



Water and carbon balance of rubber trees modelled under changing climate and management-driven disturbances

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Abstract. Rubber plantations play a critical role in the economy of Southeast Asia, yet their productivity is increasingly exposed to environmental variability and climate change. Process-based models able to represent the interactions between water and carbon dynamics are essential for assessing their current functioning and anticipating future responses. In this context, we adapted the CASTANEA-MAESPA model to simulate the biophysical functioning of mature rubber plantations in Thailand. We included in that model a newly developed module for latex production which takes into account management practices and links tapping-related processes to overall carbon allocation and growth. The model results were compared to water and carbon fluxes and stock data at a flux tower experimental site in the central-east Thailand (CRRC) and water fluxes and latex yield data at a research station in southern Thailand (SKRS). Good agreement is found between the simulated model outputs and the measured water and carbon fluxes and stocks at both sites. The model estimated at CRRC a gross primary productivity (GPP) of 25.95 t C ha⁻¹ yr⁻¹ for a 25-year-old rubber plantation, close to the observed 26.98 t C ha⁻¹ yr⁻¹. Simulated latex yield was 1.64 t C ha⁻¹ yr⁻¹ versus 1.80 t C ha⁻¹ yr⁻¹ observed, and simulated wood biomass was 117.96 t C ha⁻¹ compared with 123.15 t C ha⁻¹ observed, at CRRC. Overall, this work provided scientifically grounded results to understand latex production in Southeast Asia, while also identifying key knowledge gaps, particularly regarding the determinants of rubber leaf phenology.

Keywords: Southeast Asia, Rubber plantation, CASTANEA-MAESPA model, Water and carbon fluxes, Latex yield, Climate change



1 Introduction

Rubber tree (*Hevea brasiliensis*) is the main source of natural rubber (NR), a key industrial material widely used in products such as tires and medical equipment (Li et al., 2025; Mooibroek and Cornish, 2000). Southeast Asia (SEA) produces 83% of global NR, with Thailand and Indonesia as leading producers (FAOSTAT, 2025). However, rising demand, limited productivity gains, and climate change threaten future NR supply (ANRPC, 2025; Inkonkoy, 2021). Understanding how rubber tree growth and yield are linked to environmental factors is key to assessing how rubber-based systems respond to climate change.

Several studies have investigated environmental influences on rubber tree physiology and phenology, including the effects of temperature on latex flow and regeneration (Golbon et al., 2015; Nguyen and Dang, 2016; Yu et al., 2014), the role of soil moisture on growth (Clermont-Dauphin et al., 2013), and the impacts of water deficit (Carr, 2012; Isarangkool Na Ayutthaya et al., 2011), photoperiod (Yeang, 2007), and temperature (Azizan et al., 2023; Zhai et al., 2017) on leaf phenology. Despite these advances, the direct influence of key environmental factors such as temperature on core physiological processes remains poorly understood, and their impact on latex yield under changing climate has yet to be quantified (Pinizzotto et al., 2021). A major challenge is that these environmental factors do not act independently i.e., they can influence multiple physiological processes simultaneously and interact with one another, making it difficult to isolate their individual contributions from observations alone. A systemic approach is therefore needed to integrate these processes and identify the dominant and complementary roles of environmental drivers in determining the functioning and productivity of rubber plantations. Process-based modelling provides a suitable framework for this purpose because it explicitly represents the causal mechanisms linking environmental conditions to physiological processes and, ultimately, to plantation-level outcomes such as latex production. By integrating these mechanisms within a common framework, such models can be used to disentangle the effects of individual environmental drivers, explore their interactions, and quantify how changes in environmental conditions may translate into changes in tree development and latex yield. This approach thus offers a means to move beyond empirical associations toward a mechanistic understanding of rubber tree responses to environmental variability and climate change.

Among the process-based models applied to rubber trees, very few are able to simulate the carbon fluxes from acquisition to allocation and loss including the carbon exports related to latex yield. Notable exceptions include the Water, Nutrient and Light Capture in Agroforestry Systems (WaNuLCAS) (Van Noordwijk and Lusiana, 1999) and the Land Use Change Impact Assessment (LUCIA) (Marohn and Cadisch, 2011) models. In WaNuLCAS, latex yield is calculated as a proportion of daily net primary production (NPP), which reflects carbon gained through photosynthesis and depends on resource availability (light, water, nutrients). This carbon pool is empirically reduced under water stress and by tapping intensity. A user-defined coefficient then allocates a fixed fraction of the adjusted NPP to latex (Van Noordwijk and Lusiana, 1999; Yang et al., 2019). LUCIA adopts a similar structure but lacks a reserve pool, meaning latex carbon is allocated directly from daily NPP without intermediate storage, and it does not account directly for environmental stress effects on yield (Yang et al., 2019). While



65 WaNuLCAS provides a more comprehensive framework for latex yield simulation, it has some limitations. First, its simplified representation of rainfall infiltration on soil versus runoff can result in uncertain water availability estimates, which in turn affect predictions of tree growth and latex yield under drought (Boithias et al., 2012). Moreover, its single empirical water-stress factor, based on soil water content, can fail to capture dynamic stomatal responses under very dry or high vapor pressure deficit (VPD) conditions, leading to over- or under-estimations of water use and latex flow (Boithias et al., 2012). Finally, the NPP to latex partitioning coefficient does not vary with environmental conditions. In fact, WaNuLCAS is fundamentally a resource competition and agroforestry systems model (Van Noordwijk et al., 2011), whereas LUCIA is a spatially explicit dynamic model primarily designed to assess the impacts of land-use change on agricultural productivity and environmental functions (Marohn and Cadisch, 2011). Neither WaNuLCAS nor LUCIA includes an explicit atmospheric CO₂ concentration driver that directly influences photosynthesis through CO₂ response functions such as Farquhar-type photosynthesis (Farquhar et al., 1980) or Ball-Berry stomatal conductance formulations (Ball et al., 1987). Consequently, the CO₂ fertilisation effect and its interactions with temperature and soil water availability are not mechanistically represented in these models (Marohn and Cadisch, 2011; Van Noordwijk et al., 2011; Van Noordwijk and Lusiana, 1999). In fact, accounting for the interactive effects of CO₂, temperature and soil water dynamics is essential for improving process-based rubber tree growth models under a changing climate. A process-based modelling framework that explicitly represents these physiological processes is therefore needed to better assess rubber tree functioning and productivity under a changing climate. Integrating a latex yield module into a comprehensive ecophysiological model designed for tropical tree species, able to simulate complete carbon and water cycles, will allow us to overcome limitations of earlier latex yield models.

To address this, we applied the coupled ecophysiological process-based model CASTANEA-MAESPA model (Dufrêne et al., 2005; Duursma and Medlyn, 2012), for the first time to rubber tree and developed a new latex yield module to explicitly simulate latex production in rubber plantations. The CASTANEA-MAESPA model combines CASTANEA's strengths in carbon allocation and tree growth (Dufrêne et al., 2005) with MAESPA's detailed simulation of soil water dynamics, plant hydraulics, and leaf photosynthesis (Duursma and Medlyn, 2012). CASTANEA-MAESPA provides a comprehensive ecophysiological framework better suited to tropical tree plantations, particularly those with deep rooting systems (Christina et al., 2017; Cornut et al., 2023a, b), enabling simulation of integrated carbon and water cycles, while offering the flexibility needed to incorporate processes specific to rubber trees. The objectives of this study were to: (1) adapt the coupled CASTANEA-MAESPA model to rubber plantations; (2) develop and integrate a new module to simulate latex production; and (3) assess the ability of the resulting model to simulate water fluxes and the full carbon balance of rubber plantations, including tree growth, latex export and other carbon fluxes.



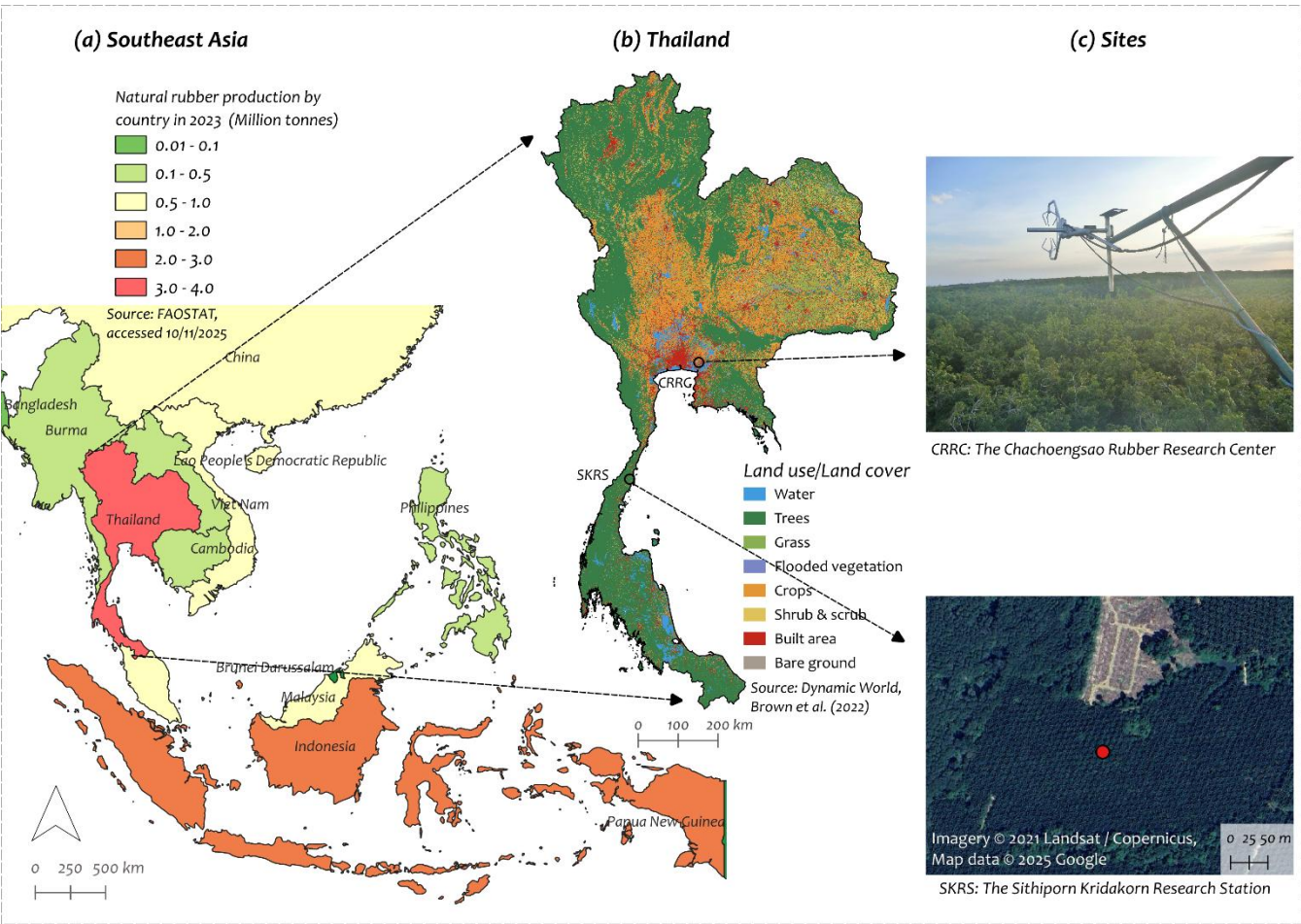
2 Materials and methods

95 2.1 Study areas

The study was conducted at two rubber plantations in Thailand: The Chachoengsao Rubber Research Center (CRRC) of the Rubber Authority of Thailand (RAOT) and the Sithiporn Kridakorn Research Station (SKRS) of Kasetsart University (Fig. 1).

CRRC is located in eastern Thailand (Fig. 1.b and 1.c: 13°34'N, 101°04'E; 69 m elevation). The site has been equipped with an eddy covariance flux tower monitoring micrometeorological and biophysical data since 2006. The region has a tropical monsoon climate with a unimodal rainfall pattern, marked by a rainy season from May to November. From 2015 to 2019, the average annual precipitation recorded on the site was 1349 mm with a high interannual variability (range: 810-2052 mm), and the average annual air temperature was 27.4 °C (range: 26.9-27.8 °C, *e.i.*, upper suitability range for rubber (Gohet et al., 2015)) (Figure 2 shows the annual precipitation and temperature anomaly data for CRRC from 1994 to 2020). The soil is classified as sandy clay loam. In the top 0-10 cm layer, it has 53.4% sand, 18.6% silt, and 28.0% clay. Soil mean pH is 5.3, with a bulk density of 1.57 Mg m⁻³ (Satakhun et al., 2013). The monoclonal rubber tree plot (*Hevea brasiliensis*, clone RRIM 600) was planted in a regular grid in 1994 at a density of 571 tree ha⁻¹. Fertilizer was applied twice a year at a total rate of 1 kg per tree annually, using a 30-5-18 NPK formulation (500 g per application). The first application occurred in May, after leaf fall at the start of the rainy season, and the second in September or October, at the end of the rainy season. A more detailed description of the site can be found in Satakhun et al. (2013) and Kanpanon et al. (2015).

SKRS is located in Prachuap Khirikhan province, Thailand (Fig. 1.b and 1.c: 10°59'13.35" N, 99°29'22.41" E), 333 km from CRRC. The site lies at the boundary between Thailand's equatorial and tropical monsoon climatic zones. From 2018 to 2021, the mean annual precipitation was 1805.7 mm, and the average air temperature was 26.26 °C. The soil is deep with a sandy-loam texture; the topsoil (0-30 cm) contains 71.4% sand, 20.9% silt, 7.7% clay, and has a pH of 4.9 (Chotiphan et al., 2019). The site hosts a monoclonal rubber tree plantation (*Hevea brasiliensis*, clone RRIM 600), established in 2007 at a density of 500 trees ha⁻¹. The plantation is part of a fertilization experiment reported in Chotiphan et al. (2019). The treatment selected for our study is representative of current fertilisation practices in Thailand: 180 g N, 80 g P, and 170 g K per tree per year, applied in two doses in June and October. Additional site details are provided in Chotiphan et al. (2019) and Epron et al. (2025).



120 **Figure 1: Overview of the study area. (a) Southeast Asia: Natural rubber production by country in 2023 (million tonnes). (b)**
125 **Thailand: Land Use and Land Cover based on Dynamic World data (Brown et al., 2022), with the locations of the study sites**
130 **highlighted. (c) Study sites: (top) Chachoengsao Rubber Research Center (CRRC), showing the eddy covariance tower; (bottom)**
Sithiporn Kridakorn Research Station (SKRS), with a zoomed-in of Google Earth image indicating the site location.

2.2 CASTANEA-MAESPA model description overview

125 The CASTANEA-MAESPA model (Cornut et al., 2023b, a) was used in this study as a coupled ecophysiological model
combining the strengths of both CASTANEA (Dufrêne et al., 2005) and MAESPA (Duursma and Medlyn, 2012) models.
CASTANEA is an ecophysiological model designed to simulate carbon and water balance in even-aged, monospecific forest
stands, originally developed for temperate beech forests (Dufrêne et al., 2005). It has since been used for various temperate
and Mediterranean species (Davi et al., 2006; Delpierre et al., 2012; Le Maire et al., 2005). While CASTANEA is good at
130 simulating carbon allocation and tree growth (Guillemot et al., 2017), its assumptions of a constant rooting depth, its use of a
simplified soil water bucket model and choice of leaf conductance model limit its applicability to tropical tree species, which
often have deep rooting systems. MAESPA model (Duursma and Medlyn, 2012), on the other hand, does not simulate carbon



allocation but provides more detailed simulations of soil water dynamics, plant hydraulics, and leaf photosynthesis. It incorporates the Tuzet leaf conductance model (Tuzet et al., 2003), which links leaf water potential, soil water potential and stomatal conductance to compute photosynthesis at a leaf scale (Christina et al., 2017). MAESPA has been successfully used in tropical contexts, including simulations of energy and water balances for an eucalyptus plantation in Brazil (Christina et al., 2017, 2018; Vezy et al., 2018), and agroforestry system in Costa Rica (Vezy et al., 2018). A full description and evaluation of the CASTANEA-MAESPA model is provided in Cornut et al. (2023b, a) in the context of tropical Eucalypt (*Eucalyptus grandis* x *urophylla*) plantations. In table 1, we provide a summary of the main model components and processes, along with the key references and input parameters.

Table 1: Description of the main processes simulated in the CASTANEA-MAESPA model.

Model component	Main process & key reference	Main forcing variables / inputs	Main parameters	Main simulated variables / states
Radiation interception	Multilayer radiative transfer based on a modified SAIL model (Verhoef, 1984, 1985). Direct and diffuse radiation are calculated through the canopy	Global radiation; leaf area index (LAI); solar geometry; canopy structure	Leaf reflectance/transmittance; mean leaf angle; clumping factor (Agreg); LAI	Absorbed photosynthetically active radiation (aPAR); vegetation and soil net radiation (Rnveg, Rnsoil)
Energy balance	Leaf/canopy energy balance associated with the radiative-transfer and evapotranspiration calculations; leaf and soil temperatures are obtained by closing the energy budget	Absorbed radiation; air temperature; humidity; wind; conductances	Leaf/soil emissivity; aerodynamic properties; conductances	Leaf temperature (Tleaf); soil temperature (Tsoil); net radiation (Rn)
Leaf photosynthesis	C3 biochemical photosynthesis model of Farquhar et al. (1980); assimilation limited by Rubisco carboxylation or RuBP regeneration	aPAR; atmospheric carbon dioxide (Ca); Tleaf; stomatal conductance (gs)	Maximum carboxylation rate (Vcmax); maximum electron transport rate (Jmax/Vjmax); quantum efficiency (α); curvature (θ)	Leaf net assimilation (A); Gross Primary Production (GPP)
Stomatal conductance	Tuzet-type stomatal model, coupling assimilation and leaf water status: $gs=f(A, \psi_{leaf})$ (Tuzet et al., 2003)	Assimilation (A); leaf water potential (ψ_{leaf})	Two-slope coefficients G11, G12 from Christina et al. (2017)	Stomatal conductance (gs)



Plant hydraulics, leaf water potential & transpiration	Soil-Plant-Atmosphere (SPA) hydraulic approach inherited through MAESPA (Duursma and Medlyn, 2012), based on Williams et al. (1996)	Soil water status; radiation; atmospheric demand; gs; root profile	Plant hydraulic conductivity; soil/root hydraulic parameters	Soil, root and leaf water potential (ψ_{soil} , ψ_{root} , ψ_{leaf}); transpiration (Tr); root water uptake
Rainfall interception & canopy evaporation	CASTANEA partitions precipitation into canopy interception, throughfall and stemflow; intercepted water can evaporate from leaves and bark	Precipitation; LAI; wood area index (WAI); atmospheric evaporative demand	Leaf and bark water-storage capacities; interception coefficients	Intercepted water; throughfall; stemflow; canopy/leaf evaporation
Soil water balance & soil evaporation	MAESPA simulates infiltration, evaporation, drainage, root water uptake and soil water status using a multilayer soil profile	Throughfall; stemflow; evaporation/transpiration demand; root distribution	Soil hydraulic properties; rooting profile; plant hydraulic parameters	Soil water content (SWC) by layer; ψ_{soil} ; drainage; soil evaporation (E_{soil}); root water uptake
Leaf phenology & canopy dynamics	Daily leaf-cohort model adapted for deciduous rubber trees: leaf production depends on tree-height increment; leaf area and mass expand sigmoidally (Cornut et al., 2023a; this study)	Tree-height increment (ΔH); cohort age; tree height (H), weather data	f_p , κ , Leaf Life Span (LLS), L_{Amax} , k_{LA} , $t_{50\text{LA}}$, BF_{max} , k_{BF} , $t_{50\text{BF}}$	Number of leaves (N); Leaf area (LA); leaf biomass (BF); Leaf area index (LAI)
Carbon allocation	Daily allocation of net primary production (NPP) among leaves, soluble sugars (SS), roots and woody organs. Original partitioning framework follows McMurtrie & Wolf (1983) / Thornley & Johnson (1990); the eucalypt version uses target and allometric functions.	NPP; soluble-sugar biomass (BSS); LAI; fine-root biomass (BFR); woody biomass	p_{SS} , p_{FR} , λ ; coarse-root allocation (GCR); organ allocation coefficients	BSS; leaf, BFR, Coarse-Root (BCR), trunk (Btrunk), branch (BBr) and bark (Bbark) biomass
Maintenance respiration	N-based maintenance respiration with exponential temperature	Living organ biomass; organ N concentration (Norgan); organ temperature (Torg)	Respiration per unit N (MRN); Q_{10} ; reference temperature (TMR)	Organ maintenance respiration (RMorgan); total maintenance respiration (RM)



	dependence following Ryan (1991).			
Growth respiration	Growth respiration based on organ construction costs, following Penning de Vries et al. (1974) and Penning de Vries (1975) (Cornut et al., 2023b).	Daily organ biomass increment (ΔB_{organ}); age for trunk	Organ construction/growth-respiration cost (CR_{organ} / GR_{Corgan})	Organ growth respiration (GR_{organ}); total growth respiration (GR)
Organ turnover & litterfall	Leaves, fine roots, branches and bark undergo turnover; resulting necromass enters litter or dead-branch pools.	Organ biomass; organ/cohort age; lifespan	Leaf life span (LLS); branch, bark and fine-root turnover/lifespan parameters	Leaf/branch/bark/root mortality; litterfall; dead-branch biomass; litter inputs
Latex yield	Tapping creates an artificial carbon sink. Daily latex production is represented as the sum of contributions from current growth assimilates and storage reserves (this study)	NPP, BSS, trunk average diameter	Allocation parameters, tapping frequency, tapping season	Latex yield

2.3 Model input and calibration data

2.3.1 Weather input data

- 145 The weather input data used for the simulations include global radiation ($W m^{-2}$), air temperature ($^{\circ}C$), relative humidity (%), wind speed ($m s^{-1}$), and precipitation (mm). At CRRC, data sources varied by period: on-site station measurements were used for the period 2015-2018 and NASA's POWER dataset (2025) provided historical data from 1994 to 2011 (Fig. 2). At SKRS we used on-site station weather data collected from 2019 to 2021. A detailed summary of all weather datasets, along with references, is presented in tables S1.
- 150 Missing data in the meteorological station dataset, primarily caused by device malfunctions, were addressed using multiple imputation via Predictive Mean Matching (PMM), implemented in R through the *mice* function from the *mice* package (Buuren and Groothuis-Oudshoorn, 2011). Measured weather data from meteorological stations are at a half-hourly timestep. In contrast, data obtained from NASA POWER have coarser temporal resolutions, ranging from hourly to daily. To harmonize all datasets to a common half-hourly resolution, we applied variable-specific interpolation methods. For continuous variables
- 155 such as temperature, radiation, relative humidity, and wind speed, linear interpolation was applied. The linear interpolation



was performed using the *na.approx* function of the zoo package (Zeileis and Grothendieck, 2005) in R. For precipitation, values were evenly distributed by dividing the total amount across the required number of timesteps. Table S2 presents a comprehensive summary of the meteorological input data, detailing the measurement periods, sampling frequencies, and the instruments or methods used.

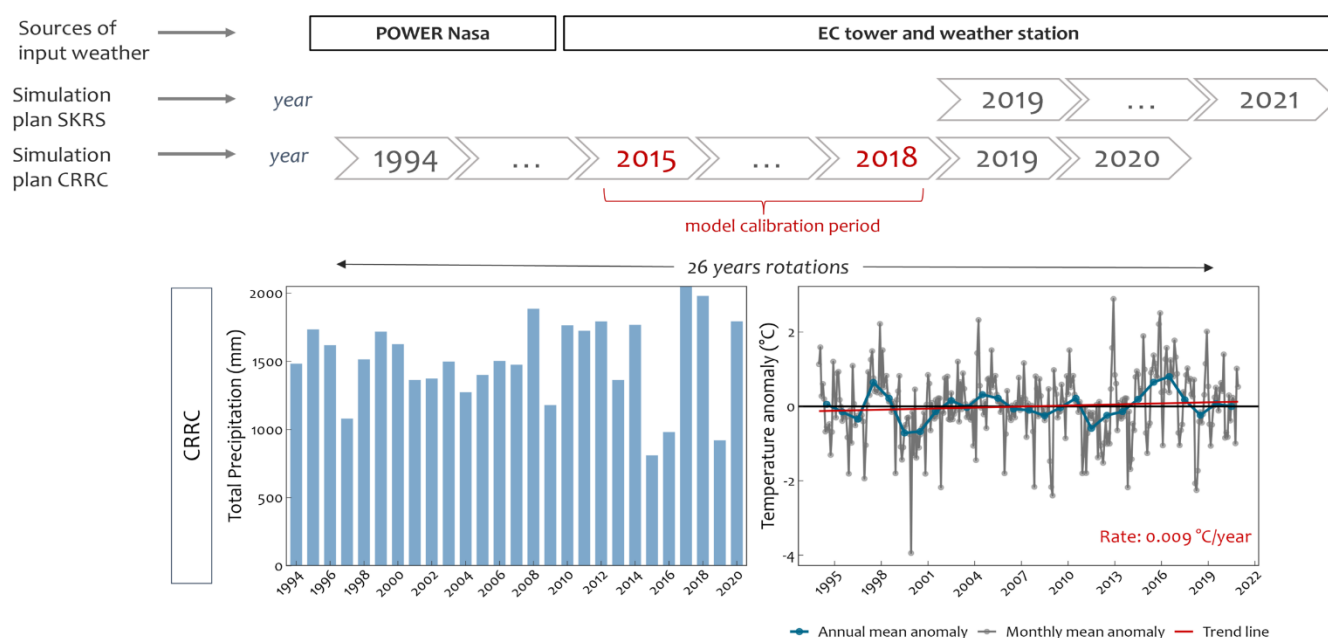


Figure 2: Overview of the simulation framework for CRRC and SKRS. The figure presents the weather forcing inputs, the precipitation and temperature anomalies during the 26-year rotation period at CRRC.

2.3.2 In situ measurements of carbon and water

Parametrization and calibration data available at the CRRC site included phenological measurements (litterfall biomass and leaf area index), latex yield, tree morphological data (e.g., girth), soil texture, and half-hourly measurements of energy, water, and carbon (C) fluxes from the on-site eddy covariance (EC) tower. Energy fluxes included net radiation above the canopy and latent and sensible heat fluxes. Water fluxes included evapotranspiration from the soil-plant system (calculated from latent heat flux), and soil water content. Carbon fluxes included net ecosystem exchange (NEE), which was partitioned into gross primary production (GPP) and ecosystem respiration (Reco). A comprehensive description of the water and C fluxes data used at CRRC (2015-2019) and partitioning method can be found in Wang et al., (2022). Photosynthetic parameters were also measured at the CRRC site in 2006 and 2007 when trees were 12 to 13-year-old. Measurements included dark respiration (R_d), the maximum rate of carboxylation (V_{cmax}), and the maximum rate of electron transport (J_{max}), which are key parameters in the photosynthesis model. Soil texture data (10-90 cm depth) were obtained from Satakhun et al. (2013). Tree biomass was estimated using tree inventory data and allometric equations developed by Hytönen et al. (2018). Leaf Area Index (LAI) was



175 estimated from hemispherical canopy photographs using Gap Light Analyzer (GLA) following Fraze et al. (1999). Monthly latex yield was recorded from 2012 to 2020 for two tree densities. The tapping system used was S/2 d/2 7d7 10m (*i.e.*, half-spiral cuts (S/2) were made on the trees, every two days (d/2), 7 days out of 7 (7d7) for 10 months (10m)), with tapping conducted from May to January, on fertilized plots.

At the SKRS site, data included soil water content and latex yield. Soil measurements were obtained from Chotiphan et al. (2019), while tree biomass was estimated from inventory data using allometric equations developed by Hytönen et al. (2018). In addition to flux measurements, daily yield records have been collected since 2014 as part of an experimental trial evaluating the effects of fertilization and stimulation treatments (Chotiphan et al., 2019). These complementary observations provide additional information for validation the latex production model on another site, although data available at SKRS is more limited than the CRRC site. The tapping system at SKRS followed S/2 d/2 7d7 10m (May-February), meaning trees were tapped every two days for 10 months from May to February of the following year (Chotiphan et al., 2019).

A summary of all measured variables at both sites, including the periods, the frequencies, and the instruments or methods used is provided in Table S2.

2.4 Adapting CASTANEA-MAESPA to rubber tree

2.4.1 Soil hydraulic parameterization

190 At both sites, soil water content was parameterized using soil texture, organic carbon content, and bulk density. These variables were used as inputs to the pedotransfer functions developed by Vereecken et al. (1989) to estimate the van Genuchten soil water retention parameters. Soil hydraulic conductivity was subsequently derived from soil porosity using the equation proposed by Ottoni et al. (2019). A detailed description of the soil water balance scheme implemented in the model, together with the associated equations, is provided in Christina et al. (2017). The estimated soil water retention and hydraulic conductivity parameters for CRRC and SKRS sites (3 upper layers) are reported in Table S3.

2.4.2 Modelling rubber phenology

At both sites, rubber trees exhibited deciduous behaviour, with defoliation occurring between December and January, reaching complete leaf loss by January. Refoliation begins in early February and the first leaf flush is fully developed in April. Two to three new leaf flushes occur and expand from early May to August (Fig. S1).

200 The original phenology model for Eucalyptus is a cohort-based canopy dynamics model, as detailed in Cornut et al. (2023a) (see Table1). The model was modified to simulate the deciduous behaviour of rubber trees while retaining the cohort-based structure that fits the periodic growth pattern of rubber canopy (Hallé, 1968). This structure assumes that each cohort consists of leaves with uniform physiological traits, growth patterns, and lifespans, defined by leaf number per square meter of ground,



individual leaf area, and leaf mass (Cornut et al., 2023a). Leaf production during leaf growth period, in terms of number of
205 leaves produced per day, is driven by tree primary growth. New leaves are vertically distributed in the canopy according to a
gamma distribution. Individual leaf area expansion within a cohort follows a sigmoid derivative function, defined by an
inflection point where 50% of the maximum area is reached and a rate of increase at that date. Leaf mass per area follows a
similar expansion pattern (Cornut et al., 2023a).

Various environmental factors have been proposed in the literature to explain rubber tree leaf phenology such as water deficit
210 (Carr, 2012; Rivano et al., 2016), photoperiod (Yeang, 2007), cold stress (Chen et al., 2022; Zhai et al., 2017), precipitation
(Zhai et al., 2017), and temperature (Azizan et al., 2023). However, the literature provides no clear consensus on the dominant
drivers or their relative importance. Given this variability, we tested several approaches to simulate rubber canopy dynamics,
informed by literature findings, expert knowledge and our dataset. Among the different approaches evaluated, a temperature-
based seasonal index provides a good empirical predictor of phenological transitions at our sites. This formulation was adapted
215 from temperate deciduous trees phenology models already implemented in CASTANEA (Dufrêne et al., 2005), but here it is
used as a proxy for seasonal progression rather than a real physiological chilling or warming requirement.

In this framework, leaf production is initiated once cumulative exposure to low temperatures exceed a predefined threshold.
Accumulation starts on a specified date, and all days contribute to a thermal index based on deviation below a base temperature:

$$S_{prod}(t) = \sum_{i=N_{START0}}^t \max(0, T_0 - T(i)) \quad (1)$$

220 Leaf production is triggered when: $S_{prod}(t) > S_{max}$

where: $T(i)$ was the daily mean temperature (°C); T_0 was the base temperature defining the seasonal reference threshold; N_{START0}
was the start day of accumulation; $S_{prod}(t)$ was the cumulative thermal index, and S_{max} was the threshold of cumulative thermal
index triggering leaf production.

The onset of leaf production is then defined as:

$$225 \quad t_{start} = \min\{t : S_{prod}(t) > S_{max}\} \quad (2)$$

Leaf production is restricted to a finite re-foliation window: $t \in [t_{start}, t_{start} + D_{refo}]$

The duration of this window depends on tree height:

$$D_{refo} = \text{round} \left(D_{min} + \frac{(H - H_{min}) \cdot (D_{max} - D_{min})}{H_{max} - H_{min}} \right) \quad (3)$$

230 where: D_{refo} was the refoliation period (ranging between 14 days (D_{min}) and 25 days (D_{max}) depending on height); H was tree
height and H_{min} , H_{max} were reference minimum and maximum heights.

Daily leaf production was computed following Cornut et al.(2023a) as:

$$N(t) = \frac{\Delta H + f_p}{1 + f_p} \cdot k \quad (4)$$



where $N(t)$ was the daily leaf production ($n_{\text{leaves}} \text{ m}^{-2}_{\text{ground}}$), ΔH was the height increment (m), f_p was a flattening factor controlling the relationship between growth and leaf production, and k was a conversion factor from height increment to leaf production

235 $(n_{\text{leaves}} \text{ m}^{-2}_{\text{ground}} \text{ m}^{-1}_{\text{height}})$.

Similarly, to leaf re-foliation, leaf fall is triggered by cumulative exposure to low temperatures, starting from a specified date. This accumulation begins on a defined initiation date, with each day contributing to a thermal index based on deviations below a base temperature. Leaf senescence is initiated when the cumulative thermal index exceeds a predefined threshold and continues until complete canopy defoliation is reached. Leaf loss follows an exponential decay formulation:

240
$$L_c(t) = L_c(t_0) \cdot \exp(-k_f \cdot J(t)) \quad (5)$$

where $L_c(t)$ was number of leaves remaining ($n_{\text{leaves}} \text{ m}^{-2}_{\text{ground}}$); $L_c(t_0)$ was the initial leaf amount at the onset of senescence; k_f was the senescence rate parameter, and $J(t)$ was the time elapsed since senescence initiation.

During simulations, this deciduous behaviour is activated for rubber only after the third year of the rotation onward. In fact, the juvenile phase of rubber tree is characterized by continuous vegetative flushes and a persistently evergreen canopy due to

245 continuous leaf replacement (Carr, 2012). Seasonal leaf shedding becomes pronounced only after physiological maturity, typically around 3 to 4 years of age (Carr, 2012).

2.4.3 Temperature responses of respiration

Previous versions of CASTANEA-MAESPA used a fixed Q_{10} parameter in the exponential functions used to simulate respiration. However, Q_{10} is temperature-dependent and generally declines at high temperatures (Atkin and Tjoelker, 2003),

250 and incorporating a temperature-dependent Q_{10} improves respiration predictions (Heskel et al., 2016). We then implemented Heskel's global polynomial model within CASTANEA-MAESPA to simulate leaf respiration:

$$R = \exp(a + bT + cT^2) \quad (6)$$

where R representing leaf respiration ($\mu\text{mol m}^{-2} \text{ s}^{-1}$) and T temperature ($^{\circ}\text{C}$). Parameters a , b , and c were explored within ranges reported for broadleaf tropical species, and the final values were selected based on model performance at the ecosystem scale.

255 Because leaf respiration was not directly measured, evaluation was performed indirectly: simulated leaf respiration was added to the other simulated components of respiration to obtain total simulated ecosystem respiration, which was then compared against observed ecosystem respiration. The parameter set was $a = -3.6757$, $b = 0.0961$ and $c = -0.0008$. Refer to Cornut et al. (2023b) for a complete description of autotrophic respiration in the other tree organs, including the associated equations. A brief description of maintenance and growth respiration processes as simulated in the CASTANEA-MAESPA model is

260 provided in Table 1. Modified key parameters values are presented in Table S4.

2.4.4 Development and integration of a latex yield module into CASTANEA-MAESPA

Since latex does not flow out naturally from the rubber trees, there is no direct proportionality between biomass, biomass increment, and rubber yield. The rubber trees must be tapped, *i.e.*, the bark of their trunk severed by manual tapping, in order to harvest the latex. Then, the tapping practices (number and position of the tapping cuts, tapping frequency, duration of the tapping season...) have a strong impact on latex yield and consequently on the mobilisation of carbon to regenerate the exported latex. One of the main levers is the tapping frequency that in current practices varies from tapping every day (d1) to every 5 days (d5), tapping every other day (d2) being a standard. In low tapping frequency systems, to compensate the lower number of tapping days, the trees are stimulated by the application of an ethylene releasing paste applied to the tapping cut. This prolongs the latex flow and activates the latex metabolism, achieving a higher yield per tapping day and similar total yield (Gohet et al., 2016; Shuib and Yusoff, 2015; Wiangsamut et al., 2024). A long-term study in Ivory Coast compared different tapping frequencies (*e.g.*, d2, d3, d4, d5, and even d6) and found that, after 10 years of tapping, yearly latex yield could largely be maintained with appropriate use of stimulant even in low frequency (Gohet et al., 2016).

The latex yield model integrated into CASTANEA-MAESPA is inspired from WaNuLCAS model (Van Noordwijk and Lusiana, 1999), as applied and adapted by Yang et al. (2019) with several modifications. It integrates both management practices and biological processes. The carbon produced by leaf photosynthesis (GPP), is first converted to NPP by considering autotrophic respiration. NPP is allocated to storage (used for leaves production), and fine roots, the remaining resources being allocated towards stem, wood, branches, and coarse roots. A comprehensive description of assimilate allocation to tree organs in the CASTANEA-MAESPA model, including the governing equations, can be found in Cornut et al. (2023b), while Christina et al. (2017) detail the representation of water balance and leaf photosynthesis in MAESPA, together with the associated equations (Table1). Once tapping begins, part of the assimilates initially allocated to wood growth is redirected toward latex production. In addition, stored carbon reserves contribute to latex synthesis, particularly during periods of low leaf area (Fig. 7), according to observed allocation patterns obtained from ¹³C labelling experiments (Duangngam et al., 2020; Kanpanon et al., 2015).

Daily latex production is represented as the sum of contributions from current assimilates and storage reserves:

$$Y_{lat} = G_{lat} + S_{lat} \quad (7)$$

With:

$$G_{lat} = DB_g \cdot R_y \cdot SI \quad (8)$$

$$S_{lat} = BSS \cdot R_s \cdot a \quad (9)$$

where Y_{lat} (gC m²) was the total latex yield, G_{lat} (gC m²) was the assimilates redirected from growth toward latex synthesis; S_{lat} (gC m²) was the stored carbon reserves contributing to latex; DB_g (gC m²) was the carbon available for wood growth (simulated by CASTANEA-MAESPA); BSS (gC m²) was the storage reserve pool (simulated by CASTANEA-MAESPA); R_y (unitless) was the ratio of growth assimilate redirected toward latex, SI (unitless) was a climatic suitability index, R_s was the



fraction of reserves mobilized toward latex production, and a (unitless) was a correction factor accounting for increased reserve mobilization under very low leaf area conditions.

295 This resource allocation strategy reflects findings that tapping rubber trees creates an artificial latex sink and results in reduced radial growth compared to untapped trees due to competitive resource allocation, as observed in studies at CRRC by Silpi et al. (2006). However, rapid reduction in growth may reflect not only competition for carbon but also responses to repeated tapping wounds. Tapped trees have also been shown to contain more starch in their wood than untapped trees, suggesting that allocation to reserves may be prioritized over radial growth under tapping conditions (Silpi et al., 2006, 2007). Moreover, if
300 trees are tapped during leafless periods, latex flow continues meaning that a large proportion of resources for latex production is coming from reserves. Isotopic experiments confirmed that both recent photosynthates and reserves contribute to latex biosynthesis of tapped trees (Duangngam et al., 2020; Kanpanon et al., 2015).

The proportion of resources allocated to latex production varies with tapping frequency. When tapping occurs less frequently, the model increases the fraction of assimilates directed to latex on each tapping day, compensating partially for untapped days.

305 This relationship is represented through a linear interpolation between minimum and maximum allocation coefficients:

$$R_y = \begin{cases} R_{ymin}, & T_f < T_{fmin} \\ \left(R_{ymin} + \frac{T_f - T_{fmin}}{T_{fmax} - T_{fmin}} \cdot (R_{ymax} - R_{ymin}) \right), & T_{fmin} \leq T_f \leq T_{fmax} \\ R_{ymax}, & T_f > T_{fmax} \end{cases} \quad (10)$$

where T_f was the tapping frequency, T_{fmin} and T_{fmax} defined the lower and upper tapping frequency bounds, and R_{ymin} and R_{ymax} defined the lower and upper allocation bounds. The model also includes the optional simulation of ethephon application, an ethylene-releasing stimulant commonly used in rubber plantations to enhance latex flow (Attanayake et al., 2018; d'Auzac,
310 2018; Lacote et al., 2010). When applied, the allocation coefficient is forced to its maximum value. These assumptions remain subject to refinement as new empirical data become available regarding the effects of tapping intensity.

To account for the direct effects of climate on latex flow a climatic suitability index (SI) was introduced within the latex allocation scheme. This index modulates carbon allocation to latex production using weekly rolling averages of maximum temperature, minimum temperature, and soil water content. The use of 7-day averages reflects the delayed physiological
315 response of latex production to environmental conditions rather than instantaneous climatic forcing. Climatic suitability was represented as a bounded linear stress function derived from normalized deviations from optimal environmental conditions:

$$SI = 0.5 + 0.5 \cdot \max(0, 1 - SI_T - SI_W) \quad (11)$$

With:

$$SI_T = \frac{|T_{max}^{avg} - T_{max}^{opt}|}{\Delta T_{max}} + \frac{|T_{min}^{avg} - T_{min}^{opt}|}{\Delta T_{min}} \quad (12)$$

$$320 \quad SI_W = \frac{|W^{avg} - W^{opt}|}{\Delta W} \quad (13)$$



where ΔT_{max} and ΔT_{min} were temperature tolerance ranges; ΔW was the soil water tolerance range; T_{max}^{avg} , T_{min}^{avg} , and W^{avg} were the weekly rolling averages of maximum temperature, minimum temperature, and soil water content; T_{max}^{opt} , T_{min}^{opt} , and W^{opt} were the optimal climatic conditions for latex production derived from field observations. SI was the climatic suitability index that penalized deviations from the optima conditions. SI was constrained between 0.5 and 1.0 to reflect partial inhibition of latex flow under suboptimal conditions (even if carbohydrates are available as recently photosynthetized or as reserves) and provides a parsimonious representation of climatic limitations, while avoiding the unrealistic assumption of a complete suppression of production.

Tapping operations are restricted by both phenological and management constraints. Tapping is initiated only when trees reach a minimum stem diameter threshold, reflecting usual practice. Stem diameter at breast height (DBH) is estimated from woody biomass using the allometric relationship adapted from Hytönen et al. (2018):

$$DBH = \left(\frac{DM_{wood} \cdot 10^4}{a \cdot C_f \cdot \rho_{tree} \cdot 10^3} \right)^{\frac{1}{b}} \quad (14)$$

Where DBH was the diameter at breast height (cm), DM_{wood} was the wood biomass as simulated by CASTANEA ($gC\ m^{-2}$), 10^4 was for the conversion from m^2 to ha, 10^3 was for the conversion from g to kg, C_f was the carbon fraction of rubber dry wood, ρ_{tree} was the tree density ($tree\ ha^{-1}$), $a = 0.05155$ and $b = 2.783$ were allometric parameters from Hytönen et al. (2018). Tapping is typically carried out outside the refoliation period, during the defined active tapping season extending (e.g., from May to January at CRRC). Following latex extraction, the carbon available for wood growth (DB_g) and storage pools (BSS) were updated to maintain mass balance within the allocation framework.

A summary of the key leaf photosynthesis parameter values and latex yield model parameter values is presented in Tables S4.

2.5 Statistical analysis and simulation workflow

Model performance was evaluated using R (R Core Team, 2025). Model accuracy and overall goodness-of-fit were assessed by comparing simulated values ($\hat{y}_i$) against observed values (y_i), where $\bar{y}$ and $\bar{\hat{y}}$ represents the mean of observed and simulated values, and n is the total number of observations. Three metrics were used to quantify model performance. The coefficient of determination (R^2) was calculated to assess the proportion of variance in the observed data explained by the model, ranging from 0 to 1 with values closer to 1 indicate a stronger linear relationship:

$$R^2 = \left(\frac{\sum_{i=1}^n (y_i - \bar{y})(\hat{y}_i - \bar{\hat{y}})}{\sqrt{\sum_{i=1}^n (y_i - \bar{y})^2 \sum_{i=1}^n (\hat{y}_i - \bar{\hat{y}})^2}} \right)^2 \quad (15)$$

The model efficiency (EF), also known as the Nash-Sutcliffe efficiency (NSE) was used to assess the predictive power of the model by comparing the variance of the prediction errors to the variance of the observed data. An EF value of 1 indicates

perfect agreement between predicted and observed values, while values close to or below zero suggest poor model performance:

$$EF = 1 - \frac{\sum_{i=1}^n (y_i - \hat{y}_i)^2}{\sum_{i=1}^n (y_i - \bar{y})^2} \quad (16)$$

RMSE was used to quantify the average magnitude of prediction errors, providing a measure of the model's overall accuracy. Lower RMSE values reflect smaller differences between observed and predicted values, indicating better model performance:

$$RMSE = \sqrt{\frac{1}{n} \sum_{i=1}^n (y_i - \hat{y}_i)^2} \quad (17)$$

At the CRRC site, one rotation cycle, covering a 26-year period (1994-2019) was simulated. In addition, a 4-year simulation (2018-2021) was conducted at the SKRS site to evaluate the latex yield module under contrasting site conditions (Fig. 2). Latex yield simulations were conducted at the CRRC site during the model parameterization phase, and the SKRS site was used as validation.

3 Results

3.1 Water fluxes of the rubber plantations at CRRC and SKRS sites

At CRRC, simulated soil water content (SWC) aligned well with the observations for both layer 1 (depth = 0.33 m) and layer 3 (depth = 1.0 m). The model reproduces the minimum and maximum SWC as well as the interannual dynamics, except for layer 1 in 2018, where both minimum and maximum SWC were underestimated. Overall agreement is good for layer 1 (Fig. 3a and Fig. S2a; RMSE = 0.03 mm³·mm⁻³, R² = 0.49, EF = 0.40) and even better for layer 3 (Fig. 3c and Fig. S2b; RMSE = 0.03 mm³·mm⁻³, R² = 0.65, EF = 0.61) although the model did not capture the first SWC peak in 2016 (Fig. 3c). At SKRS, simulated SWC generally agrees well with observations, but performance decreases with depth. For layer 1, the model captures the minimum, maximum, and seasonal dynamics satisfactorily (Fig. 3d and Fig. S2d; RMSE = 0.02 mm³·mm⁻³, R² = 0.84, EF = 0.56). In layer 2, the model overestimates the minimum SWC and, in some years, the maximum as well (Fig. 3e and Fig. S2e; RMSE = 0.03 mm³·mm⁻³, R² = 0.77, EF = -0.16). Conversely, in layer 3 the model tends to underestimate both the minimum and maximum SWC. Although discrepancies occur in some years, the seasonal dynamics are reasonably well captured (Fig. 3f and Fig. S2f; RMSE = 0.02 mm³·mm⁻³, R² = 0.46, EF = -0.33). In the first soil layer, observed SWC was higher in CRRC than SKRS.

The overall seasonal dynamics of half-hourly evapotranspiration (ET) were well simulated by the model at the calibration site (CRRC) (Fig. 3g and Fig. S2c; RMSE = 0.04 mm m⁻², R² = 0.75, EF = 0.73), indicating strong agreement at high temporal resolution. At the daily time step, ET showed R² = 0.49, RMSE = 1.07 mm d⁻¹, and EF = 0.27, suggesting moderate correlation but reduced model efficiency (Fig. 4a and Fig. S3a). At the monthly time step, R² was 0.52, RMSE was 26.16 mm month⁻¹, and EF was 0.35, reflecting a slight improvement in explained variance compared to the daily scale, although overall efficiency



remained moderate (Fig. S3d). In 2016, the model overestimated the measured temporal dynamics at the end of the dry season and at the beginning of the rainy season (Fig. 3g and Fig 4a). This mismatch led to an overestimation of cumulative annual ET in 2016 (Fig. 3g). Aside from that year, the model's annual cumulative ET agreed closely with the eddy-covariance measurements for all other years (Fig. 3g).

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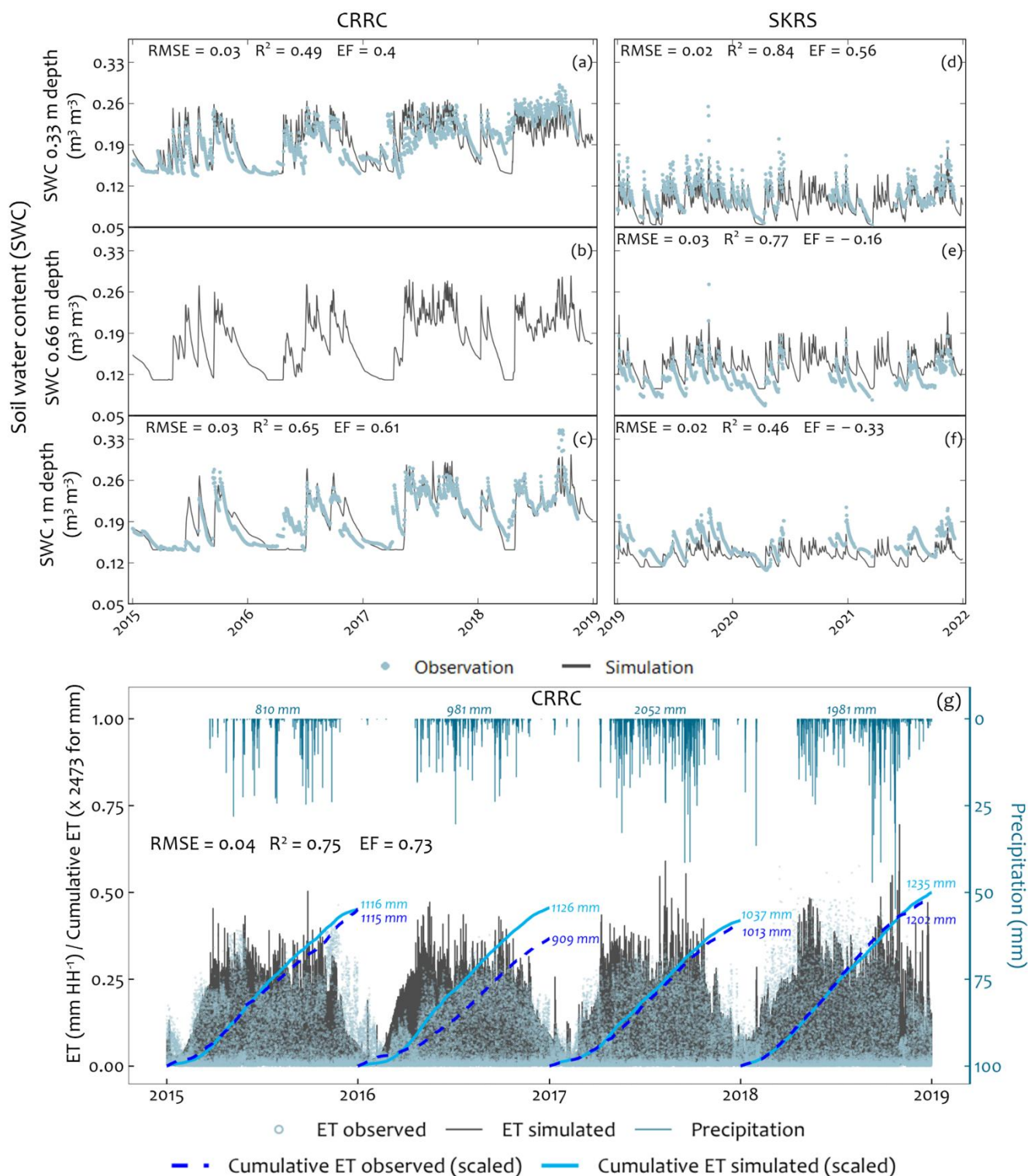




Figure 3: Time series of simulated and observed soil water content (SWC) and evapotranspiration (ET) at the two study sites (CRRC: 2015-2018; SKRS: 2019-2021). Daily regression statistics (RMSE, R^2 , and EF) are shown in the top-left corner of each plot. (a-c) Half-hourly SWC at CRRC for layer 1 (depth = 0.33 m), layer 2 (depth = 0.66 m), and layer 3 (depth = 1.0 m); the black solid line represents the simulated SWC and the light blue dots represent the observed SWC. (d-f) Half-hourly SWC at SKRS for layer 1 (depth = 0.33 m), layer 2 (depth = 0.66 m), and layer 3 (depth = 1.0 m); the black solid line represents the simulated SWC and the light blue dots represent the observed SWC. (g) Half-hourly and cumulative annual ET with daily precipitation (mm day⁻¹) shown on top in dark cyan line, along with total annual precipitation values; the black solid line represents the simulated ET and the blue dots represent the observed ET; cumulative annual simulated ET is shown as a light blue solid line and cumulative annual observed ET as a dark blue dashed line.

3.2 Phenology and carbon fluxes of the rubber plantation at CRRC site

The implementation of a rubber-specific phenology model allowed the representation of the deciduous behaviour of the rubber tree. However, the evaluation of simulated LAI was limited by the availability of only two years of measurements (2017 and 2018) and a relatively small number of observations. Therefore, the comparison with simulations mainly provides an indication of the seasonal trends rather than a robust assessment of model performance. Measured LAI were of the same order of magnitude as the simulated values. The model successfully reproduced the lowest observed LAI values (0.3 m² m⁻²); however, it anticipated the LAI decline at the end of 2017. Moreover, it was not able to reproduce the highest LAI values measured in 2018 (3.8 m² m⁻²) (Fig. 4b). Overall, the model underestimated LAI in both years, despite the improved representation of seasonal dynamics (Fig. 4b; RMSE = 1.13, R^2 = 0.52, EF = -1.25).

The seasonal dynamics of measured daily gross primary production (GPP) and net ecosystem production (NEP) were generally well captured by the model (Fig. 4c and 4d). The model, however, overestimated both GPP and NEP at the onset of the 2016 rainy season. Agreement between observations and simulations improved in 2017 and 2018 for daily GPP and daily NEP. During these periods, the model generally overestimated NEP, except in 2017, whereas it more accurately represented GPP in 2017 and 2018. For annual cumulative fluxes, the model slightly overestimated GPP in 2015 and 2016 and slightly underestimated it in 2017 and 2019 (Fig. 4c). A similar pattern was observed for NEP, although with larger discrepancies (Fig. 4d). Between 2015 and 2018, daily measured GPP ranged from 0 to 14 g C m⁻² d⁻¹, whereas simulated values ranged from 0.09 to 12.62 g C m⁻² d⁻¹. Daily measured NEP varied between -6.15 and 9.91 g C m⁻² d⁻¹, while simulated NEP ranged from -2.79 to 8.77 g C m⁻² d⁻¹. On an annual basis, measured GPP ranged from 2.34 to 2.70 kg C m⁻² yr⁻¹ (annual average: 2.54 kg C m⁻² yr⁻¹), compared with simulated estimates of 2.48 to 2.69 kg C m⁻² yr⁻¹ (annual average: 2.60 kg C m⁻² yr⁻¹). Annual measured NEP varied between 0.90 and 1.47 kg C m⁻² yr⁻¹ (annual average: 1.19 kg C m⁻² yr⁻¹), whereas simulated NEP ranged from 1.13 to 1.35 kg C m⁻² yr⁻¹ (annual average: 1.27 kg C m⁻² yr⁻¹). These comparisons indicate that the model reproduces both the magnitude and variability of measured carbon fluxes reasonably well, although some discrepancies persist. In fact, the model explained 65% and 57% of the variability in daily GPP (Fig. 4c and Fig. S3b; RMSE = 1.89, R^2 = 0.65, EF = 0.61) and NEP (Fig. 4d and Fig. S3c, RMSE = 1.9, R^2 = 0.57, EF = 0.53). At the monthly time scale, model performance improved relative to the daily scale. For GPP, RMSE was 45.51, R^2 was 0.72, and EF was 0.70 (Fig. S3e). For NEP, RMSE was 48.47, R^2 was 0.67, and EF was 0.58 (Fig. S3f), indicating a modest increase in explained variance. Model performance improved further when evaluated at the half-hourly time step, with both GPP (Fig. S4e; RMSE = 0.07, R^2 = 0.88, EF = 0.81) and NEP (Fig. S4f;



RMSE = 0.1, $R^2 = 0.78$, EF = 0.77) closely matching the measured values. This showed the ability of the model to better capture short-term fluctuations in carbon fluxes, demonstrating its capacity to reproduce diurnal patterns.

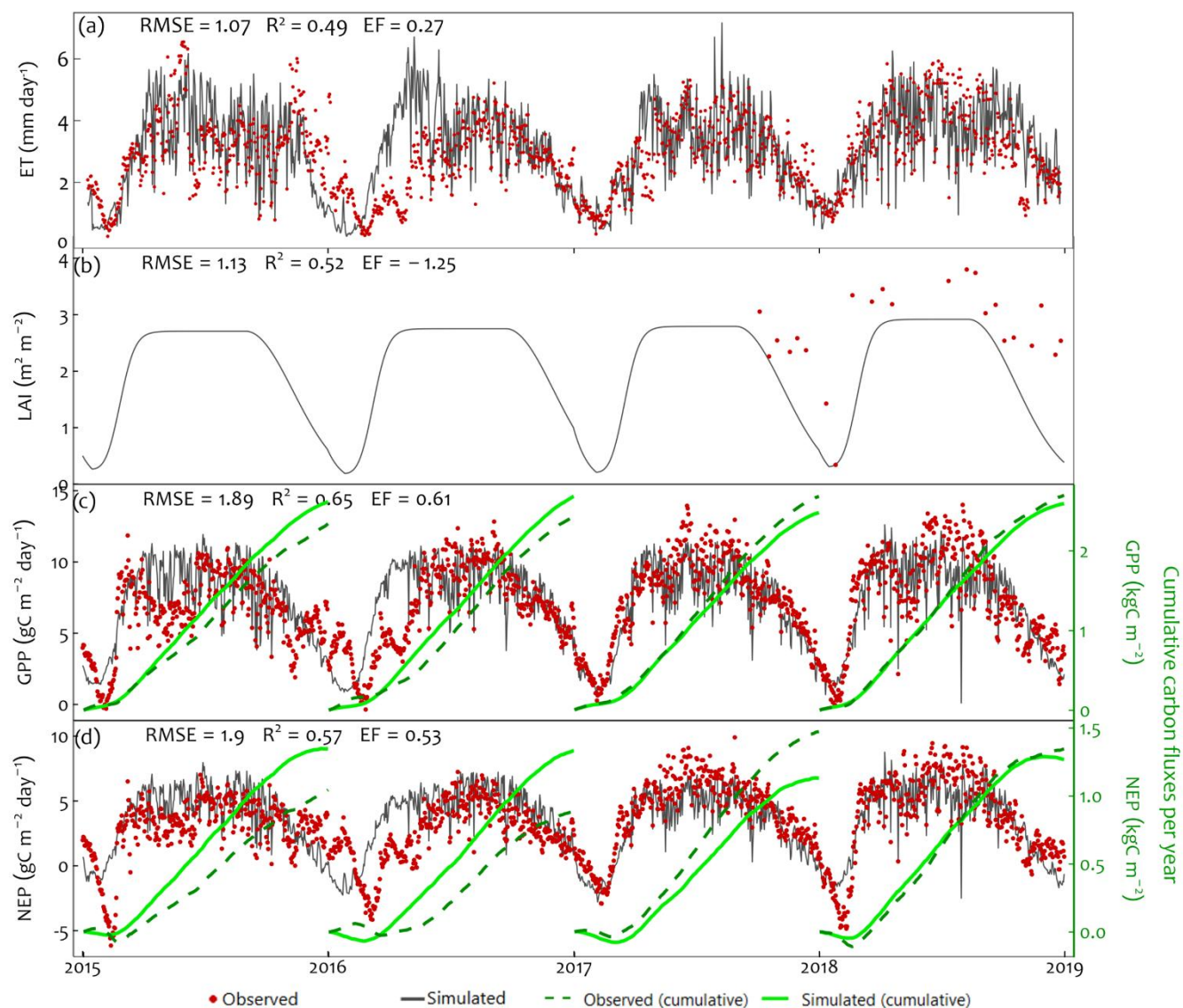


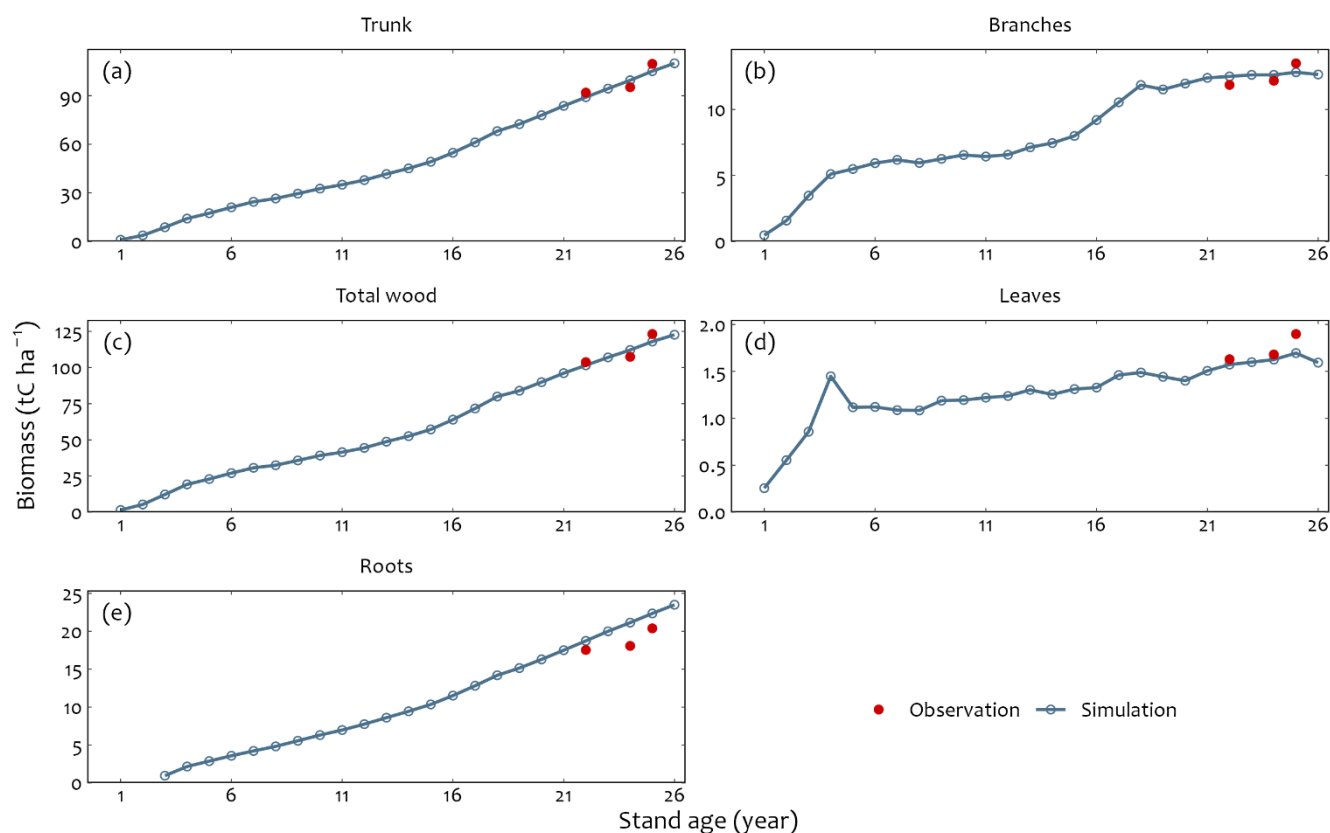
Figure 4: Time series of daily simulated and observed evapotranspiration (ET), leaf area index (LAI), gross primary production (GPP), and net ecosystem production (NEP) at CRRC (2015-2018). Daily regression statistics (RMSE, R^2 , and EF) are shown in the top-left corner of each plot. (a) Daily simulated ET is shown as a black line and observed ET as red dots. (b) Daily simulated LAI is shown as a black line and observed LAI as red dots. (c) Daily simulated GPP is shown as a black line and observed GPP as red dots; cumulative annual simulated GPP is shown as a light green solid line and cumulative annual observed GPP as a dark green dashed line. (d) Daily simulated NEP is shown as a black line and observed NEP as red dots; cumulative annual simulated NEP is shown as a light green solid line and cumulative annual observed NEP as a dark green dashed line.



430 The model simulation showed a negative net ecosystem carbon balance (NECB) of during the first year, indicating a net carbon loss during establishment (Fig. S5a). From the second year onward, simulated NECB became positive, ranging from 1.79 to 14.28 t C ha⁻¹ yr⁻¹, indicating that the plantation generally functioned as a net carbon sink. Simulated NECB peaked at 18 years after establishment, following a period of increasing biomass development. Thereafter, simulated NECB remained positive and reached 10.35 t C ha⁻¹ yr⁻¹ at the end of the rotation (Fig. S5a).

3.3 Biomass accumulation in rubber plantation at CRRC site

435 The model reproduced well the observed biomass allocation among rubber tree organs at the available measurement years. Observed biomass data were available only at rotation years 22, 24 and 25, and simulated values at these years closely matched measurements for trunk and branch biomass (Fig. 5a and 5b). Leaf biomass was well simulated at years 22 and 24 but was underestimated at year 25 (Fig. 5d), while root biomass was generally slightly overestimated across the three measurement years. At year 25, simulated trunk and branch biomass reached 105.14 and 12.81 t C ha⁻¹, compared with observed values of 109.65 and 13.49 t C ha⁻¹, respectively (Fig. 5a and 5b). Simulated leaf and root biomass were 1.69 and 22.35 t C ha⁻¹, compared with measured values of 1.89 and 20.38 t C ha⁻¹, respectively (Fig. 5d and 5e). Beyond these measurement years, the model was used to simulate biomass dynamics continuously from plantation establishment to the end of the 26-year rotation, providing an estimate of biomass accumulation and allocation throughout the rotation. Over this period, the model simulated a mean change in total woody biomass stocks of 6.5 t C ha⁻¹ (Fig. S5c).



445 **Figure 5: Measured and simulated biomass of rubber tree organs at CRRC: (a) trunk, (b) branches, (c) total wood, (d) leaves, and (e) roots. Simulated biomass is shown in blue, and observed biomass in red. Observations are estimates derived from tree inventory data using Hytönen et al. (2019) allometric equation.**

3.4 Latex yield modelling at CRRC and SKRS sites

According to the usual practice in Thailand, each production year starts around mid-April and stops around next February.
 450 Trees are not tapped from March to April (resting period corresponding to the refoliation). There are some variations according to actual start and end of the rainy season, explaining the different number of yield months between tapping years.

At CRRC (the calibration site), measured yearly latex yields between 2012/2013 to 2019/2020 ranged from 0.92 to 1.73 tC ha⁻¹ year⁻¹ (average: 1.38 tC ha⁻¹ year⁻¹), while simulated yields ranged from 1.22 to 1.63 tC ha⁻¹ year⁻¹ (average: 1.52 tC ha⁻¹ year⁻¹) over the same period (Fig. 6a-6h). Across the simulated periods at CRRC, yearly latex production showed a consistent
 455 interannual pattern with some discrepancies between observed and simulated values. Overall, the model captured the yearly magnitude but exhibited both overestimations (e.g., 2012/2013, 2013/2014, 2016/2017) and underestimations (e.g., 2014/2015, 2017/2018) (Fig 6a-6h). Agreement between simulated and observed yields was better at the yearly scale than at the monthly scale. At the monthly scale, the model tended to simulate higher yields during the rainy season, whereas measured yields were



more variable, without clear seasonal pattern. Yield peaks were often, but not always, measured at the end of the season. As a
460 result, the model did not accurately capture monthly yield dynamics, even though yearly totals were generally well represented.
Simulated monthly yields ranged from 0.07 to 0.24 tC ha⁻¹ month⁻¹ (average: 0.17 tC ha⁻¹ month⁻¹), while measured yields
ranged from 0.04 to 0.39 tC ha⁻¹ month⁻¹ (average: 0.15 tC ha⁻¹ month⁻¹) (Fig. 6a-6h).

At SKRS (the validation site), measured annual yields between 2018/2019 to 2021/2022 ranged from 1.31 to 2.23 tC ha⁻¹ year⁻¹
465 (average: 1.68 tC ha⁻¹ year⁻¹), whereas simulations ranged from 1.77 to 2.04 tC ha⁻¹ year⁻¹ (average: 1.94 tC ha⁻¹ year⁻¹) (Fig.
6i-6l). The model overestimated yields except in 2020/2021. Simulations tended to show higher monthly yields during the
rainy-season, while there was no systematic monthly pattern in measured data. During tapping months, simulated yields ranged
from 0.07 to 0.30 tC ha⁻¹ month⁻¹, and measured yields ranged from 0.04 to 0.36 tC ha⁻¹ month⁻¹ (Fig. 6i-6l).

Overall, yearly simulated yield was in the same range as measured one, at both sites. The model explained 35% of the observed
monthly variability at CRRC (Fig. S6a; RMSE = 0.08 tC ha⁻¹ month⁻¹, R² = 0.35 and EF = 0.28) but only 13% at SKRS (Fig.
470 S6b; RMSE = 0.12 tC ha⁻¹ month⁻¹, R² = 0.13 and EF = -1.64), demonstrating moderate ability at CRRC and limited ability to
reproduce monthly fluctuations at SKRS.

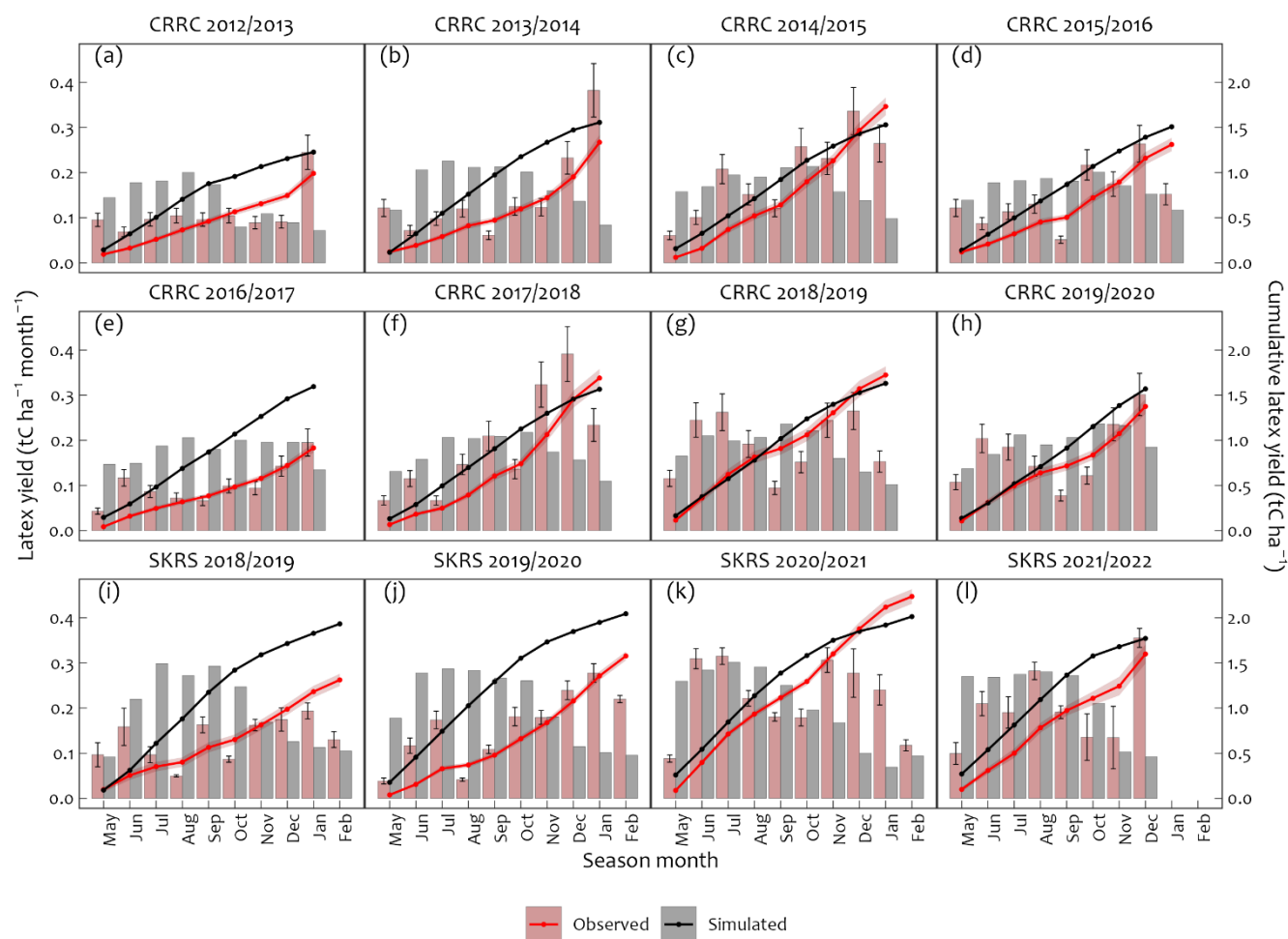


Figure 6: Time series of monthly simulated and observed latex yield at CRRC (2012-2019) and SKRS (2018-2021). Panels (a-h) show CRRC (2012-2019), and panels (i-l) show SKRS (2018-2021). Grey bars represent simulated monthly latex yield, and light red bars represent observed monthly latex yield. Solid black lines show simulated cumulative annual latex yield, and solid red lines show observed cumulative annual latex yield. Shaded areas around the red lines indicate the standard deviation of cumulative observation, and black vertical lines denote the standard deviation of monthly observations. CRRC is the parameterization site and SKRS the validation site.

4 Discussion

4.1 Simulating water and carbon fluxes and stocks in rubber plantations

Our simulations generally show good agreement between the measured and simulated soil water content (SWC) in the upper three soil layers at both sites (CRRC: layer 1 (0- 0.33 m) and layer 3 (0.99-1.99 m) and SKRS: layer 1 (0- 0.33 m), layer 2 (0.33-0.99 m), and layer 3 (0.99-1.99 m)). This is particularly important given strong concerns about the use of water by rubber plantations (Carr, 2012; Clermont-Dauphin et al., 2013) and recent findings indicating that rubber trees primarily absorb water

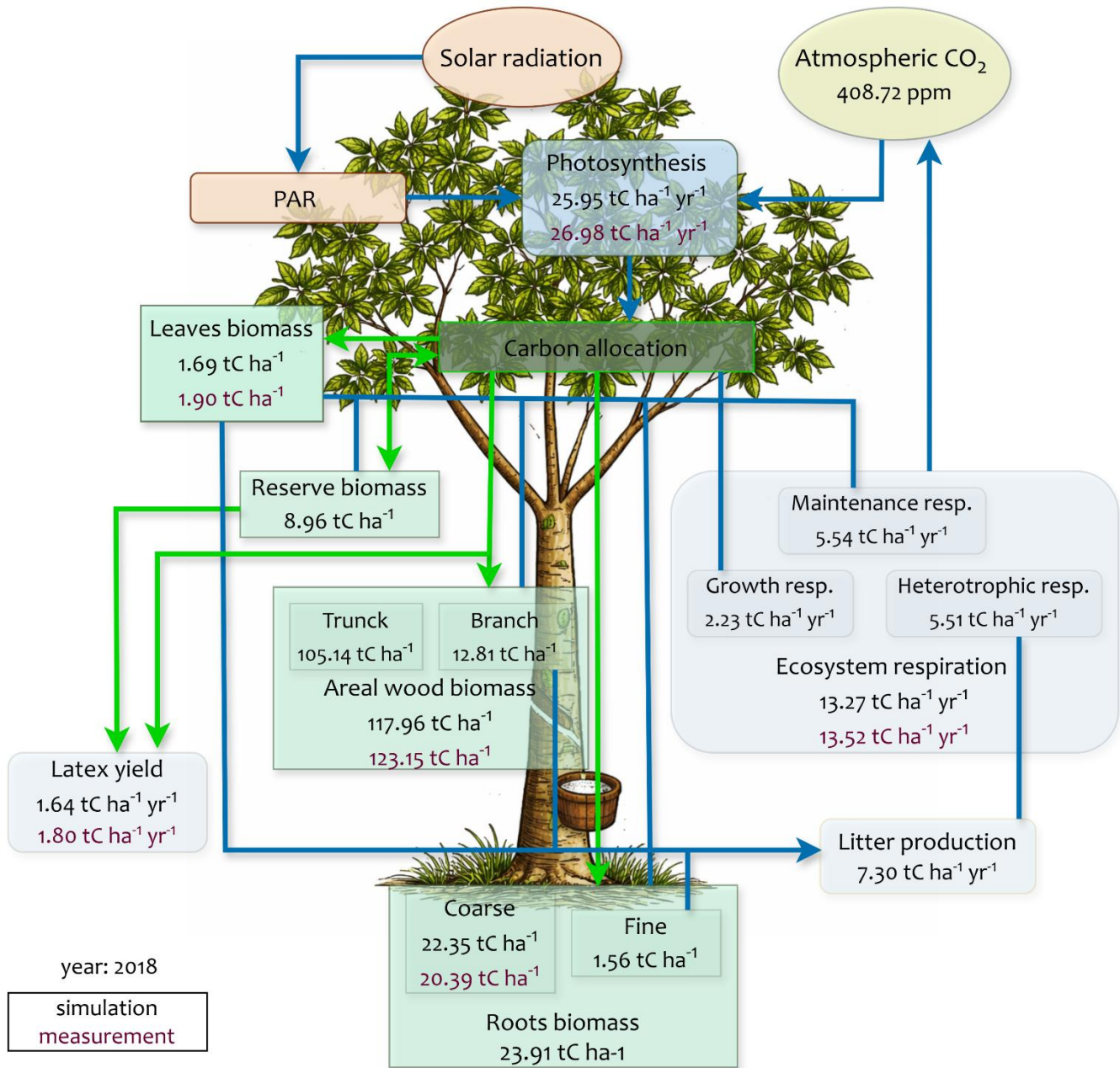


485 from the 5–50 cm depth interval (Song et al., 2022). The simulation results showed a well-marked temporal variability in SWC dynamics, with SWC remaining at its lowest levels for a longer period at CRRC, corresponding to the longer dry season at this site compared with SKRS. The MAESPA water balance model used for rubber is based on the Richards equation and has been previously applied successfully to simulate water balance in tropical eucalypt forests characterized by deep rooting systems (Christina et al., 2017). These modeling results demonstrate the model’s ability to reasonably simulate soil water dynamics
490 across different tropical tree-based systems, provided appropriate site-scale parameterization.

At the CRRC site, the lowest measured evapotranspiration (ET) during the 2015–2018 period occurred in 2016 (909 mm) (Fig. 3g). In that year, measured daily data showed that both ET (Fig. 4a) and GPP (Fig. 4c) declined sharply after a modest initial peak at the onset of the year. The model produced its largest positive bias in 2016, overestimating annual ET by approximately 217 mm relative to observations. This overestimation is primarily attributable to the model’s excessive simulation of ET during
495 the early stages 2016 (end of the previous dry season and the onset of the subsequent wet season), where it failed to capture the observed decline in ET (Fig. 3g and Fig. 4a), likely associated with drought-induced physiological limitations (*e.i.*, high temperature, elevated VPD (Fig. S7b: highest VPD observed in 2015 and 2016 at CRRC) and low SWC (Fig. 3a–3c)) on leaf development and stomatal conductance (Isarangkool Na Ayutthaya et al., 2011; Law et al., 2002). This overestimation could also indicate that the model is tapping water resources from deeper soil layers than is the case in reality. Both ET and GPP are
500 known to be highly sensitive to drought stress (Yang et al., 2016). In addition, a study assessing the environmental controls on net ecosystem exchange (NEE) over a young rubber plantation in northeastern Thailand have shown that VPD, SWC, and air temperature can have a major influence on carbon balance (Chayawat et al., 2019). Indeed, the CRRC site experienced persistent drought conditions from April 2015 to August 2016 (Wang et al., 2022). This period coincided with the second strongest El Niño event in Mainland Southeast Asia (MSEA) since 1950, which triggered an extended and severe drought
505 characterized by extreme precipitation deficits and record-high air temperatures (Burton et al., 2018; Santoso et al., 2017; Thirumalai et al., 2017; Wang et al., 2022). The 2016 model’s results for ET and GPP indicate room to improve the representation of drought-driven delays in leaf dynamics (shedding and refoliation). The current temperature-driven phenology scheme does not fully account for the combined effects of high VPD and low SWC, which can hinder leaf development, induce stomatal closure in young leaves, and limit increase in GPP and ET (Chen et al., 2010; Law et al., 2002). This temperature-
510 driven phenology simulation performs generally well at our study sites, producing canopy dynamics that align with observed patterns. Nonetheless, further research is required to refine the model and deepen our understanding of rubber tree phenology particularly regarding the influence of environmental drivers on leaf flushing, shedding, maturation, and flowering. In this context, remote sensing offers opportunities to complement field observations by enabling continuous, spatially explicit monitoring of canopy phenology. Satellite and UAV based observations can capture changes in canopy greenness and
515 structure, providing indicators of leaf emergence, senescence, and development. Integrating these observations with environmental variables such as temperature, rainfall, and soil moisture could improve understanding of phenological drivers.



The CRRC site was a carbon sink during the period from 2015 to 2018. The average measured and simulated GPP at CRRC over this period were 2.54 and 2.60 kg C m⁻² yr⁻¹ (Fig. 4c), respectively, while the average annual measured and simulated NEP were 1.19 and 1.35 kg C m⁻² yr⁻¹, respectively (Fig. 4d). The measured and simulated NEP at CRRC fall within the range of NEP variation estimated for most temperate forests with high nutrient availability (0 to 1.5 kg C m⁻² yr⁻¹) (Fernández-Martínez et al., 2014). For comparison, a secondary-growth natural forest in Thailand at a similar latitude than CRRC exhibited an annual average NEP of 0.75 ± 0.25 kg C m⁻² yr⁻¹, while another monoculture rubber plantation in southern Thailand showed 1.07 ± 0.14 kg C m⁻² yr⁻¹ (Wang et al., 2022). Both values are lower than the measured and simulated annual average NEP observed at CRRC. Similarly, in a 20-22 years rubber plantation in Danzhou (Hainan province, China), Yang et al. (2023) measured an average annual NEP of 0.91 kg C m⁻² yr⁻¹, also lower than CRRC values. This high carbon sequestration potential of the CRRC site was previously shown by Satakhun et al. (2019), who reported that the rubber plantation acted as a substantial carbon sink, with an annual average NEP (*i.e.*, CO₂ sequestration: proxy of -NEE) of 1.00 kg C m⁻² yr⁻¹ (*approx.* 36.7 t CO₂ ha⁻¹ yr⁻¹) during the period 2013-2016. The CRRC site is fertilized; both measured and simulated ecosystem respirations (Reco) at the site are relatively low; for example, in 2018, measured and simulated values were 1.32 and 1.35 kg C m⁻² yr⁻¹, respectively (Fig. 7). Previous studies have shown that fertilization and weed control can reduce carbon allocation to roots as well as to fungal symbionts and root exudates, while increasing allocation to woody biomass, thereby lowering both autotrophic and heterotrophic respiration (*i.e.*, overall Reco) (Janssens et al., 2010; Vicca et al., 2012). In this case, a greater proportion of carbon may have been directed toward above-ground growth, enhancing NEP. Broadly fertilized plantation forests can exhibit higher NEP than naturally regenerating forests. This pattern has been demonstrated in a study based on 35 eddy-covariance measurements conducted across China (Zhu et al., 2022). All of these studies suggest that the high NEP at CRRC can be attributed to enhanced nutrient availability (trees are fertilized twice yearly (1 kg tree⁻¹ yr⁻¹, 30-5-18 NPK), coupled with potentially reduced below-ground competition (root:shoot ratio *approx.* 0.175). In addition, the CRRC site exhibits high photosynthetically active radiation (PAR) levels, even during the rainy season (Fig. S7a), which promotes increased carbon uptake. All of these highlight the importance of local environmental and management factors in modulating ecosystem carbon dynamics. The model demonstrates strong capability in representing overall carbon fluxes (e.g., photosynthesis, respiration, latex yield) and stocks (e.g., trunk, branches, leaves, and root biomass), as shown in Figure 7, which compares simulated and observed carbon dynamics in 2018. Model performance could be further enhanced by explicitly accounting for the effects of soil fertilization on productivity (Cornut et al., 2023b, a).



545 **Figure 7: Full carbon balance of a 24-year-old rubber plantation (2018).** Right-angled boxes represent state variables, rounded boxes
represent flow variables, and elliptical boxes represent meteorological forcing variables. Each arrow indicates a flow from one
550 compartment to another with green arrows showing carbon allocation toward tree organs and latex production. Values of stocks
and fluxes are shown inside the boxes. Simulated values are indicated in black, and observed values are indicated in red.

The simulated cumulative total biomass for the 26-year-old rubber plantation at CRRC was 179.40 tC ha⁻¹, compared with a
550 measured total biomass of 145.43 tC ha⁻¹ at 25 years of age (Fig. 5). This estimate remains within the range reported for mature



rubber plantations in Southeast Asia. For example, in Thailand, a total biomass of 157 and 289 tC ha⁻¹ has been reported for a 20- and 30-year-old stand, respectively (Hytönen et al., 2019). Similarly, Saengruksawong et al. (2012) reported 141 tC ha⁻¹ for a 20 year old plantation in northeastern Thailand, indicating variability among sites. In another study in China, Yang et al. (2019) reported 121 tC ha⁻¹ measured for a 35 year old plantation. Although biomass accumulation in rubber tree plantations
555 generally increases with age, the variability observed across studies likely reflects differences in stand density, site conditions, and management practices.

Between 2012 and 2019, the annual average measured and simulated latex yields at CRRC were lower than those recorded at SKRS between 2018 and 2021, with differences of -0.34 and -0.45 t C ha⁻¹ yr⁻¹ for measured and simulated values, respectively (Fig. 6). The CRRC site is considered relatively marginal for rubber cultivation due to its lower precipitation relative to
560 traditional equatorial areas like SKRS. Nevertheless, average latex production at CRRC (measured: 1.4 t C ha⁻¹ yr⁻¹ and simulated: 1.53 t C ha⁻¹ yr⁻¹) remains within an acceptable range compared to reported yield for other rubber plantations in the region. For comparison in the Nabang reserve (Xishuangbanna, China) Yang et al. (2019) estimated for 40 year rubber plantations with different density and at different elevation latex yield ranging from 0.6 to 1.9 t C ha⁻¹ yr⁻¹. At the SKRS site, previous experimental work demonstrated that fertilization and intensive tapping practices (ethephon stimulation) can increase
565 latex yield. The study reported 5 to 8 percent yield increase when medium and high NPK application rates were used, compared to unfertilized plots (Chotiphan et al., 2019). The medium yield observed at CRRC, despite lower precipitation relative to optimal sites (Gohet et al., 2016), can be attributed to fertilization and elevated PAR (Fig. S7a: at CRRC, PAR up to 2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and $R_n > 750 \text{ W m}^{-2} \text{HH}^{-1}$ sometime, even during the rainy season), both of which enhance carbon uptake as compared to wetter but more cloudy areas (Wang et al., 2022). In fact, fertilization would likely have stronger effect in a poorer
570 soil. It is worth noting that the simulated latex yield presented here represents a yield determined mainly by the intrinsic physiological capacity to accumulate photosynthates according to environmental conditions, and to convert them into latex. It does not consider the latex flowing capacity, which also depends on climatic factors (Rao et al., 1998), but also on genetic factors (Chao et al., 2017). Also, the model does not take into account, disease caused by pathogens and physiological disorders such as tapping panel dryness and bark necrosis (Herlinawati et al., 2022; Pellegrin et al., 2004). This explains the observed
575 overestimation of annual average yield at both sites (overestimation of 0.13 and 0.24 t C ha⁻¹ yr⁻¹ at CRRC and SKRS, respectively). Overestimation may also result from other operational constraints affecting tapping, such as availability and skills of tappers or quality of planting material. Moreover, the model represents the direct influence of climate on latex production through a climate suitability factor in the latex-yield submodule. This factor is currently formulated using linear, additive penalties with fixed tolerance thresholds. Such an approach simplifies the computations but does not reflect the
580 inherently nonlinear and interactive nature of biological responses. Consequently, while the current formulation provides a valuable first approximation, future model development would benefit from refining tolerance parameters and exploring nonlinear or multiplicative penalty structures to enhance biological realism. Future experiments combining contrasting



temperature and soil moisture conditions could help quantify nonlinear climate responses and refine the tolerance thresholds used in the model.

585 The simulated NECB indicates that the rubber plantation functioned predominantly as a net carbon sink (Fig. S5a), with carbon losses occurring only during the establishment year. Thereafter, NECB increased with biomass accumulation, reaching the highest carbon sequestration rate at 18 years after establishment. Despite continuous carbon removal through latex harvesting, NECB remained positive during the later stages, indicating that carbon gains through biomass accumulation exceeded losses from respiration, litter decomposition, and latex export. Overall, these results suggest that the rubber plantation maintained a
 590 substantial capacity for net carbon sequestration throughout most of the simulated period.

4.2 Uncertainties, limitations and future perspectives for simulating rubber productivity

With the latex yield module incorporated into the adapted version of CASTANEA-MAESPA for rubber, the model provides a useful framework for investigating the implications of future climate change for rubber growth and productivity by linking environmental conditions with plant physiological processes, growth, and latex production. Overall, the model reasonably
 595 reproduced the main water and carbon dynamics and biomass accumulation across the two study sites. It also captured the general magnitude of latex production. These results support its use for exploring the physiological responses of rubber plantations to changes in environmental conditions. Nevertheless, the evaluation indicates that further refinement is needed, particularly in the representation of phenology and the regulation of latex production.

An important consideration when interpreting the latex simulations is the distinction between simulated production potential
 600 and observed farm yield. The model estimates the latex production that is physiologically achievable under the simulated environmental conditions while accounting for management practices that are currently explicitly represented in the model. An effort has already been made to incorporate management through a flexible framework in which tapping frequency can be modified, thereby affecting latex flow. This is an important feature because tapping frequency can substantially influence latex production, as demonstrated in the literature (Gohet et al., 2016). However, several other management and operational factors
 605 remain difficult to represent, including the number of effective tapping days resulting from labor availability, field accessibility, temporary interruptions in tapping, farmer decisions to modify or skip tapping, and variations in tapping intensity. Weather conditions during tapping, particularly rainfall, may also prevent or reduce harvesting. These factors can contribute to differences between simulated and observed yields when realized production is lower than the simulated potential. For example, at SKRS, a substantial number of tapping days were lost each year because approximately 90% of rainy days occurred
 610 during the tapping period, from May to February (Chotiphan et al., 2019). Moreover, when rainfall occurs after tapping, but before harvesting (typically at night), the latex is produced by the tree, but lost by overflowing from the harvesting cup. The trees then use carbohydrate resources in the way described by the model, but the yield is unaccounted for in measurements, inducing a gap with simulations. However, management constraints alone cannot explain all discrepancies between simulations and observations. In some periods, simulated yield was lower than observed yield, indicating that differences also arise from



615 uncertainties in the representation of physiological processes and their environmental controls. For example, the model may
not fully capture short-term variations in carbon allocation to latex and carbohydrate reserves. Discrepancies may also arise
because the model does not account for pathogen-induced diseases and physiological disorders, such as tapping panel dryness
and bark necrosis (Herlinawati et al., 2022; Pellegrin et al., 2004), which can affect latex production. Consequently,
discrepancies between simulated and observed yields should be interpreted as the combined result of model uncertainty and
620 importantly, management and harvesting conditions.

Overall, the model provides a useful framework for estimating the physiological production potential of rubber plantations
under different environmental conditions. Its ability to reproduce major water and carbon dynamics, biomass accumulation,
and the general magnitude of latex production demonstrates its potential for climate-impact assessment. Importantly, the model
can be used to explore the production that is physiologically achievable under given environmental conditions, while
625 recognizing that realized farm yields may depart from this potential in either direction because of model uncertainty,
management and harvesting conditions. This distinction provides a valuable basis for assessing how much rubber production
could potentially be maintained under future climates and for identifying the management conditions required to realize that
production potential. Beyond latex production, the simulated biomass dynamics provided an opportunity to assess other
dimensions of plantation performance, including wood production and carbon sequestration potential. In particular, the model
630 was used to estimate the NECB, thereby integrating carbon gains through photosynthesis and biomass accumulation with
carbon losses through respiration, decomposition, and latex export. This broader perspective could contribute to a more
comprehensive valuation of rubber plantations, considering not only their capacity for latex production but also their potential
contribution to carbon sequestration and biomass production under current and future climates. Such an approach could provide
a basis for evaluating trade-offs between production and carbon services and for identifying management conditions that
635 support both productive and climate-resilient rubber plantations.

5 Conclusion

Overall, our results show that the adapted CASTANEA-MAESPA model adequately represents the main water and carbon
dynamics of mature rubber plantations, including soil water content, evapotranspiration, photosynthesis, respiration, net
ecosystem productivity, biomass accumulation, and latex production. The model reproduced the general magnitude of latex
640 yield, while discrepancies between simulated and observed yields highlight the influence of management and harvesting
conditions, as well as physiological and biological processes that are not explicitly represented in the model. By explicitly
accounting for carbon allocation to latex production, the model provides an integrated framework for quantifying carbon
stocks, carbon sequestration, and carbon export through latex in mature rubber plantations. Consequently, this framework can
support assessments of rubber plantation functioning and productivity under current and future environmental conditions.
645 Future model development should improve the representation of rubber phenology, physiological disorders, and nonlinear



responses to climatic conditions to better capture variations in latex production and carbon dynamics, thereby strengthening assessments of rubber plantation productivity and carbon sequestration under climate change.

Author contribution. Y.A., Conceptualization, Methodology, Writing - original draft, Writing - review & editing, G.M., Y.N., P.T., Conceptualization, Methodology, Writing - review & editing, C.F., N.D., I.C., P.K., J.S., O.D., D.S., Writing - review & editing

Competing interests. The authors declare that they have no conflict of interest.

Code availability. The CASTANEA-MAESPA model, adapted for rubber trees and presented in this study, will be made available upon request to the corresponding author.

Data availability. Data will be made available upon request from the corresponding author.

Financial support. This work was supported by the project “Forecasting impacts of climate change and workforce availability on natural rubber commodity chain in South-East Asia” (FORSEA) funded by the Agence Française de Développement (AFD), FEXTE Program.

Acknowledgments. The stay of P. Thaler and G. le Maire in Thailand was financially supported by the Office of the Thailand Ministry of Higher Education, Science, Research and Innovation and the Thailand Science Research and Innovation through the Kasetsart University Reinventing University program 2023. The Hevea Research Platform in Partnership (HRPP) facilitated all the data collection.

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