



1 **Seasonal dynamics and spatial drivers of mangrove gross primary productivity**
2 **revealed by tower and satellite observations**

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15 **Abstract:** Mangrove gross primary productivity (GPP) plays a critical role in coastal
16 carbon cycling, yet its seasonal dynamics and spatial variability remain insufficiently
17 characterized. Here, we integrated eight months of half-hourly eddy covariance
18 measurements with 10-m Sentinel-2 imagery to quantify seasonal GPP, calibrate light
19 use efficiency, and examine the spatial drivers of productivity in the Qinglangang
20 mangrove forest, Hainan Island, China. Tower-derived GPP averaged 6.67 ± 1.81 g C
21 m⁻² d⁻¹, peaking at 8.57 g C m⁻² d⁻¹ in July. Bootstrap-calibrated maximum light use
22 efficiency ($\epsilon_{\max}$) exhibited seasonal variation, with values of 1.491, 1.965, and 1.897
23 g C MJ⁻¹ APAR in spring, summer, and autumn, respectively. Incorporating sea surface
24 temperature and salinity constraints did not improve half-hourly GPP predictions,
25 indicating limited predictive value of monthly oceanic climatologies at sub-seasonal
26 timescales. The seasonally calibrated model yielded landscape-scale GPP estimates of
27 3.27 ± 2.08 , 7.14 ± 4.06 , and 3.16 ± 1.78 g C m⁻² d⁻¹ across the three seasons,
28 respectively. Spatial attribution using XGBoost and SHAP identified leaf area index as



the dominant predictor, accounting for 69.9% of total feature importance, whereas meteorological variables alone explained only 19–23% of spatial GPP variability. Random forest analysis further indicated a greater contribution of distance from the coastline than elevation. These findings demonstrate the seasonal dependence of mangrove light use efficiency and the importance of canopy structure in shaping landscape-scale productivity, providing a basis for integrating flux observations with high-resolution satellite estimates of mangrove GPP.

Keywords: Mangrove; Gross primary productivity; Light use efficiency; Eddy covariance; Sentinel-2; Sea surface salinity

1. 1. Introduction

Mangrove forests occupy less than 0.1% of Earth's vegetated land surface, yet they are among the planet's most carbon-dense ecosystems. A pantropical survey estimated mean carbon stocks of 1,023 Mg C ha⁻¹, comprising biomass, dead wood and soil organic carbon to a depth of 1 m, with the soil pool alone accounting for 49–98% of the total across sites (Donato et al., 2011). Sequestration rates in mangroves are three to five times higher per unit area than in terrestrial tropical forests (McLeod et al., 2011), and these ecosystems are estimated to contribute 10–15% of coastal sediment carbon storage (Alongi, 2014; Macreadie et al., 2021). This disproportionate role in biogeochemical cycling has led to the inclusion of mangroves in national greenhouse gas inventories and in blue carbon crediting frameworks under the Paris Agreement (Arkema et al., 2023), which has in turn increased the demand for accurate estimates of mangrove carbon fluxes at scales from individual stands to entire coastlines.

Estimates of mangrove gross primary productivity (GPP), the photosynthetic carbon uptake that supports both biomass accumulation and soil carbon storage, remain



53 poorly constrained relative to those for upland forests. Global analyses report GPP
54 values of 3.8–12.3 Mg C ha⁻¹ yr⁻¹ (Alongi, 2020), and site-level values span an order
55 of magnitude even within a single biogeographic province (Bouillon et al., 2008). Three
56 sources account for much of this spread. First, eddy covariance provides continuous
57 ecosystem-scale CO₂ flux measurements, but it has been applied at fewer than 30
58 mangrove sites worldwide, mostly in the neotropics and Australia (Barr et al., 2013;
59 Gnanamoorthy et al., 2020; Gou et al., 2023; Qiao et al., 2024). Fewer than five flux
60 records have been published for Southeast Asian mangroves, although the region
61 contains roughly one-third of global mangrove area (Hamilton & Friess, 2018). Records
62 for subtropical Chinese mangroves, which lie at the northern latitudinal limit of the
63 global distribution, are scarcer still: a single multi-year record exists for the Dongzhai
64 Harbor site on Hainan Island (Gou et al., 2023; Gou et al., 2024). Second, partitioning
65 net ecosystem exchange (NEE) into GPP and ecosystem respiration (Reco) introduces
66 model-dependent uncertainty, because the choice of respiration model, the filtering of
67 nighttime data and the extrapolation of nighttime-derived parameters to daytime
68 conditions all generate systematic biases. These biases have been quantified for
69 terrestrial forests (Reichstein et al., 2005; Lasslop et al., 2010) but not for mangroves.
70 Third, converting tower GPP into spatially explicit estimates requires a model linking
71 canopy light absorption to carbon assimilation, and the parameters governing that link
72 have not been empirically calibrated for mangroves.

73 The Vegetation Photosynthesis Model (VPM; Xiao et al., 2004) is the most widely
74 used light-use-efficiency (LUE) framework for satellite-based GPP estimation. It



expresses canopy production as the product of a maximum light use efficiency ($\epsilon_{\max}$, g C MJ⁻¹ of absorbed photosynthetically active radiation, APAR) and a set of dimensionless environmental scalars, each bounded between 0 and 1, that downregulate photosynthesis under suboptimal temperature, elevated atmospheric water demand and leaf ageing. The model has been applied across a range of terrestrial biomes, including temperate deciduous forests (Xiao et al., 2004), alpine grasslands and croplands (Yan et al., 2009). In these applications $\epsilon_{\max}$ is normally obtained by fitting a non-linear regression between half-hourly tower GPP and PAR, using only data collected under near-optimal conditions. The standard VPM scalars, however, were designed for terrestrial ecosystems and do not represent the coastal oceanographic environment that distinguishes mangroves from upland forests. Mangroves occupy the intertidal zone, where root-zone temperature tracks seawater rather than air temperature (Alongi, 2014). Salinity in the intertidal zone is controlled by freshwater input, tidal exchange and evaporation, and affects stomatal conductance, carboxylation efficiency and photosystem II quantum yield through osmotic rather than matric water-potential effects (Ball & Farquhar, 1984; Krauss et al., 2008; Reef & Lovelock, 2015). Periodic tidal inundation imposes root-zone hypoxia with no analogue in terrestrial LUE models (Li et al., 2014; Qiao et al., 2025). Consistent with these mechanisms, a global synthesis identified salinity and tidal range, rather than temperature or vapour pressure deficit, as the strongest correlates of inter-site variation in mangrove productivity (Sun et al., 2024), an LUE model including SST and salinity scalars outperformed its terrestrial counterpart for Chinese mangroves (Zheng & Takeuchi, 2022), and tower work in the



97 Florida Everglades reported a decline in mangrove CO₂ uptake of roughly 5% per 10
98 ppt increase in salinity (Barr et al., 2013). What remains unresolved is how these
99 oceanographic controls partition at a single site, how much each contributes relative to
100 the standard terrestrial scalars, and whether a scalar built from a monthly climatology
101 can resolve variation at the sub-seasonal scales at which tower fluxes are measured.

102 Sentinel-2, with 10-m spatial resolution, a 5-day revisit and three red-edge bands,
103 has substantially improved the capacity for high-resolution mangrove monitoring. Red-
104 edge vegetation indices are more sensitive to mangrove LUE than broadband NDVI
105 (Pastor-Guzman et al., 2018; Liu & Zhu, 2024), and cloud-based processing platforms
106 allow continuous Sentinel-2 time series to be generated across mapped mangrove
107 extents (Binh et al., 2024). Machine learning methods, including random forest for
108 predictor ranking and XGBoost combined with SHAP (SHapley Additive exPlanations)
109 for non-linear multivariate attribution, have become widely used for resolving the
110 spatial drivers of ecosystem function from high-dimensional remote sensing datasets
111 (Pichler & Hartig, 2023; Malerba et al., 2023). Satellite-based GPP products for
112 mangroves nevertheless continue to rely on fixed $\epsilon_{\max}$ values of 1.0–1.5 g C MJ⁻¹
113 derived from terrestrial calibrations (Zhang et al., 2017; Zheng & Takeuchi, 2022; Sun
114 et al., 2024), which do not represent the seasonal dynamics seen in tower records.
115 Season-specific, empirically calibrated $\epsilon_{\max}$ values have not been reported for an
116 individual mangrove site, and machine learning attribution has not been used to
117 partition the contributions of canopy structure (leaf area index, LAI), coastal proximity
118 (distance from coastline, tidal elevation) and meteorological forcing (precipitation,



119 radiation, temperature, CO₂) to landscape-scale spatial variation in mangrove GPP.

120 Here we combine eight months (March–October 2023) of half-hourly eddy
121 covariance measurements with Sentinel-2 imagery for the Qinglangang mangrove
122 forest, Hainan Island, China (19.615°N, 110.798°E). We derive season-specific,
123 bootstrap-calibrated $\epsilon_{\max}$ values, scale them to 10-m Sentinel-2 imagery, and apply
124 random forest and XGBoost to resolve the spatial drivers of mangrove GPP. We also
125 test whether representing the coastal oceanographic setting explicitly improves the
126 calibration, by comparing an ocean-enhanced VPM with the standard terrestrial
127 formulation and evaluating all three configurations as predictive models. Four
128 hypotheses were tested: (H1) $\epsilon_{\max}$ varies seasonally and is underestimated when only
129 terrestrial scalars are used; (H2) among the environmental scalars, salinity accounts for
130 more of the seasonal variation in $\epsilon_{\max}$ than temperature does; (H3) because the
131 oceanographic scalars are built from monthly climatologies they act as a seasonal
132 correction rather than improving sub-seasonal prediction; and (H4) canopy structure,
133 rather than climate, is the primary determinant of landscape-scale spatial variation in
134 GPP.

135 **2. Materials and methods**

136 **2.1 The study area**

137 This study was conducted in the Qinglan Bay mangrove reserve on the
138 northeastern coast of Hainan Island, China. The flux tower is located at 19.615°N,
139 110.798°E and the bay centre lies near 19°34'N, 110°45'E (Fig. 1). The reserve is the
140 second largest mangrove reserve in Hainan Province and covers a wetland area of



141 approximately 3,000 ha, of which 2,732 ha is mangrove forest supporting 24 of the 28
142 mangrove species recorded in China. The regional climate is controlled by the tropical
143 East Asian monsoon, with a warm-wet season from May to October and a cool-dry
144 season from November to April, producing seasonal contrasts in SST (22–31 °C), sea
145 surface salinity (28–34 PSU) and river discharge. The site has been under active
146 restoration since the late 1980s, and remote-sensing reconstructions document
147 substantial recovery of mangrove cover and an associated increase in carbon sink
148 capacity over the intervening decades (Jia et al., 2022). The South China Sea
149 experiences pronounced interannual variability in surface salinity, driven by monsoon
150 freshwater flux and modulated by the El Niño–Southern Oscillation (Liu et al., 2011;
151 Wu et al., 2025).

152 2.2 Eddy covariance measurements and flux processing

153 Continuous measurements of CO₂, H₂O and energy fluxes were collected at the
154 Qinglangang mangrove flux tower (19.615°N, 110.798°E; canopy height ~6.0 m;
155 sensor height 18.5 m). The eddy covariance system comprised a Gill WindMaster Pro
156 3-D sonic anemometer paired with a LI-COR LI-7500DS open-path CO₂/H₂O gas
157 analyser (LI-COR Biosciences, Lincoln, NE, USA). Raw 10-Hz data were processed in
158 EddyPro 7.0 (LI-COR Biosciences) following the standard FLUXNET protocol:
159 double-axis rotation for tilt correction (Kaimal & Finnigan, 1994), block averaging over
160 30-min intervals, Webb–Pearman–Leuning density correction (Webb et al., 1980) and
161 spectral correction following the analytical transfer-function approach of Moncrieff et
162 al. (1997).

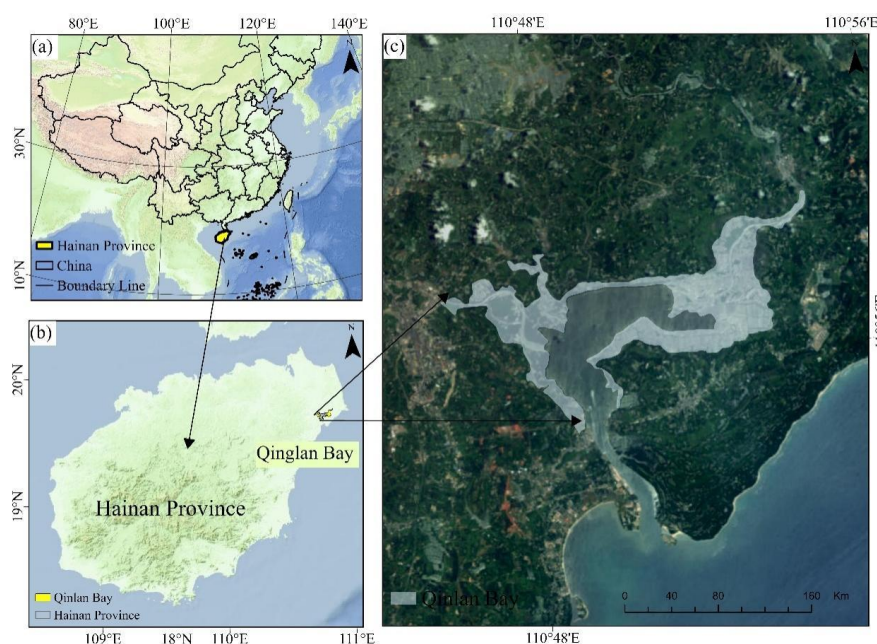


Fig. 1 The study area. a, Location of Hainan Island on the southeastern coast of China. b, Hainan Island showing the Qinglangang Protected Zone boundary. c, Sentinel-2 false-color composite overlain with the protected zone boundary.

Quality control (QC) of the half-hourly fluxes followed the two-flag scheme of Foken and Wichura (1996). A record was retained only if (i) the combined steady-state and integral turbulence characteristics test score (FC_SSITC_TEST) was 0 or 1, (ii) $|FC| < 30 \mu\text{mol m}^{-2} \text{s}^{-1}$, and (iii) $u^* \geq 0.10 \text{ m s}^{-1}$ during nighttime periods (NIGHT = 1). Measurements ran from 8 March to 9 October 2023 and yielded 8,374 valid half-hourly records (4,899 daytime, 3,475 nighttime). Seasons were defined from the Hainan climatological monsoon cycle as spring (March–April), summer (May–August) and autumn (September–October).

2.3 NEE partitioning and ecosystem respiration modelling



Net ecosystem exchange ($NEE = FC$) follows the micrometeorological sign convention (negative = net carbon uptake). Gross primary production was calculated from the NEE partitioning identity:

$$GPP = R_{eco} - NEE \quad (1)$$

where R_{eco} is ecosystem respiration. At night ($GPP = 0$), NEE is equal to R_{eco} , so the temperature dependence of R_{eco} was characterised using the Lloyd–Taylor (LT) model (Lloyd and Taylor, 1994):

$$R_{eco}(T_k) = R_{ref} \cdot \exp \left\{ E_0 \cdot \left[\frac{1}{T_{ref} - T_0} - \frac{1}{T_k - T_0} \right] \right\} \quad (2)$$

where R_{ref} ($\mu\text{mol m}^{-2} \text{s}^{-1}$) is the reference respiration at $T_{ref} = 283.15 \text{ K}$ (10°C), E_0 (K) is the activation energy parameter, $T_0 = 227.13 \text{ K}$ (-46.02°C) is a fixed lower temperature limit and T_k (K) is the measured air temperature. To reduce the influence of random flux errors on parameter estimation, nighttime data were aggregated into 1°C air-temperature bins ($16.5\text{--}36.5^\circ \text{C}$) and the Lloyd–Taylor model was fitted to bin-median R_{eco} values (minimum $N = 5$ per bin) by weighted non-linear least squares, with weights proportional to $1/\sqrt{N}$. The fitted model was extrapolated to daytime T_a to obtain R_{eco} for each daytime half-hour. Daily GPP ($\text{g C m}^{-2} \text{d}^{-1}$) was computed by integrating the valid half-hourly fluxes:

$$GPP_{\text{daily}} = \sum [GPP_{\text{hh}} \times 1800 \text{ s} \times 12 \text{ g} \cdot \text{mol}^{-1} \times 10^{-6} \text{ mol} \cdot \text{umol}^{-1}] \quad (3)$$



Days with fewer than 10 valid daytime records were excluded from further analysis, retaining 204 days across the study period.

2.4 Vegetation Photosynthesis Model framework

The Vegetation Photosynthesis Model (VPM; [Xiao et al., 2004](#)) parameterises GPP as:

$$\text{GPP} = \epsilon_{\max} \times \text{APAR} \times \prod \text{Scalar}_i \quad (4)$$

where $\epsilon_{\max}$ ($\text{g C MJ}^{-1} \text{ APAR}$) is the maximum light use efficiency, APAR ($\mu\text{mol m}^{-2} \text{ s}^{-1}$) is absorbed photosynthetically active radiation, and Scalar_i (range 0–1) are dimensionless environmental stress scalars. In this study APAR was estimated from measured incoming shortwave radiation:

$$\text{APAR} = \text{SW_IN_POT} \times 0.45 \times 2.114 \quad (5)$$

where 0.45 is the fraction of total solar radiation in the PAR waveband and $2.114 \mu\text{mol J}^{-1}$ is the photon-energy conversion factor. This treats all incident PAR as absorbed, so the $\epsilon_{\max}$ values below are expressed per unit incident rather than absorbed PAR. Three nested configurations were evaluated:

V1 (terrestrial baseline): $\text{GPP} = \epsilon_{\max} \times \text{APAR} \times T_{\text{scalar}}(T_a)$

V2 (+SST): $\text{GPP} = \epsilon_{\max} \times \text{APAR} \times T_{\text{scalar}} \times S_{\text{scalar}}(\text{SST})$

V3 (+SST+SSS, ocean-enhanced): $\text{GPP} = \epsilon_{\max} \times \text{APAR} \times T_{\text{scalar}} \times S_{\text{scalar}} \times$



217 Salscalar(SSS)

218 **2.4.1 Air temperature scalar (Tscalar)**

219 The air temperature scalar is a bell-shaped function that equals zero at and below
220 $T_{\min}$ and at and above $T_{\max}$ and reaches unity at T_{opt} . This rational form is bounded
221 and smooth across the interval and exactly zero at both thermal limits:

$$222 \quad T_{\text{scalar}}(T_a) = \frac{(T_a - T_{\min})(T_a - T_{\max})}{(T_a - T_{\min})(T_a - T_{\max}) - (T_a - T_{\text{opt}})^2}$$

223 (6)

224 with $T_{\min} = 0^\circ\text{C}$, $T_{\text{opt}} = 28^\circ\text{C}$ and $T_{\max} = 45^\circ\text{C}$.

225 **2.4.2 Sea surface temperature scalar (Sscalar)**

226 Mangrove photosynthesis is closely coupled to coastal ocean thermal conditions
227 through air–sea heat exchange and tidal water temperature. The SST scalar was
228 therefore parameterised with the same functional form as Eq. (6):

$$229 \quad S_{\text{scalar}}(\text{SST}) = \frac{(\text{SST} - \text{SST}_{\min})(\text{SST} - \text{SST}_{\max})}{(\text{SST} - \text{SST}_{\min})(\text{SST} - \text{SST}_{\max}) - (\text{SST} - \text{SST}_{\text{opt}})^2}$$

230 (7)

231 with $\text{SST}_{\min} = 18^\circ\text{C}$, $\text{SST}_{\text{opt}} = 27.5^\circ\text{C}$ and $\text{SST}_{\max} = 38^\circ\text{C}$. The SST time
232 series is described in Section 2.8; twelve monthly values for the Hainan east coast grid
233 cell centred at 19.6°N , 110.8°E were linearly interpolated to daily values by fractional-
234 month weighting.

235 **2.4.3 Sea surface salinity scalar (Salscalar)**



236 Elevated salinity suppresses mangrove photosynthesis through osmotic and ionic
237 stress (Krauss et al., 2008). Because the salinity–productivity relationship declines
238 monotonically above a reference value, a sigmoid decay function was adopted:

$$239 \quad \text{Sal}_{\text{scalar}}(\text{SSS}) = \frac{1}{1 + \exp[k_{\text{sal}} \times (\text{SSS} - \text{SSS}_{\text{opt}} - \delta)]}$$

240 (8)

241 with $\text{SSS}_{\text{opt}} = 32$ PSU, $k_{\text{sal}} = 0.8$ PSU⁻¹ and $\delta = 2$ PSU. The function decays
242 monotonically with increasing salinity and reaches 0.83 at 32 PSU, with its inflection
243 at $\text{SSS}_{\text{opt}} + \delta = 34$ PSU. Because these parameters are not calibrated to observed
244 productivity, the seasonal enhancement they produce depends on their assumed values;
245 a sensitivity analysis is reported in Section 3.3. A monthly SSS climatology for the
246 northern South China Sea (~19.6°N, 110.8°E) was interpolated to daily values in the
247 same way.

248 **2.5 Light response curves and seasonal ϵ_{max} estimation**

249 Seasonal light response curves were constructed by binning half-hourly GPP
250 observations into 31 equal-width PAR intervals (0–2500 $\mu\text{mol m}^{-2} \text{s}^{-1}$). We used the
251 rectangular hyperbola (Michaelis–Menten) model:

$$252 \quad \text{GPP} = \frac{\alpha \times \text{PAR} \times P_{\text{max}}}{\alpha \times \text{PAR} + P_{\text{max}}} - R_{\text{d}}$$

253 (9)

254 The model was fitted to bin-mean GPP ($N \geq 8$ per bin) by non-linear least squares.
255 Here α ($\mu\text{mol CO}_2 \mu\text{mol}^{-1} \text{photon}$) is the apparent quantum yield, P_{max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)



256 is the light-saturated gross photosynthesis, and R_d ($\mu\text{mol m}^{-2} \text{s}^{-1}$) is daytime dark
257 respiration. R_d was treated as a free parameter bounded between 0.30 and $8.0 \mu\text{mol m}^{-2}$
258 s^{-1} , initialised at max ($1.0, 0.15 \times \text{Reco}$ at 25°C). The season-specific maximum light
259 use efficiency ϵ_{max} was derived as:

$$\epsilon_{\text{max}} (\text{g C MJ}^{-1} \text{ APAR}) = \alpha \times 55.2 \quad (10)$$

262 where 55.2 is the unit-conversion factor (g C MJ^{-1} per $\mu\text{mol CO}_2 \mu\text{mol}^{-1} \text{ photon}$). To
263 isolate the contribution of each scalar to ϵ_{max} , GPP was normalised by the scalar product
264 appropriate to each configuration before re-fitting Eq. (9). Because dividing GPP by a
265 scalar product smaller than one necessarily raises the fitted ϵ_{max} , this quantifies how
266 much each scalar changes the calibrated parameter; it does not establish that the
267 configuration predicts GPP better, so Section 3.3 also evaluates the three as predictive
268 models.

269 **2.6 Bootstrap uncertainty quantification of ϵ_{max}**

270 Uncertainty in seasonal ϵ_{max} was quantified by 500-iteration bootstrap resampling.
271 Within each iteration the binned PAR–GPP dataset for a given season was resampled
272 with replacement, Eq. (9) was re-fitted, and ϵ_{max} was computed from Eq. (10). The
273 bootstrap median was taken as the point estimate and the 2.5th–97.5th percentile
274 interval as the 95% confidence interval. Iterations that failed to converge (parameter-
275 bounds violation or more than 10,000 function evaluations) were discarded. To match
276 the temporal resolution of the oceanographic scalars, the bootstrap was performed on
277 20 equal-frequency PAR bins, so that the resampling reflects variation among bins



rather than among individual half-hourly records; the wider intervals this produces are reported throughout.

2.7 Environmental threshold detection via segmented regression

Non-linear GPP responses to air temperature (T_a) and vapour pressure deficit (VPD) were characterised by segmented (piecewise linear) regression on high-light observations ($\text{PAR} > 500 \mu\text{mol m}^{-2} \text{s}^{-1}$). Observations were aggregated into 20 equal-frequency bins across each environmental variable, and a two-segment model was fitted:

$$\text{GPP} = \begin{cases} \beta_1 \cdot X + \alpha_1 & (X \leq \tau) \\ \beta_2 \cdot X + \alpha_2 & (X > \tau) \end{cases} \quad (11)$$

The model was fitted with the breakpoint τ swept systematically across the variable range, and the τ maximising the overall R^2 was selected as the threshold. Because the EddyPro output VPD_EP was systematically affected by sensor saturation in the high-humidity mangrove environment, VPD was recalculated from the measured H_2O mixing ratio and barometric pressure as:

$$\text{VPD} = e_s(T_a) - e_a \quad (12)$$

where e_s is the saturation vapour pressure (calculated with the Tetens formula) and e_a is the actual vapour pressure derived from the H_2O mixing ratio and air pressure. Season-specific VPD half-saturation values (VPD_0 , the VPD at which GPP declined to 50% of its low-VPD maximum) were used to construct a diagnostic water-stress scalar:

$$W_{\text{scalar}} = \frac{1}{1 + \exp[k \times (\text{VPD} - \text{VPD}_0)]}$$



299 (13)

300 with $k = 8.0 \text{ kPa}^{-1}$. The W scalar was used for diagnostic analysis only and was excluded
301 from the operational VPM GPP estimates, because open-path sensor humidity data are
302 of limited reliability in the mangrove environment.

303 **2.8 Auxiliary datasets for the oceanographic scalars**

304 The SST and salinity scalars used in the tower calibration were built from
305 monthly climatological values, not from retrievals matched to the flux record, because
306 the campaign covers a single eight-month period. Twelve monthly values for the Hainan
307 east coast grid cell (19.6°N, 110.8°E) were specified for each variable and interpolated
308 to daily values. The scalars can be reproduced and the salinity sensitivity in Section 3.3
309 traced to specific inputs. Both series represent the regional climatology rather than
310 conditions in 2023. The salinity cycle is small (1.1 PSU across the three seasons,
311 comparable to the uncertainty of coastal satellite salinity retrievals) whereas the
312 temperature cycle spans 4.4 °C, and because the scalars vary only monthly they can
313 represent a seasonal shift in ϵ_{max} but not sub-seasonal variation.

314 **2.9 SHAP-based interpretable machine learning analysis**

315 To quantify the relative contributions of canopy structure, climatic forcing and
316 coastal proximity to spatial variation in mangrove GPP, we used an interpretable
317 machine-learning framework based on Extreme Gradient Boosting (XGBoost) coupled
318 with SHapley Additive exPlanations (SHAP) (Chen & Guestrin, 2016; Lundberg & Lee,
319 2017). XGBoost is a tree-ensemble algorithm that iteratively minimises prediction error
320 through gradient boosting and has shown strong predictive performance in non-linear



ecological applications (Pichler & Hartig, 2023). For each season, pixel-level GPP was modelled as a function of six predictors: leaf area index (LAI), precipitation, solar radiation, land surface temperature (LST), photosynthetically active radiation (PAR) and atmospheric CO₂. LAI was an independent gridded product rather than the greenness index used as fAPAR in the upscaling chain (Section 2.9), so the canopy predictor is not a term of the GPP calculation. Land surface temperature came from Landsat thermal imagery, precipitation from GPM IMERG V07, solar radiation from ERA5, and PAR from the same ERA5 fields checked against CERES. Atmospheric CO₂ came from the NOAA Global Monitoring Laboratory monthly mean background concentration, which carries no spatial structure. All predictors were resampled to the 10-m Sentinel-2 grid; precipitation is in millimetres per season and CO₂ in parts per million. The XGBoost prediction is expressed as:

$$\hat{y}_i = \sum_{k=1}^K f_k(x_i), f_k \in \mathcal{F} \quad (14)$$

where $\hat{y}$ denotes the predicted GPP value, K is the total number of regression trees, and f_k denotes an individual decision tree. Model training minimises a regularised objective function:

$$\mathcal{L}^{(t)} = \sum_{i=1}^n l(y_i, \hat{y}_i^{(t-1)} + f_t(x_i)) + \Omega(f_t) \quad (15)$$

where l is a differentiable loss function and Ω penalizes model complexity to reduce overfitting. Model performance was evaluated using the coefficient of determination



(R) and root mean square error (RMSE). To interpret model predictions, we applied SHAP, an explainable artificial intelligence framework derived from cooperative game theory (Lundberg & Lee, 2017). SHAP decomposes model predictions into additive contributions of individual predictors:

$$g(z') = \phi_0 + \sum_{j_1}^M \phi_j z'_{j_1} \quad (16)$$

where $g(z')$ is the prediction from the simple, interpretable linear model that approximates the complex XGBoost model, ϕ_0 is the baseline model output, M is the total number of features, ϕ_j represents the marginal contribution of feature j . The Shapley value is calculated as

$$\phi_j = \sum_{S \subseteq F \setminus \{j\}} \frac{|S|!(M - |S| - 1)!}{M!} [f_{S \cup \{j\}}(x) - f_S(x)] \quad (17)$$

where F is the full predictor set and $\mathcal{S}$ denotes all possible feature subsets. SHAP values were estimated with the TreeSHAP algorithm (Lundberg et al., 2020). Model performance is reported for a randomly held-out subset of the pixel sample; because neighbouring pixels are spatially autocorrelated, a random split places near-duplicate observations in both training and test data and the resulting R^2 is an upper bound on predictive skill. No confidence interval is available for the importance ranking.

3. Results

3.1 Seasonal GPP dynamics and photosynthetic light response



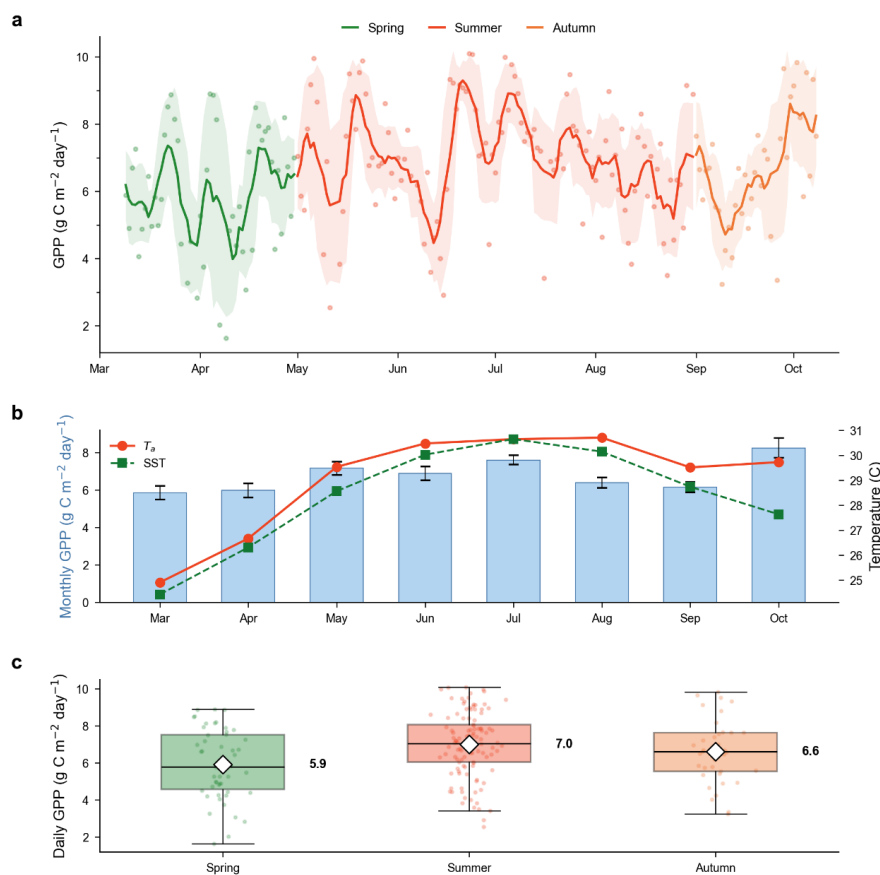
362 Half-hourly CO₂ fluxes were measured in the Qinglangang mangrove forest
363 (19.615°N, 110.798°E) from 8 March to 9 October 2023 with an open-path eddy
364 covariance system. Following quality control ($u^* \geq 0.10 \text{ m s}^{-1}$, stationarity test score $\leq$
365 1, $|FC| < 30 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$), 8,374 valid records were retained (4,899 daytime, 3,475
366 nighttime). Nighttime ecosystem respiration was well described by the Lloyd–Taylor
367 model (binned $R^2 = 0.79$), yielding a reference respiration of $4.05 \text{ } \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ at
368 25 °C ($R_{\text{ref}} = 295.3 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$ at the 10 °C reference temperature) and a Q_{10} of 2.25
369 (20–30 °C; Fig. S1). Daytime GPP, derived as $\text{GPP} = \text{Reco}(\text{Ta}) - \text{NEE}$ and integrated
370 to daily totals, averaged $6.67 \pm 1.81 \text{ g C m}^{-2} \text{ day}^{-1}$ across 204 valid days, rising from
371 5.93 ± 1.85 in spring (March–April) to 7.01 ± 1.72 in summer (May–August) and
372 declining to 6.61 ± 1.85 in autumn (September–October; Fig. 2a,c). Monthly GPP
373 reached a maximum of $8.57 \text{ g C m}^{-2} \text{ day}^{-1}$ in July, and the highest single-day value
374 ($10.09 \text{ g C m}^{-2} \text{ day}^{-1}$) was recorded in mid-July (Fig. 2b).

375 Diurnal GPP profiles were strongly unimodal in all three seasons, with uptake
376 peaking between 10:30 and 12:00 local time (Fig. 3). The peak of the seasonal mean
377 diurnal profile increased from $14.0 \text{ } \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in spring to 17.1 in summer and
378 17.6 in autumn, paralleling the seasonal progression of the daily integrals (Fig. 3a–d).
379 Summer and autumn profiles were consistently $4\text{--}5 \text{ } \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ above spring
380 values throughout the daylight period. In all seasons the afternoon decline was more
381 gradual than the morning rise, an asymmetry consistent with progressive stomatal
382 limitation as afternoon vapour pressure deficit increases.

383 Seasonal light response curves, fitted with the rectangular hyperbola model (GPP



384 $= \alpha \times \text{PAR} \times P_{\text{max}} / (\alpha \times \text{PAR} + P_{\text{max}}) - R_d$ to 31 PAR bins ($N \geq 8$ per bin), reproduced
385 the binned observations closely ($R^2 = 0.965\text{--}0.992$; Fig. 4a–c). The apparent quantum
386 yield (α) increased from $0.0166 \pm 0.0013 \mu\text{mol CO}_2 \mu\text{mol}^{-1}$ photon in spring to 0.0225
387 ± 0.0014 in summer and 0.0234 ± 0.0031 in autumn (Fig. 4d), giving ϵ_{max} of 0.915,
388 1.244 and 1.292 g C MJ⁻¹ APAR from Eq. (10). Daytime dark respiration was low in
389 spring and summer ($\sim 0.30 \mu\text{mol m}^{-2} \text{s}^{-1}$) and rose to 1.03 in autumn. Summer and
390 autumn rates exceeded spring rates across almost the full PAR range (Fig. 4e). The fitted
391 light-saturation parameter P_{max} was 151, 75 and 125 $\mu\text{mol m}^{-2} \text{s}^{-1}$ but was poorly
392 constrained: the highest adequately supported PAR bin lay near 1,300 $\mu\text{mol m}^{-2} \text{s}^{-1}$, and
393 an unconstrained refit returned P_{max} 6–30% lower with a compensating change in α ,
394 so P_{max} is an upper bound rather than a measured photosynthetic capacity.



395

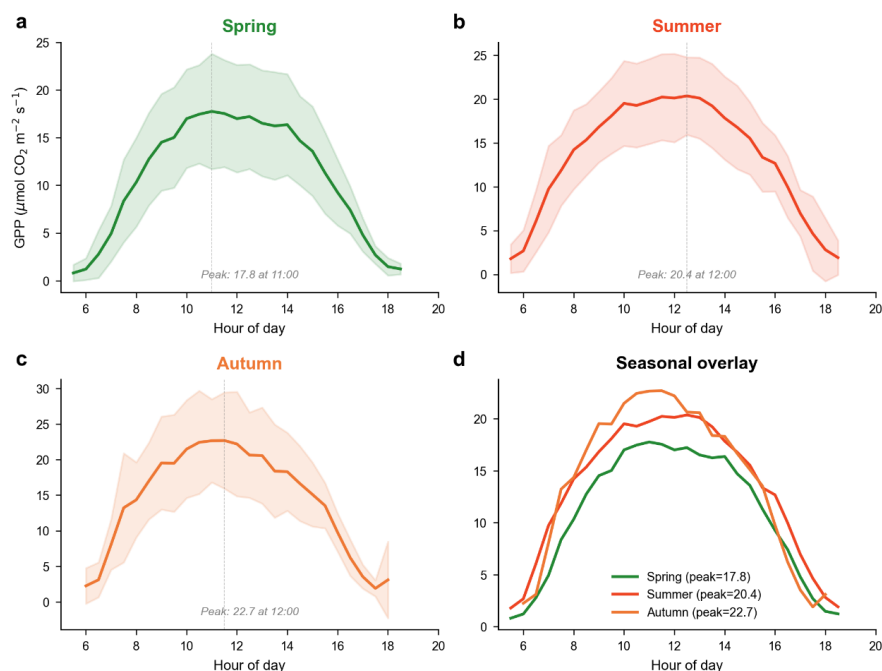
396 **Fig. 2 Seasonal dynamics of mangrove GPP. a,** Daily GPP ($\text{g C m}^{-2} \text{ day}^{-1}$) with 7-day

397 moving average (solid line) and ± 1 SD envelope. Season colours: spring (green),

398 summer (red), autumn (orange). **b,** Monthly mean GPP (blue bars, $\pm$ SEM) overlain

399 with mean air temperature (T_a , red) and sea surface temperature (SST, teal). **c,** Seasonal

400 boxplots with jittered daily values and mean (diamonds). $n = 204$ days.

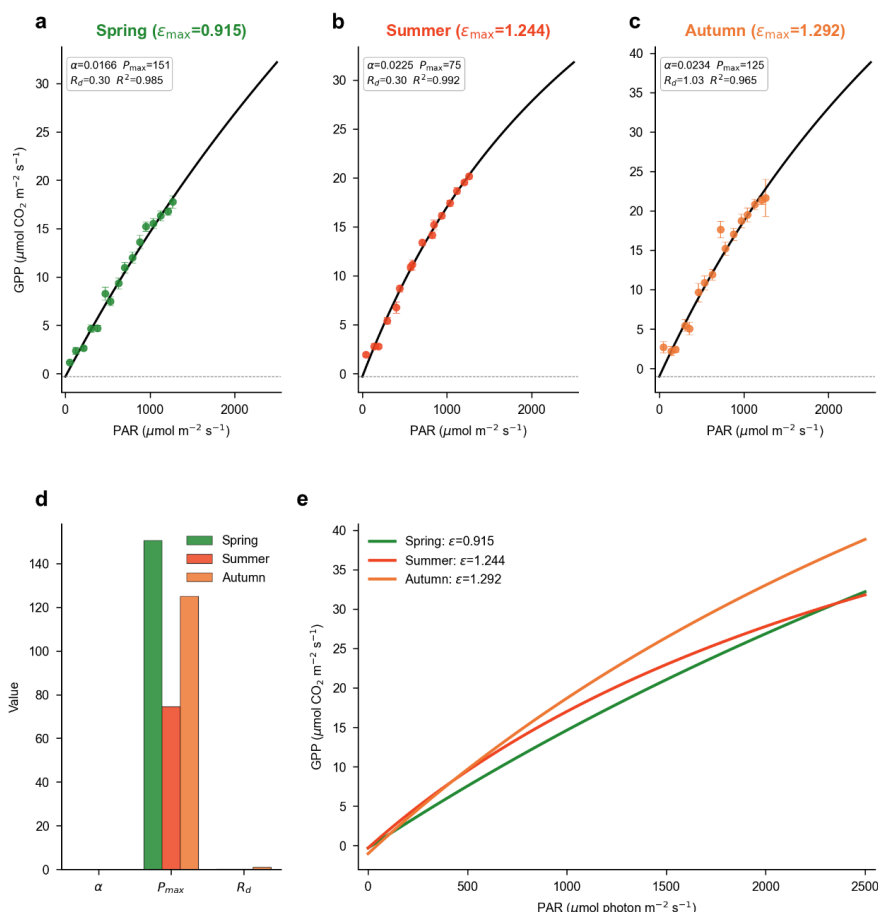


401

402 **Fig. 3 Diurnal GPP variation by season. a–c,** Mean diurnal GPP (± 1 SD shaded) for

403 spring (a), summer (b), and autumn (c). Dashed line marks peak timing; peak value and

404 hour annotated. **d,** Seasonal overlay of mean diurnal profiles.



405

406 **Fig. 4 Light response curves and photosynthetic parameters. a–c,** Binned GPP (31

407 PAR bins, $N \geq 8$ per bin; $\pm$ SEM) with rectangular hyperbola fits for each season. Inset

408 reports fitted parameters (α , $P_{\max}$, R_d , R^2) and derived $\epsilon_{\max}$. **d,** Comparison of α , $P_{\max}$,

409 and R_d across seasons. **e,** Overlay of seasonal light response curves.

410 3.2 Environmental drivers of mangrove carbon uptake

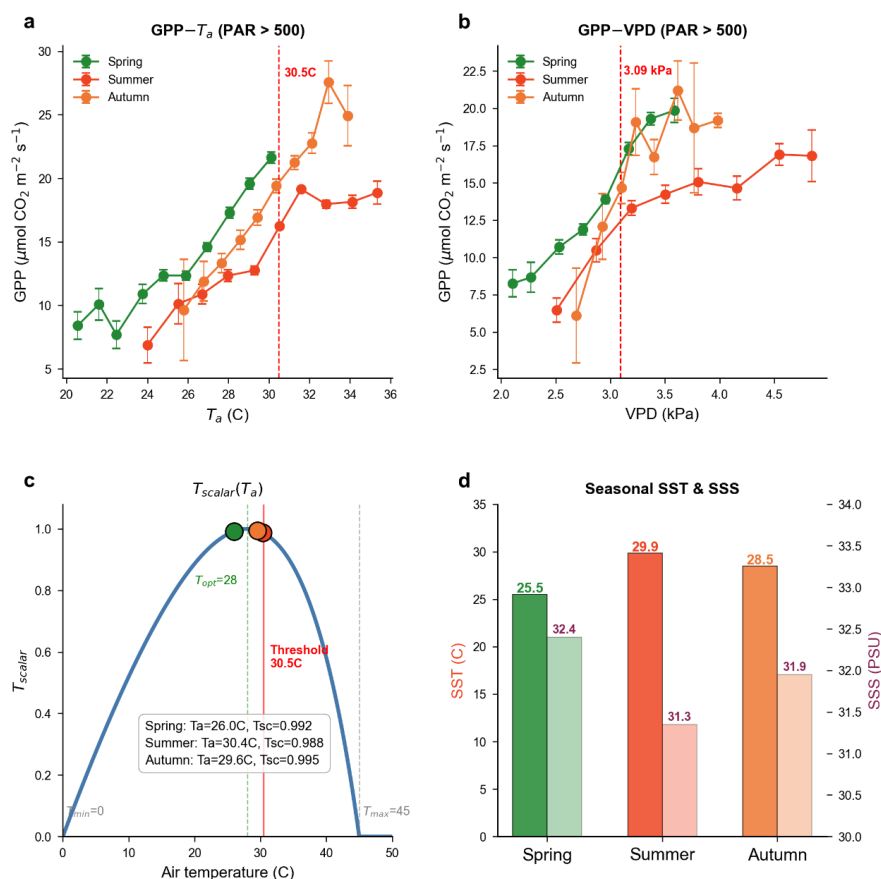
411 Air temperature exerted pronounced non-linear control on GPP under high-light

412 conditions ($\text{PAR} > 500 \mu\text{mol m}^{-2} \text{s}^{-1}$; $n = 3,487$). Segmented regression on temperature-

413 binned GPP identified an inflection point at 30.5°C , below which GPP increased



414 approximately linearly with T_a and above which it plateaued (Fig. 5a). Despite this
415 empirical threshold, the VPM temperature scalar ($T_{min} = 0\text{ }^{\circ}\text{C}$, $T_{opt} = 28\text{ }^{\circ}\text{C}$, $T_{max} =$
416 $45\text{ }^{\circ}\text{C}$) remained near-saturated in all seasons (0.979–0.987), because seasonal mean T_a
417 ($26.0\text{--}30.4\text{ }^{\circ}\text{C}$) fell within the broad optimal envelope of the bell-shaped function (Fig.
418 5c). Vapour pressure deficit, calculated from the H_2O mixing ratio to avoid sensor
419 saturation in the humid mangrove environment, was negatively correlated with GPP
420 (Fig. 5b); the VPD threshold at which GPP declined to 50% of its low-VPD maximum
421 increased from 1.0 kPa in spring to 2.5–2.7 kPa in summer and autumn, consistent with
422 progressive stomatal acclimation. Seasonal SST and SSS, spanning $25.5\text{--}29.9\text{ }^{\circ}\text{C}$ and
423 $31.3\text{--}32.4\text{ PSU}$ respectively, followed opposing annual cycles driven by monsoon
424 forcing (Fig. 5d).



425

426 **Fig. 5 Environmental controls on mangrove GPP.** a, GPP vs. T_a under high light

427 (PAR > 500). Red dashed line: segmented regression threshold (30.5 °C). b, GPP vs.

428 VPD under high light. Red line: half-saturation threshold. c, $T_{scalar}(T_a)$ function (T_{min}

429 = 0, T_{opt} = 28, T_{max} = 45 °C). Coloured circles mark seasonal T_a ; inset reports values.

430 Red line: GPP– T_a threshold. d, Seasonal mean SST (solid bars) and SSS (hatched bars).

431 Oceanic conditions exerted a seasonally variable influence on mangrove

432 photosynthetic capacity (Fig. 6). SST along the Hainan east coast (MODIS Aqua

433 climatology) was 25.5 ± 1.4 °C in spring, 29.9 ± 0.9 °C in summer and 28.5 ± 1.1 °C

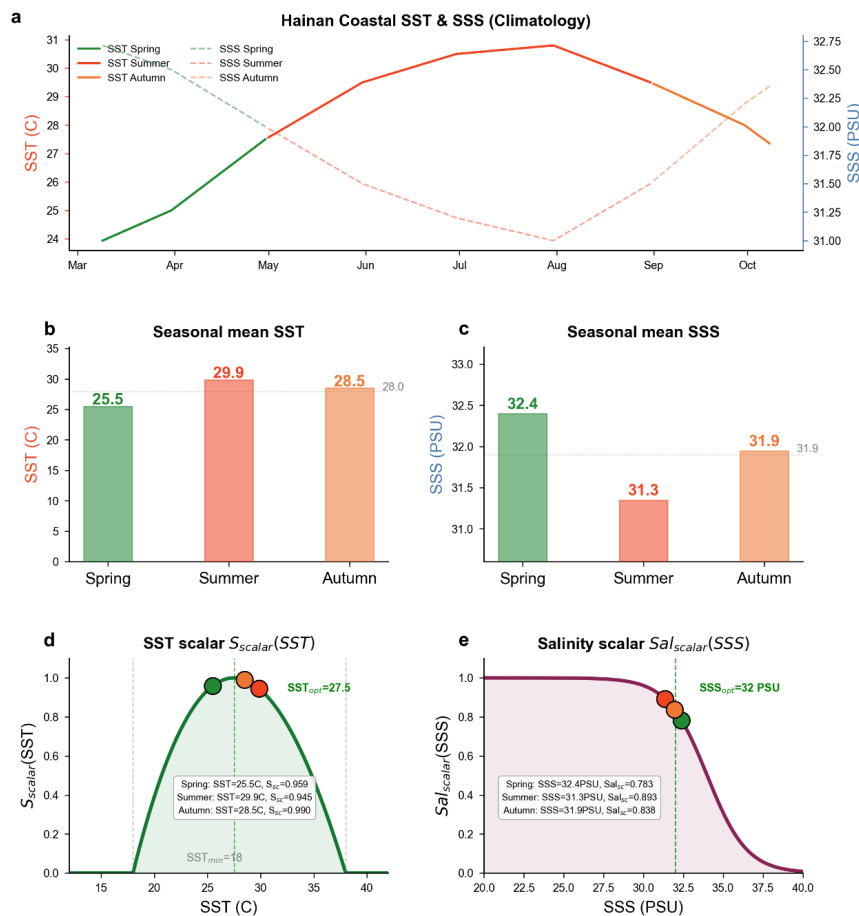
434 in autumn (Fig. 6a,b). Parameterised as a bell-shaped function with SST_{opt} = 27.5 °C,



435 the SST scalar peaked in autumn (0.987) and reached its minimum in summer (0.938),
436 because summer SST exceeded the optimum by 2.4 °C whereas autumn SST fell closest
437 to it (Fig. 6d). SSS (SMAP/SMOS climatology) declined from a dry-season maximum
438 of 32.4 ± 0.3 PSU in spring to a monsoon-driven minimum of 31.3 ± 0.3 PSU in summer
439 before recovering to 31.9 ± 0.3 PSU in autumn (Fig. 6a,c).

440 The salinity scalar ($SSS_{opt} = 32$ PSU, $ksal = 0.8$ PSU⁻¹, $\delta = 2$ PSU), a sigmoid
441 decay function, translated the modest SSS range into larger differences in scalar
442 magnitude: 0.781 in spring, 0.891 in summer and 0.836 in autumn (Fig. 6e). The
443 composite oceanic stress index ($S_{scalar} \times S_{alscalar}$) identified spring as the most ocean-
444 limited season (0.740) and summer as the most favourable (0.836). Among the three
445 scalars, T_{scalar} varied negligibly (range 0.008), S_{scalar} varied modestly (range 0.049)
446 and $S_{alscalar}$ contributed the largest share of the seasonal amplitude (range 0.110).
447 Because the salinity scalar is built from a monthly climatology, these differences
448 represent a seasonal offset applied to ϵ_{max} rather than a driver resolved at the half-
449 hourly timescale of the flux record.

450



451

452 **Fig. 6 Oceanic drivers: SST and salinity scalars.** **a**, Seasonal SST (solid) and SSS
453 (dashed) time series. **b–c**, Seasonal mean SST and SSS; grey dotted line marks annual
454 mean. **d**, SST scalar function. Circles mark seasonal SST; inset reports values. **e**,
455 Salinity scalar function.

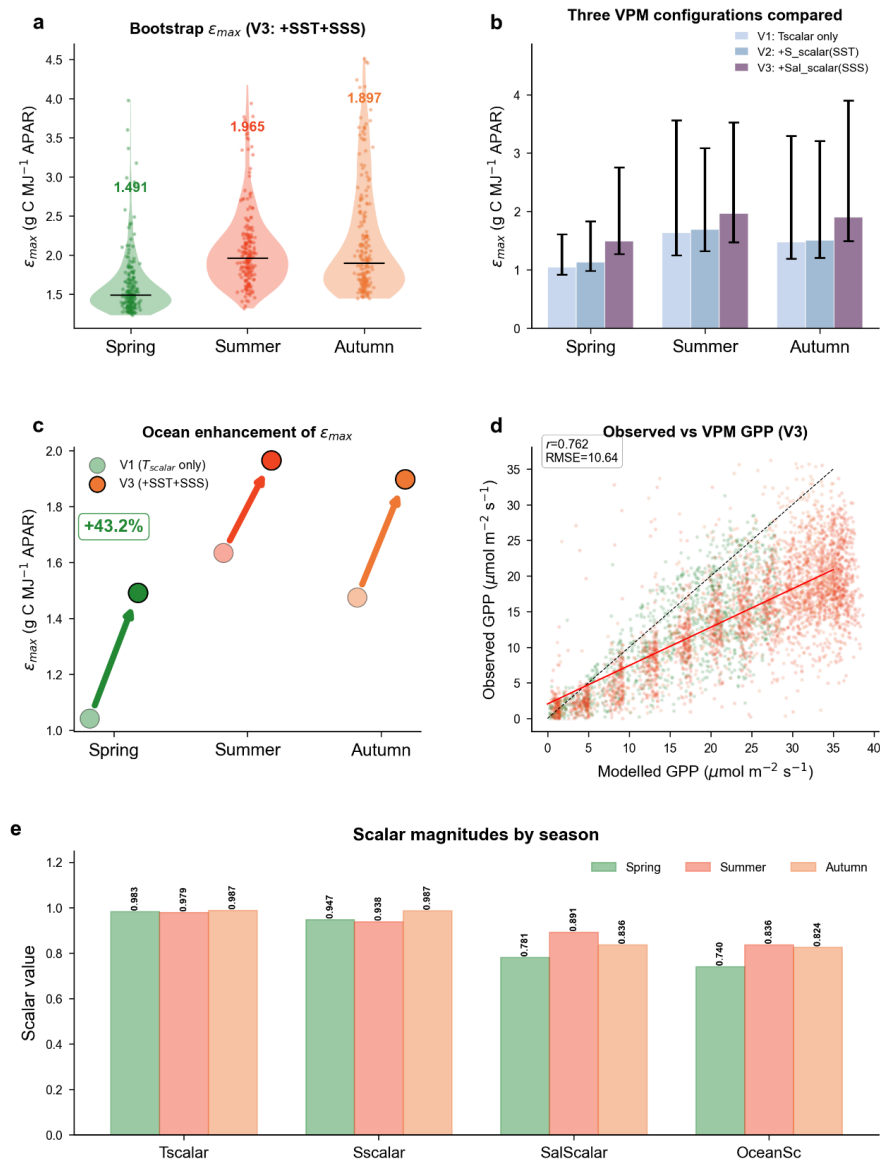
456 3.3 VPM parameter optimization and model evaluation

457 Bootstrap-derived maximum light use efficiency under the full ocean-enhanced
458 VPM configuration (V3: Tscalar + Sscalar + Salscalar; 500 iterations) was 1.491 g C
459 MJ⁻¹ APAR (95% CI 1.265–2.754) in spring, 1.965 (1.468–3.524) in summer and 1.897



(1.487–3.893) in autumn (Fig. 7a). The corresponding terrestrial baseline (V1) values were 1.041, 1.634 and 1.475 g C MJ⁻¹, and the intermediate configuration (V2, Tscalar + Sscalar) gave 1.133, 1.690 and 1.504 g C MJ⁻¹. Adding the SST scalar alone therefore changed $\epsilon_{\max}$ by 3–9%, whereas adding the salinity scalar raised it by 43.2% in spring, 20.3% in summer and 28.7% in autumn (Fig. 7b,c). The disproportionate spring enhancement is consistent with elevated dry-season salinity: correcting for osmotic stress through V3 brought the spring $\epsilon_{\max}$ much closer to the summer and autumn values, indicating that the spring depression in photosynthetic efficiency was associated primarily with salinity rather than with intrinsic phenological constraints.

Three points qualify this result. First, the 95% confidence intervals of the seasonal $\epsilon_{\max}$ values overlap substantially (Fig. 7a), so the seasons are not statistically distinguishable despite the 30% difference among their medians. Second, varying the salinity-scalar parameters over plausible ranges changed the spring enhancement from 7% to 97%, with summer 5–60% and autumn 0.4–75% (Fig. S2). Observed and modelled half-hourly GPP were strongly correlated when pooled ($r = 0.733$, RMSE = 10.83 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$; Fig. 7d), with per-season correlations of 0.733, 0.773 and 0.664, but agreement with the 1:1 line was poor: the regression slope was 0.53 and the modelled mean (22.6) exceeded the observed mean (14.3 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), reflecting the linear-in-APAR form of the VPM, which cannot represent the light saturation in Fig. 4.



480

481 **Fig. 7 VPM parameter optimization and model evaluation. a**, Seasonal ϵ_{max} (V3)
482 from 500-iteration bootstrap. Violin plots show bootstrap distributions; dots show a
483 random subset ($n = 200$). **b**, Three VPM configurations: V1 (Tscalar only), V2
484 (+Sscalar), V3 (+Salscalar). Bars show median $\pm$ 95% CI. **c**, Paired V1→V3



enhancement with percentage labels. **d**, Observed vs. VPM-modelled GPP (V3), pooled across seasons. Dashed line: 1:1; red line: regression. Inset: r and RMSE. **e**, Seasonal mean scalar values and composite oceanic stress index (OceanSc).

3.4 Coastal proximity and elevation as spatial predictors of mangrove GPP

Mean GPP across the mangrove ecosystem, from the ocean-enhanced VPM driven by Sentinel-2 imagery, was $3.27 \pm 2.08 \text{ g C m}^{-2} \text{ day}^{-1}$ in spring, 7.14 ± 4.06 in summer and 3.16 ± 1.78 in autumn (Fig. 8). Summer GPP exceeded spring and autumn by factors of 2.2 and 2.3 ($P < 0.001$, two-sample t-test). Pixel-level GPP ranged from near zero to 10.30, 16.63 and 9.81 $\text{g C m}^{-2} \text{ day}^{-1}$, and the coefficient of variation declined from 0.64 in spring to 0.57 and 0.56. Statistics are averaged over pixels with positive GPP; non-mangrove pixels were excluded, so the values describe the vegetated area rather than the full image extent. Relative to the tower record the upscaled product was low by 34% and 48% in spring and autumn but high by 39% in summer (within 250 m of the tower), and its seasonal amplitude (summer/spring = 2.2) was nearly double that of the tower record (1.2). Part of this may reflect footprint sampling, but it also shows that the maps are not yet validated and their absolute values should be treated as provisional. The seasonal pixel comparison used a two-sample t-test, for which spatial autocorrelation reduces the effective sample size, so the P value is indicative only.

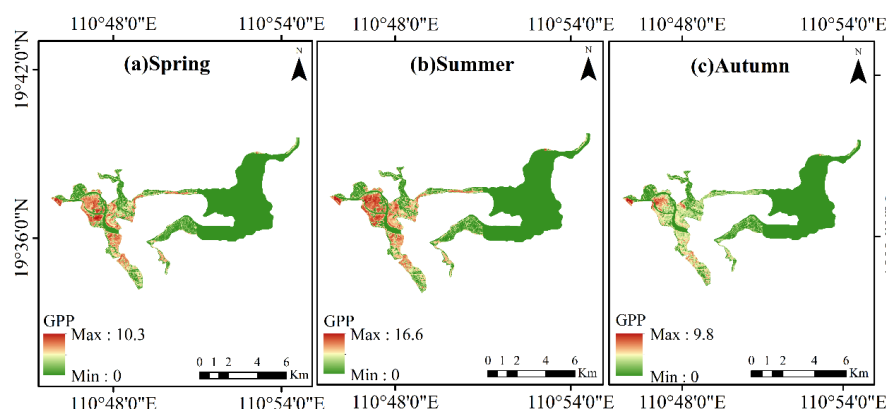
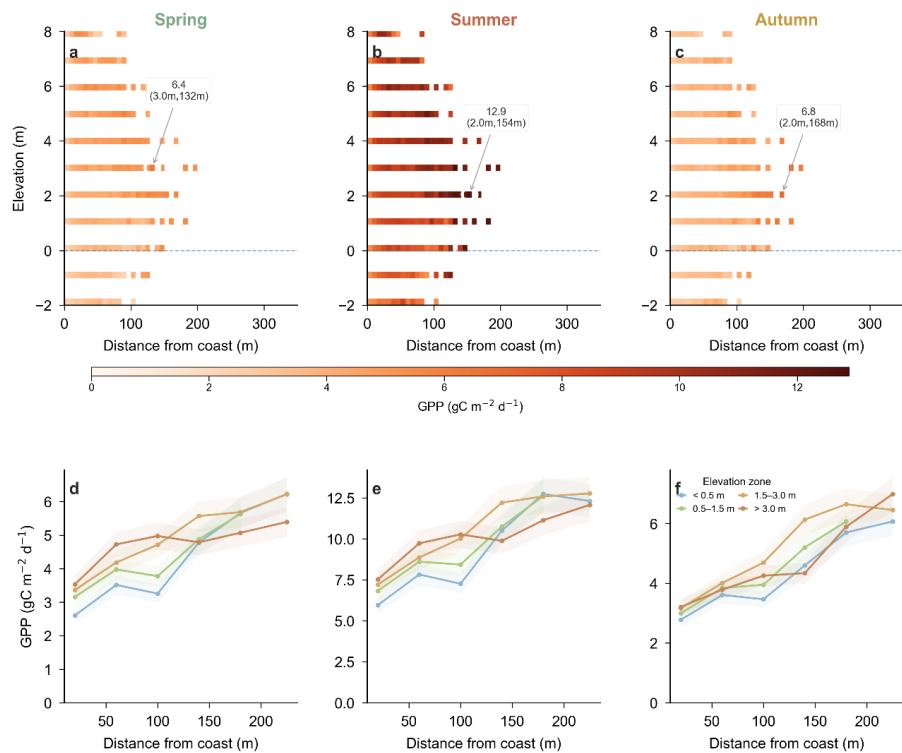


Fig. 8 Spatial distribution of seasonal mangrove gross primary productivity. a–c, Landscape GPP ($\text{g C m}^{-2} \text{ day}^{-1}$) for spring, summer and autumn.

GPP generally increased with distance from the coast in all three seasons (Fig. 9d–f), although the spring and autumn profiles flattened near 100 m: summer GPP rose from $7.1 \text{ g C m}^{-2} \text{ day}^{-1}$ within 60 m of the coast to $13.2 \text{ g C m}^{-2} \text{ day}^{-1}$ beyond 250 m, an 85% increase, and spring and autumn showed proportional gains of 94% and 110% respectively. The relationship between GPP and elevation was weaker: summer productivity increased by 31% from the low intertidal zone ($<0.5 \text{ m}$; $6.08 \text{ g C m}^{-2} \text{ day}^{-1}$) to the supratidal zone ($>3.0 \text{ m}$; $7.95 \text{ g C m}^{-2} \text{ day}^{-1}$; Fig. 9a–c). Two-dimensional niche analysis resolved peak GPP of $6.4 \text{ g C m}^{-2} \text{ day}^{-1}$ at 3.0 m elevation and 132 m from the coast in spring, $12.9 \text{ g C m}^{-2} \text{ day}^{-1}$ at 2.0 m and 154 m in summer, and $6.8 \text{ g C m}^{-2} \text{ day}^{-1}$ at 2.0 m and 168 m in autumn (Fig. 9a–c). Elevation-stratified distance profiles showed that the coastal-to-inland GPP gradient was steepest in the low intertidal zone and weakened with increasing elevation. These patterns should be interpreted with caution, because elevation was derived from a 30-m SRTM digital elevation model whose vertical accuracy over flat tidal flats is comparable to or larger than the elevation



520 contrasts discussed here.



521

522 **Fig. 9 Mangrove GPP niche space across elevation, coastal proximity and season.**

523 a–c, Two-dimensional GPP heatmaps ($\text{g C m}^{-2} \text{ d}^{-1}$) for spring (a), summer (b) and
524 autumn (c); white circles mark the seasonal productivity maximum and the dashed line
525 denotes mean sea level. d–f, GPP–distance profiles stratified by elevation zone for
526 spring (d), summer (e) and autumn (f).

527 **3.5 Canopy structure as the primary determinant of mangrove productivity**

528 An XGBoost model driven by six predictors explained 85–88% of the spatial
529 variation in GPP in all three seasons (spring $R^2 = 0.86$; summer 0.88; autumn 0.85; Figs.
530 10–12), with leaf area index (LAI) dominating feature importance in every season. LAI
531 contributed 67.9% in spring, 74.3% in summer and 67.6% in autumn, averaging 69.9%,



more than six times any other predictor. Among the meteorological variables, solar radiation ranked second in spring (10.6%) and autumn (11.4%), while PAR rose to second in summer (10.3%). Precipitation was most influential in autumn (10.3%), moderate in spring (8.4%) and least important in summer (3.2%). Land surface temperature contributed least of the six (2.4–3.8%), indicating that temperature was not limiting. Atmospheric CO₂ was assigned 8.0% of the importance in spring, but was built from a background concentration with no spatial structure, so that share should not be read as an effect. LAI alone accounts for 65%, 76% and 66% of the mapped GPP variance in the three seasons. It is a distinct variable from the greenness index used as fAPAR but is retrieved from the same Sentinel-2 reflectance, so the result identifies canopy structure as the strongest spatial correlate of GPP rather than isolating its cause.

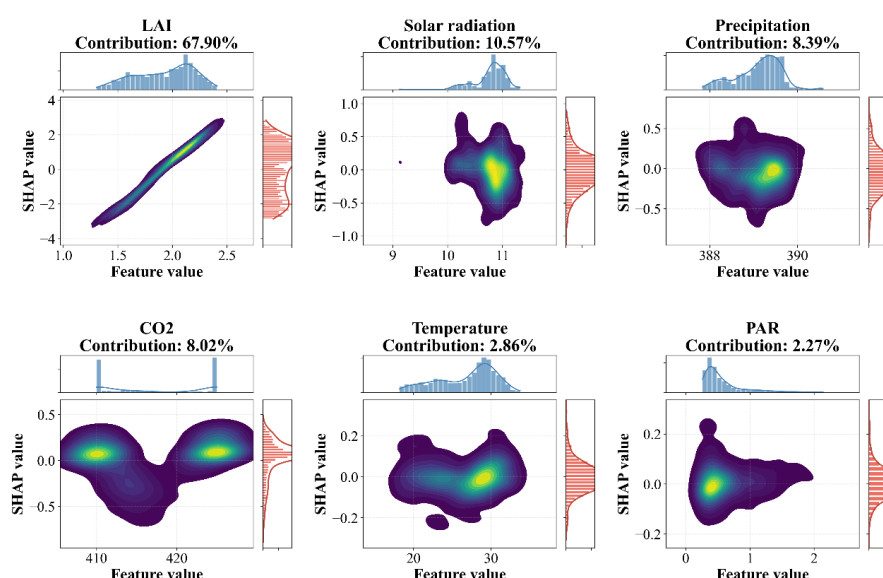


Fig. 10 SHAP dependence plots for the six predictors of spring mangrove GPP, ordered by importance.



Climate alone captured less than a quarter of the GPP variance. When LAI was excluded and the model restricted to the five meteorological predictors (precipitation, solar radiation, temperature, PAR and CO₂), explained variance fell to 19–23%. In this climate-only framework precipitation became the dominant driver, contributing 46.0% (spring), 36.0% (summer) and 47.0% (autumn) of SHAP importance, followed by solar radiation (15.5–31.1%) and temperature (9.7–11.2%). The near fourfold reduction in R² on removing LAI indicates that meteorological forcing alone cannot explain the spatial heterogeneity of mangrove carbon uptake. Canopy structure, itself an integrated product of species composition, stand age and local edaphic conditions, emerges as the proximate determinant of GPP, with precipitation and radiation imposing secondary climatic constraints.

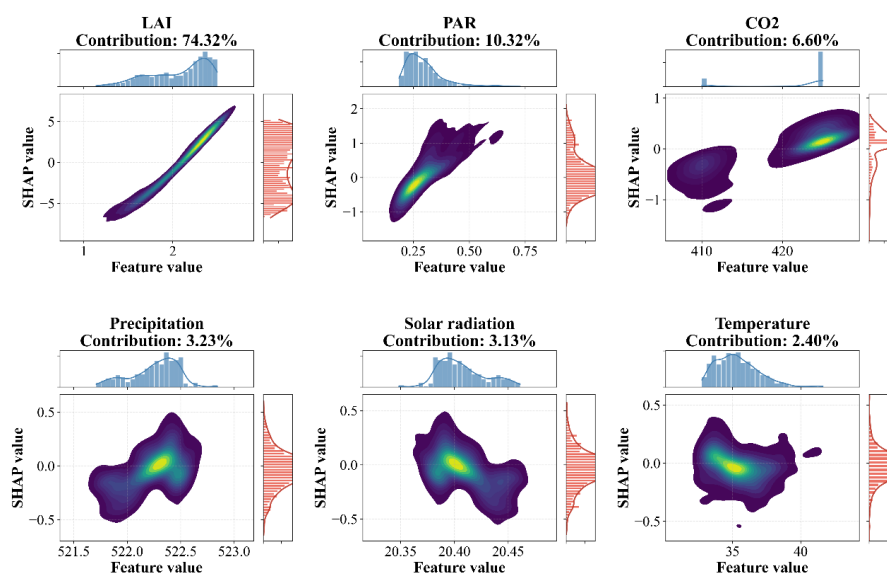


Fig. 11 SHAP dependence plots for summer mangrove GPP, ordered by importance.

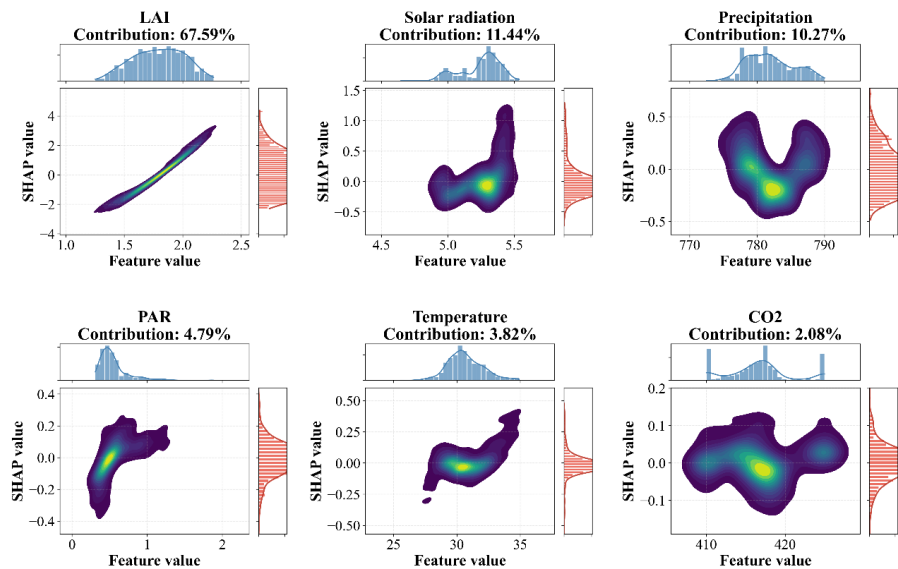


Fig. 12 SHAP dependence plots for autumn mangrove GPP, ordered by importance.

4. 4. Discussion

4.1 GPP magnitude, photosynthetic acclimation and thermal response

This study combined tower-based eddy covariance, a light-use-efficiency model calibrated against those fluxes, and machine-learning attribution of spatial drivers for a subtropical Chinese mangrove ecosystem, extending earlier work that established salinity and SST as controls on mangrove carbon exchange (Barr et al., 2013; Zheng & Takeuchi, 2022). The mean daily GPP of $6.67 \pm 1.81 \text{ g C m}^{-2} \text{ day}^{-1}$ (Fig. 2a), with a summer mean of $7.01 \text{ g C m}^{-2} \text{ day}^{-1}$ and a July maximum of $8.57 \text{ g C m}^{-2} \text{ day}^{-1}$ (Fig. 2b), lies near the upper bound of the global mangrove productivity range (Bouillon et al., 2008; Gnanamoorthy et al., 2020; Ahmed & Kamruzzaman, 2021) and exceeds the global mean of $5.1 \text{ g C m}^{-2} \text{ day}^{-1}$ reported by Alongi (2014). This is consistent with seasonal GPP estimates from the Everglades (Barr et al., 2013), Pichavaram



(Gnanamoorthy et al., 2020) and the Sundarbans (Ahmed & Kamruzzaman, 2021), and indicates that subtropical mangroves at the northern limit of their latitudinal range can sustain carbon uptake rates comparable to those of their low-latitude counterparts. The pronounced unimodal diurnal pattern, with peak assimilation between 10:30 and 12:00 (Fig. 3a–c) and no clear midday depression of the kind reported for terrestrial tropical forests (Doughty & Goulden, 2008), suggests that the canopy maintained favourable leaf water status under high ambient humidity and intertidal water supply (Reef & Lovelock, 2015; Gou et al., 2024). Light response analysis (Fig. 4) provides complementary evidence of seasonal acclimation: the apparent quantum yield increased from 0.0166 ± 0.0013 in spring to $0.0234 \pm 0.0031 \mu\text{mol CO}_2 \mu\text{mol}^{-1} \text{ photon}$ in autumn (Fig. 4d), consistent with canopy leaf area development and Rubisco investment in seasonally acclimating mangroves (Inoue et al., 2025).

Segmented regression on high-light observations identified a GPP–Ta inflection point at 30.5°C (Fig. 5a), which to our knowledge is the first empirically constrained thermal optimum reported for a subtropical mangrove ecosystem. The value exceeds thermal optima reported for temperate and boreal forests by $2\text{--}4^\circ\text{C}$ (Huang et al., 2019; Dusenke et al., 2023), consistent with thermal adaptation at 19.6°N . Air temperature alone nevertheless explained less than one-third of the high-light GPP variance (segmented regression $R^2 = 0.29$), and the VPM temperature scalar remained near-saturated in all seasons ($0.979\text{--}0.987$; Fig. 5c) because seasonal mean Ta ($26.0\text{--}30.4^\circ\text{C}$) fell within the optimal envelope. A detectable thermal threshold can therefore coexist with a perennially near-saturated Tscalar, which indicates that temperature was a real



597 but non-dominant constraint at this subtropical site. The 30.5 °C threshold matters
598 chiefly for its warming trajectory: if the thermal tracking efficiency reported for boreal
599 conifers (0.26–0.35 °C per 1 °C warming; [Dusenge et al., 2023](#)) applies to mangroves,
600 continued warming of the magnitude projected for this century ([IPCC, 2021](#)) would
601 increase the frequency of supra-optimal temperatures without commensurate
602 acclimation. Because summer SST already exceeded the mangrove optimum by 2.4 °C
603 (Fig. 6d), continued warming could shift Qinglangang from its present salinity-limited
604 regime toward one in which atmospheric and oceanic temperatures jointly constrain
605 photosynthesis.

606 **4.2 From terrestrial to ocean-enhanced VPM: framework and transferability**

607 The nested comparison of V1, V2 and V3 (Fig. 7b,c) quantifies how much each
608 oceanographic scalar changes the calibrated $\epsilon_{\max}$, addressing hypothesis H1. The SST
609 scalar alone changed $\epsilon_{\max}$ by 3–9%, reflecting the near-optimal SST regime at this
610 low-latitude site, whereas adding the salinity scalar raised $\epsilon_{\max}$ by 43.2% in spring,
611 20.3% in summer and 28.7% in autumn. The largest modification was required during
612 the dry-season salinity peak. The moderate agreement between V3-modelled and
613 observed half-hourly GPP ($r = 0.733$, $\text{RMSE} = 10.83 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$; Fig. 7d)
614 indicates that the model captures the seasonal signal but leaves substantial half-hourly
615 variance unexplained, probably reflecting tidal inundation effects (Li et al., 2014),
616 diffuse and direct radiation partitioning (Lu et al., 2022) and sub-seasonal phenology
617 (Gou et al., 2023).

618 Hypothesis H3, that the oceanographic scalars act as a seasonal correction rather



619 than a sub-seasonal driver, was supported by the predictive comparison in Section 3.3.
620 Because SST and SSS were built from monthly climatologies, they vary little within a
621 season and cannot track the weather-scale fluctuations that dominate half-hourly flux
622 variability; consequently the ocean-enhanced configuration did not improve prediction
623 and in spring performed worse than the terrestrial baseline. This distinction matters for
624 how the framework should be used. The value of the calibrated, season-specific $\epsilon_{\max}$
625 is that it makes light-use efficiency comparable across seasons and provides a
626 transferable parameter for satellite-based GPP estimation, whereas the salinity scalar
627 should be understood as a seasonal adjustment whose magnitude depends on the
628 assumed response function. The salinity sensitivity is nevertheless mechanistically
629 plausible: elevated salinity constrains mangrove water transport through osmotic effects
630 on leaf water potential (Reef & Lovelock, 2015), reduces carboxylation efficiency (Ball
631 & Farquhar, 1984) and suppresses photosystem II quantum yield (Naidoo et al., 2002),
632 and experimental work shows that these effects are themselves temperature-dependent
633 (Inoue et al., 2025). Resolving them properly will require in situ salinity and
634 temperature records co-located with the flux tower rather than monthly climatologies.

635 **4.3 Seasonal control of $\epsilon_{\max}$ by the oceanographic scalars**

636 Among the three scalars, salinity accounted for most of the seasonal variation in
637 photosynthetic light use efficiency at Qinglangang. SSS declined from a spring dry-
638 season maximum of 32.4 ± 0.3 PSU to a monsoon-driven summer minimum of $31.3 \pm$
639 0.3 PSU before recovering to 31.9 ± 0.3 PSU in autumn (Fig. 6a,c). This 1.1 PSU range,
640 though small, produced a 0.11-unit range in the salinity scalar (0.781–0.891; Fig. 6e)



641 because of the non-linear sigmoid form. Tscalar varied negligibly (range 0.008), Sscalar
642 varied modestly (range 0.049) and Salscalar contributed the largest share of the seasonal
643 amplitude (range 0.110). The composite oceanic stress index identified spring as the
644 most ocean-limited season (0.740) and summer as the most favourable (0.836). Because
645 the salinity scalar is a monthly climatology, these differences are a seasonal offset rather
646 than a resolved sub-seasonal response, and the magnitude of the resulting $\epsilon_{\max}$ change
647 depends on the assumed shape of the response function (Section 3.3).

648 This ordering is reflected in the bootstrap-derived $\epsilon_{\max}$ estimates and their nested
649 decomposition (Fig. 7a–c). Under V3, $\epsilon_{\max}$ was 1.491 g C MJ⁻¹ APAR in spring, 1.965
650 in summer and 1.897 in autumn (Fig. 7a), a seasonal range of approximately 30% whose
651 confidence intervals nonetheless overlap. The nested V1 to V3 comparison showed a
652 +43.2% spring enhancement (Fig. 7b,c), larger than in summer and autumn, which is
653 the expected signature of greater salinity limitation in spring: spring SSS lay on the
654 steeper part of the sigmoid, where the seasonal salinity change produced a
655 disproportionate decline in the scalar. The ranking of spring above summer and autumn
656 held for all 16 parameter combinations tested, indicating that the qualitative conclusion
657 is robust even though the magnitude is not. This supports hypothesis H2 in its
658 qualitative form.

659 **4.4 Spatial drivers: coastal proximity, canopy structure and the limited role of** 660 **climate**

661 Distance from coastline was the leading spatial predictor of GPP (26.6% relative
662 importance), exceeding elevation (9.8%) by a factor of 2.7, while season accounted for



663 the largest share overall. Because season contributes the majority of the random forest
664 importance, the remaining predictors should be interpreted as secondary within-season
665 structure rather than as dominant controls. The coastal-to-inland gradient integrates
666 salinity exposure, inundation frequency and groundwater influence, all of which change
667 with distance inland, and mirrors within-estuary salinity gradients documented
668 elsewhere (Barr et al., 2010; Ray et al., 2011). The landscape is also the product of an
669 active restoration history, and reconstructions of Qinglan Bay since 1988 document
670 substantial recovery of mangrove cover and increased carbon sink capacity (Jia et al.,
671 2022).

672 The XGBoost attribution (Figs. 10–12) supports hypothesis H4: LAI accounted
673 for a mean of 69.9% of total SHAP importance, more than six times any meteorological
674 predictor, and land surface temperature contributed least (2.4–3.8%). Excluding LAI
675 and retraining on the five meteorological predictors alone reduced explained variance
676 from 85–88% to 19–23%, with precipitation dominant (36–47%), consistent with
677 freshwater alleviation of salinity stress. This dominance is not an artefact of model
678 structure, since LAI is not the greenness index that enters the GPP calculation, but it
679 comes from the same reflectance data, so the result identifies canopy structure as the
680 strongest spatial correlate of the mapped GPP rather than isolating its cause. This is
681 consistent with field evidence from Hainan mangroves that species diversity and stand
682 structure jointly determine biomass and carbon storage (Bai et al., 2021), and implies
683 that species selection and planting configuration at appropriate tidal elevations offer
684 greater leverage for restoration than choosing among climatically similar sites.



685 **4.5 Limitations and future directions**

686 Several limitations should be acknowledged. The flux record spans eight months
687 and excludes the winter monsoon period; a full annual cycle with interannual
688 replication is needed to establish whether a cold-season thermal constraint emerges.
689 Both scalars were built from monthly climatologies rather than in situ measurements,
690 which limits them to seasonal resolution and means the salinity sensitivity cannot be
691 separated from the assumed shape of the response function; moored sensors co-located
692 with the tower would resolve both issues (Barr et al., 2010). Coastal satellite salinity
693 retrievals also carry much larger uncertainty than open-ocean retrievals, and the
694 seasonal SSS range here (1.1 PSU) is small relative to it. The $\epsilon_{\max}$ values derive from a
695 single tower and require validation across sites spanning a salinity gradient. The
696 upscaled maps have not been validated against the tower record and differ from it by
697 34–48% in two of three seasons; a footprint-weighted comparison is required before
698 they are used quantitatively. Tidal height was not incorporated (Li et al., 2014), the VPD
699 scalar was excluded because of open-path sensor humidity saturation, and elevation
700 came from a 30-m SRTM model whose vertical accuracy limits the sub-metre contrasts
701 in Section 3.4. Three predictors also contain artefacts: autumn LST reaches -4.1 °C,
702 autumn PAR falls below zero, and summer solar radiation is almost spatially uniform,
703 so its low importance in that season reflects the absence of spatial contrast rather than
704 the absence of an effect. The CO₂ predictor has no spatial structure of its own and its
705 reported importance should be disregarded. Finally, the VPM is linear in APAR and
706 cannot represent the light saturation evident in the light response curves.



707 In summary, this study calibrated season-specific light use efficiency for a
708 subtropical mangrove and scaled it from tower to landscape (Figs. 2–9). The season-
709 specific $\epsilon_{\max}$ values of 1.491 (spring), 1.965 (summer) and 1.897 (autumn) g C MJ⁻¹
710 APAR (Fig. 7a), combined with the ocean-enhanced VPM framework, provide a
711 calibrated pathway for regional satellite-based GPP estimation, subject to the validation
712 and sensitivity analyses noted above. Among the environmental scalars examined,
713 salinity accounted for most of the seasonal amplitude in $\epsilon_{\max}$, with spring consistently
714 the most salinity-limited season across all parameter combinations tested, whereas the
715 temperature scalars remained near-saturated. The spatial attribution adds an operational
716 dimension: the primacy of canopy structure over climate (Figs. 10–12) and of coastal
717 proximity over elevation (Fig. 9) offer quantitative guidance for siting mangrove
718 restoration. Extending this framework across the pan-tropical mangrove distribution,
719 where salinity regimes, tidal amplitudes and species assemblages vary by orders of
720 magnitude while ENSO-driven forcing modulates the oceanographic environment at
721 basin scale, is the logical next step.

722 5. Conclusion

723 Gross primary productivity in a subtropical Chinese mangrove forest was
724 calibrated and scaled from tower to landscape. Integrating eight months of eddy
725 covariance measurements with Sentinel-2 imagery produced season-specific maximum
726 light use efficiency values of 1.491, 1.965 and 1.897 g C MJ⁻¹ APAR for spring, summer
727 and autumn, offering an alternative to the fixed $\epsilon_{\max}$ assumption used in satellite-based
728 mangrove GPP products. Among the environmental scalars, salinity modified $\epsilon_{\max}$



729 most strongly, raising the spring value by 43.2% relative to the terrestrial baseline,
730 although a sensitivity analysis showed that this magnitude depends on the assumed
731 salinity response function (7–97% across the parameter range tested) while the ranking
732 of spring as the most salinity-limited season was robust. Because SST and SSS were
733 built from monthly climatologies, they act as a seasonal correction rather than
734 improving sub-seasonal prediction. The spatial analysis showed that leaf area index
735 accounted for about 70% of total SHAP importance and that coastal proximity
736 outweighed elevation as a predictor of GPP, providing spatially explicit guidance for
737 blue carbon restoration planning. Taken together, the results indicate that calibrating
738 light-use-efficiency parameters against tower observations, and representing the coastal
739 oceanographic setting explicitly, are both necessary steps toward closing the mangrove
740 carbon budget.

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745 **Data availability**

746 The eddy covariance measurements and derived maps are available from the
747 corresponding author on reasonable request. All ancillary datasets are publicly available:
748 Sentinel-2 (COPERNICUS/S2_SR_HARMONIZED), ERA5-Land
749 (ECMWF/ERA5_LAND/MONTHLY_AGGR), NOAA OISST v2.1
750 (NOAA/CDR/OISST/V2_1) and Landsat thermal imagery.



751 **Author contributions**

752 X.P. and Y.C. designed the study, analysed the data and wrote the manuscript. T.S.
753 and Z.C. conceived and supervised the study. T.W., X.C., Y.L. and S.N. collected and
754 processed the flux data. D.Z. contributed the remote-sensing analysis. All authors
755 approved the final manuscript.

756 **Competing interests**

757 The authors declare no competing interests.

758 **References**

- 759 Ahmed, S., & Kamruzzaman, M. (2021). Species-specific biomass and carbon flux in Sundarbans
760 mangrove forest, Bangladesh: Response to stand and weather variables. *Biomass and*
761 *Bioenergy*, 153, 106215. <https://doi.org/10.1016/j.biombioe.2021.106215>
762 Alongi, D. M. (2014). Carbon cycling and storage in mangrove forests. *Annual Review of Marine*
763 *Science*, 6, 195–219. <https://doi.org/10.1146/annurev-marine-010213-135020>
764 Alongi, D. M. (2020). Global significance of mangrove blue carbon in climate change mitigation.
765 *Sci*, 2(3), 67. <https://doi.org/10.3390/sci2030067>
766 Arkema, K. K., Delevaux, J. M. S., Silver, J. M., et al. (2023). Evidence-based target setting informs
767 blue carbon strategies for nationally determined contributions. *Nature Ecology & Evolution*,
768 7(7), 1045–1059. <https://doi.org/10.1038/s41559-023-02081-1>
769 Bai, J., Meng, Y., Gou, R., et al. (2021). Mangrove diversity enhances plant biomass production and
770 carbon storage in Hainan island, China. *Functional Ecology*, 35(3), 774–786.
771 <https://doi.org/10.1111/1365-2435.13753>
772 Ball, M. C., & Farquhar, G. D. (1984). Photosynthetic and stomatal responses of two mangrove
773 species, *Aegiceras corniculatum* and *Avicennia marina*, to long term salinity and humidity
774 conditions. *Plant Physiology*, 74(1), 1–6. <https://doi.org/10.1104/pp.74.1.1>
775 Barr, J. G., Engel, V., Fuentes, J. D., et al. (2010). Controls on mangrove forest–atmosphere carbon
776 dioxide exchanges in western Everglades National Park. *Journal of Geophysical Research:*
777 *Biogeosciences*, 115, G02020. <https://doi.org/10.1029/2009JG001186>
778 Barr, J. G., Engel, V., Fuentes, J. D., et al. (2013). Modeling light use efficiency in a subtropical
779 mangrove forest equipped with CO₂ eddy covariance. *Biogeosciences*, 10(3), 2145–2158.
780 <https://doi.org/10.5194/bg-10-2145-2013>
781 Binh, N. A., Hauser, L. T., Salinero-Delgado, M., et al. (2024). Monitoring mangrove traits through
782 optical Earth observation: Towards spatio-temporal scalability using cloud-based Sentinel-2
783 continuous time series. *ISPRS Journal of Photogrammetry and Remote Sensing*, 214, 135–152.
784 <https://doi.org/10.1016/j.isprsjprs.2024.06.007>
785 Bouillon, S., Borges, A. V., Castañeda-Moya, E., et al. (2008). Mangrove production and carbon
786 sinks: A revision of global budget estimates. *Global Biogeochemical Cycles*, 22, GB2013.



- 787 <https://doi.org/10.1029/2007GB003052>
- 788 Chen, T., & Guestrin, C. (2016). XGBoost: A scalable tree boosting system. In Proceedings of the
789 22nd ACM SIGKDD International Conference on Knowledge Discovery and Data Mining (pp.
790 785–794). <https://doi.org/10.1145/2939672.2939785>
- 791 Donato, D. C., Kauffman, J. B., Murdiyarso, D., et al. (2011). Mangroves among the most carbon-
792 rich forests in the tropics. *Nature Geoscience*, 4(5), 293–297. <https://doi.org/10.1038/ngeo1123>
- 793 Doughty, C. E., & Goulden, M. L. (2008). Are tropical forests near a high temperature threshold?
794 *Journal of Geophysical Research: Biogeosciences*, 113, G00B07.
795 <https://doi.org/10.1029/2007JG000632>
- 796 Dusenge, M. E., Warren, J. M., Reich, P. B., et al. (2023). Boreal conifers maintain carbon uptake
797 with warming despite failure to track optimal temperatures. *Nature Communications*, 14, 4667.
798 <https://doi.org/10.1038/s41467-023-40248-3>
- 799 Foken, T., & Wichura, B. (1996). Tools for quality assessment of surface-based flux measurements.
800 *Agricultural and Forest Meteorology*, 78(1–2), 83–105. [https://doi.org/10.1016/0168-](https://doi.org/10.1016/0168-1923(95)02248-1)
801 [1923\(95\)02248-1](https://doi.org/10.1016/0168-1923(95)02248-1)
- 802 Gnanamoorthy, P., Selvam, V., Deb Burman, P. K., et al. (2020). Seasonal variations of net
803 ecosystem (CO₂) exchange in the Indian tropical mangrove forest of Pichavaram. *Estuarine,*
804 *Coastal and Shelf Science*, 243, 106828. <https://doi.org/10.1016/j.ecss.2020.106828>
- 805 Goldberg, L., Lagomasino, D., Thomas, N., & Fatoyinbo, T. (2020). Global declines in human-
806 driven mangrove loss. *Global Change Biology*, 26(10), 5844–5855.
807 <https://doi.org/10.1111/gcb.15275>
- 808 Gou, R., Buchmann, N., Chi, J., et al. (2023). Temporal variations of carbon and water fluxes in a
809 subtropical mangrove forest: Insights from a decade-long eddy covariance measurement.
810 *Agricultural and Forest Meteorology*, 343, 109764.
811 <https://doi.org/10.1016/j.agrformet.2023.109764>
- 812 Gou, R., Chi, J., Liu, J., et al. (2024). Atmospheric water demand constrains net ecosystem
813 production in subtropical mangrove forests. *Journal of Hydrology*, 630, 130651.
814 <https://doi.org/10.1016/j.jhydrol.2024.130651>
- 815 Hamilton, S. E., & Friess, D. A. (2018). Global carbon stocks and potential emissions due to
816 mangrove deforestation from 2000 to 2012. *Nature Climate Change*, 8, 240–244.
817 <https://doi.org/10.1038/s41558-018-0090-4>
- 818 He, Z., Feng, X., Chen, Q., et al. (2022). Evolution of coastal forests based on a full set of mangrove
819 genomes. *Nature Ecology & Evolution*, 6, 738–749. [https://doi.org/10.1038/s41559-022-](https://doi.org/10.1038/s41559-022-01744-9)
820 [01744-9](https://doi.org/10.1038/s41559-022-01744-9)
- 821 Huang, M., Piao, S., Ciais, P., et al. (2019). Air temperature optima of vegetation productivity across
822 global biomes. *Nature Ecology & Evolution*, 3(5), 772–779. [https://doi.org/10.1038/s41559-](https://doi.org/10.1038/s41559-019-0838-x)
823 [019-0838-x](https://doi.org/10.1038/s41559-019-0838-x)
- 824 Inoue, T., Fujimura, T., & Noguchi, K. (2025). Growth, morphology and respiratory cost responses
825 to salinity in the mangrove plant *Rhizophora stylosa* depend on growth temperature. *Plant, Cell*
826 *& Environment*, 48, 965–977. <https://doi.org/10.1111/pce.15184>
- 827 Jia, P., Huang, W., Zhang, Z., et al. (2022). The carbon sink of mangrove ecological restoration
828 between 1988–2020 in Qinglan Bay, Hainan Island, China. *Forests*, 13(10), 1547.
829 <https://doi.org/10.3390/f13101547>
- 830 IPCC (2021). *Climate Change 2021: The Physical Science Basis*. Contribution of Working Group I



- 831 to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge
832 University Press. <https://doi.org/10.1017/9781009157896>
- 833 Kaimal, J. C., & Finnigan, J. J. (1994). Atmospheric boundary layer flows: Their structure and
834 measurement. Oxford University Press. <https://doi.org/10.1093/oso/9780195062397.001.0001>
- 835 Krauss, K. W., Lovelock, C. E., McKee, K. L., et al. (2008). Environmental drivers in mangrove
836 establishment and early development: A review. *Aquatic Botany*, 89(2), 105–127.
837 <https://doi.org/10.1016/j.aquabot.2007.12.014>
- 838 Lasslop, G., Reichstein, M., Papale, D., et al. (2010). Separation of net ecosystem exchange into
839 assimilation and respiration using a light response curve approach: Critical issues and global
840 evaluation. *Global Change Biology*, 16(1), 187–208. <https://doi.org/10.1111/j.1365-2486.2009.02041.x>
- 842 Li, Q., Lu, W., Chen, H., Luo, Y., & Lin, G. (2014). Differential responses of net ecosystem
843 exchange of carbon dioxide to light and temperature between spring and neap tides in
844 subtropical mangrove forests. *The Scientific World Journal*, 2014, 943697.
845 <https://doi.org/10.1155/2014/943697>
- 846 Liu, Y., & Zhu, X. (2024). Tracking mangrove light use efficiency using normalized difference red
847 edge index. *Ecological Indicators*, 168, 112774. <https://doi.org/10.1016/j.ecolind.2024.112774>
- 848 Liu, Q., Feng, M., & Wang, D. (2011). ENSO-induced interannual variability in the southeastern
849 South China Sea. *Journal of Oceanography*, 67, 127–133. <https://doi.org/10.1007/s10872-011-0002-y>
- 851 Lloyd, J., & Taylor, J. A. (1994). On the temperature dependence of soil respiration. *Functional*
852 *Ecology*, 8(3), 315–323. <https://doi.org/10.2307/2389824>
- 853 Lu, H., Qin, Z., Lin, S., et al. (2022). Large influence of atmospheric vapor pressure deficit on
854 ecosystem production efficiency. *Nature Communications*, 13, 1653.
855 <https://doi.org/10.1038/s41467-022-29009-w>
- 856 Lundberg, S. M., Erion, G., Chen, H., et al. (2020). From local explanations to global understanding
857 with explainable AI for trees. *Nature Machine Intelligence*, 2(1), 56–67.
858 <https://doi.org/10.1038/s42256-019-0138-9>
- 859 Lundberg, S. M., & Lee, S.-I. (2017). A unified approach to interpreting model predictions. In
860 *Advances in Neural Information Processing Systems* 30 (pp. 4765–4774).
861 <https://doi.org/10.48550/arXiv.1705.07874>
- 862 Macreadie, P. I., Costa, M. D. P., Atwood, T. B., et al. (2021). Blue carbon as a natural climate
863 solution. *Nature Reviews Earth & Environment*, 2(12), 826–839.
864 <https://doi.org/10.1038/s43017-021-00224-1>
- 865 Malerba, M. E., Duarte de Paula Costa, M., Friess, D. A., et al. (2023). Remote sensing for cost-
866 effective blue carbon accounting. *Earth-Science Reviews*, 238, 104337.
867 <https://doi.org/10.1016/j.earscirev.2023.104337>
- 868 McLeod, E., Chmura, G. L., Bouillon, S., et al. (2011). A blueprint for blue carbon: Toward an
869 improved understanding of the role of vegetated coastal habitats in sequestering CO₂. *Frontiers*
870 *in Ecology and the Environment*, 9(10), 552–560. <https://doi.org/10.1890/110004>
- 871 Moncrieff, J. B., Massheder, J. M., de Bruin, H., et al. (1997). A system to measure surface fluxes
872 of momentum, sensible heat, water vapour and carbon dioxide. *Journal of Hydrology*, 188–189,
873 589–611. [https://doi.org/10.1016/S0022-1694\(96\)03194-0](https://doi.org/10.1016/S0022-1694(96)03194-0)
- 874 Naidoo, G., Tuffers, A. V., & von Willert, D. J. (2002). Changes in gas exchange and chlorophyll



- 875 fluorescence characteristics of two mangroves and a mangrove associate in response to salinity
876 in the natural environment. *Trees*, 16(2–3), 140–146. [https://doi.org/10.1007/s00468-001-](https://doi.org/10.1007/s00468-001-0134-6)
877 0134-6
- 878 Pastor-Guzman, J., Dash, J., & Atkinson, P. M. (2018). Remote sensing of mangrove forest
879 phenology and its environmental drivers. *Remote Sensing of Environment*, 205, 71–84.
880 <https://doi.org/10.1016/j.rse.2017.11.009>
- 881 Pichler, M., & Hartig, F. (2023). Machine learning and deep learning: A review for ecologists.
882 *Methods in Ecology and Evolution*, 14(4), 994–1016. [https://doi.org/10.1111/2041-](https://doi.org/10.1111/2041-210X.14061)
883 210X.14061
- 884 Qiao, P., Dong, Y., Gu, X., et al. (2024). Warming stimulates mangrove carbon sequestration in
885 rising sea level at their northern limit: An in situ simulation. *Limnology and Oceanography*,
886 69(9), 2138–2151. <https://doi.org/10.1002/lno.12655>
- 887 Qiao, P., Chen, L., Krauss, K. W., et al. (2025). Rising sea level reduces carbon sequestration and
888 CO₂ and N₂O fluxes while promoting CH₄ flux from mangroves. *Cell Reports Sustainability*,
889 2(9), 100520. <https://doi.org/10.1016/j.crsus.2025.100520>
- 890 Ray, R., Ganguly, D., Chowdhury, C., et al. (2011). Carbon sequestration and annual increase of
891 carbon stock in a mangrove forest. *Atmospheric Environment*, 45(28), 5016–5024.
892 <https://doi.org/10.1016/j.atmosenv.2011.04.074>
- 893 Reef, R., & Lovelock, C. E. (2015). Regulation of water balance in mangroves. *Annals of Botany*,
894 115(3), 385–395. <https://doi.org/10.1093/aob/mcu174>
- 895 Reichstein, M., Falge, E., Baldocchi, D., et al. (2005). On the separation of net ecosystem exchange
896 into assimilation and ecosystem respiration: Review and improved algorithm. *Global Change*
897 *Biology*, 11(9), 1424–1439. <https://doi.org/10.1111/j.1365-2486.2005.001002.x>
- 898 Sun, Z., An, Y., Kong, J., et al. (2024). Exploring the spatio-temporal patterns of global mangrove
899 gross primary production and quantifying the factors affecting its estimation, 1996–2020.
900 *Science of the Total Environment*, 908, 168262.
901 <https://doi.org/10.1016/j.scitotenv.2023.168262>
- 902 Webb, E. K., Pearman, G. I., & Leuning, R. (1980). Correction of flux measurements for density
903 effects due to heat and water vapour transfer. *Quarterly Journal of the Royal Meteorological*
904 *Society*, 106(447), 85–100. <https://doi.org/10.1002/qj.49710644707>
- 905 Wu, X., Yao, F., & Wang, D. (2025). Interannual variability of the summer surface salinity in the
906 southern South China Sea driven by the summer monsoon. *Journal of Geophysical Research:*
907 *Oceans*, 130, e2025JC022399. <https://doi.org/10.1029/2025JC022399>
- 908 Xiao, X., Hollinger, D., Aber, J., et al. (2004). Satellite-based modeling of gross primary production
909 in an evergreen needleleaf forest. *Remote Sensing of Environment*, 89(4), 519–534.
910 <https://doi.org/10.1016/j.rse.2003.11.008>
- 911 Yan, H., Fu, Y., Xiao, X., et al. (2009). Modeling gross primary productivity for winter wheat–maize
912 double cropping system using MODIS time series and CO₂ eddy flux tower data. *Agriculture,*
913 *Ecosystems & Environment*, 129(4), 391–400. <https://doi.org/10.1016/j.agee.2008.10.017>
- 914 Zhang, Y., Xiao, X., Wu, X., et al. (2017). A global moderate resolution dataset of gross primary
915 production of vegetation for 2000–2016. *Scientific Data*, 4, 170165.
916 <https://doi.org/10.1038/sdata.2017.165>
- 917 Zheng, Y., & Takeuchi, W. (2022). Estimating mangrove forest gross primary production by
918 quantifying environmental stressors in the coastal area. *Scientific Reports*, 12, 2238.

<https://doi.org/10.5194/egusphere-2026-5811>

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