	974	1074	10	--	--	876	-10	904	-7	965	-1	919	-6	1443	48	1460	50
	2012	2318	2318	0	1902	-18	1702	-27	1649	-29	1772	-24	1688	-27	1482	-36	1543	-33
	2013	1276	1227	-4	1653	30	1931	51	1954	53	1850	45	1961	54	1572	23	1589	25
	2014	1405	1127	-20	1896	35	1306	-7	1352	-4	1246	-11	1495	6	1355	-4	1476	5
	2015	1514	--	--	--	--	1252	-17	1294	-15	1185	-22	1388	-8	1406	-7	1470	-3
	2011-2015	7487	5746 ^b	-4 ^b	5451 ^c	9 ^c	7067	-6	7153	-4	7018	-6	7451	0	7258	-3	7538	1

^aRE = $[(GPP_{pred} - GPP_{obs}) / GPP_{obs}] \times 100$ % (Kang et al., 2014).

^bSum excludes 2015 due to the large gap in GCC_{cam} during peak growing season which makes gap-filling GCC_{cam} challenging and consequently annual integrated GPP_{pred} highly uncertain that year. The RE compares GPP_{pred} against GPP_{obs} across 2011-2014.

^cSum excludes 2011 and 2015 due to the limited number of NDVI_{tower} in those years (Figure 3). The RE compares GPP_{pred} against GPP_{obs} across 2012-2014.

10. Figures

Figure 1. Flux tower locations and climatological footprints for the two restored wetlands. For the climatological footprints, data were separated by year at the Mayberry wetland since vegetation height and percent cover along with tower height changed throughout the study. Data were not separated by year at West Pond since tower height remained the same throughout the study and vegetation cover and height was roughly similar between years. At both wetland sites, the contours represent the 85 % flux footprints.

Figure 2. Examples of the digital camera images for West Pond (a) and Mayberry (b)-(d). As noted in the above, the field of view (FOV) changed a number of times throughout the study at the Mayberry wetland. Panels (b)-(d) show the major changes in the FOV at Mayberry. Polygons indicated the region of interest (ROI) for extracting image greenness.

Figure 3. Time series of daily GPP (gray line; g C m⁻² d⁻¹) and GCC_{cam} (camera-derived green chromatic coordinate, black circles) for (a) West Pond and (b) Mayberry, and time series of daily GPP (gray line; g C m⁻² d⁻¹) and NDVI_{tower} (tower-based normalized difference vegetation index, black circles) for (c) West Pond, and (d) Mayberry. The dashed vertical lines in (b) indicate the dates when the FOV changed at Mayberry (Figure 2).

Figure 4. Scatter plots of daily GPP (g C m⁻² d⁻¹) vs. GCC_{cam} for (a) West Pond, and (b) Mayberry, and vs. NDVI_{tower} for (c) West Pond, and (d) Mayberry). Linear (black) and quadratic lines (dashed black) are superimposed. Different years are represented by different symbols (2011 = squares, 2012 = circles; 2013 = upward-pointing triangles; 2014 = downward-pointing triangles; 2015 = diamonds).

Figure 5. Time series of daily GPP (gray line; $\text{g C m}^{-2} \text{d}^{-1}$) and normalized vegetation indices (VI_{norm}) obtained from Landsat (see Table 1 for the description of each VI) for (a) West Pond and (b) Mayberry. Indices were normalized between 0 and 1 to allow all Landsat-derived VIs to be plotted on the same figure.

Figure 6. Modeled daily GPP ($\text{g C m}^{-2} \text{d}^{-1}$; black circles), where GCC_{cam} was used as the

vegetation index (VI) in the light use efficiency (LUE) model, and observed daily GPP (g C m^{-2}

d^{-1} ; gray line) for (a) West Pond, and (b) Mayberry. For both wetlands, data from all years except

2014 were used in model parameterization and data from 2014 were used in model validation. (c)

and (d) show data-model agreement for the West Pond and Mayberry wetlands, respectively,

where the black circles indicate the parameterization period, and the light gray circles indicate

the validation period. Solid black and solid gray lines indicate the line of best fit for the

parameterization and validation periods, respectively, and the dotted line indicates the 1:1 line

(see Table 3 for model performance statistics).

Figure 7. Modeled daily GPP ($\text{g C m}^{-2} \text{d}^{-1}$; black circles), where EVI_L was used as the VI in the LUE model, and observed daily GPP ($\text{g C m}^{-2} \text{d}^{-1}$; gray line) for (a) West Pond, and (b) Mayberry. For both wetlands, data from all years except 2014 were used in model parameterization and data from 2014 were used in model validation. (c) and (d) show data-model agreement for the West Pond and Mayberry wetlands, respectively, where the black circles indicate the parameterization period, and the light gray circles indicate the validation period. Solid black and solid light gray lines indicate the line of best fit for the parameterization and validation periods, respectively, and the dotted line indicates the 1:1 line (see Table 3 for model performance statistics).