

Atmospheric dryness effects on canopy chlorophyll fluorescence and Gross Primary Production (GPP) in a deciduous forest during heat waves

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ABSTRACT

Sun-Induced chlorophyll Fluorescence (SIF) is the most promising remote-sensing proxy of Gross Primary Production (GPP) in terrestrial ecosystems. However, the estimation of GPP using SIF is challenging when plants experience stress, particularly during extreme climatic events whose frequency is projected to increase in the future. Recently, the feasibility of canopy-level active chlorophyll fluorescence measurements (LED-induced chlorophyll fluorescence), which directly measure the apparent fluorescence yield (F_{yieldLIF}), has provided new perspectives on detecting the responses of plants to stress. This study was conducted during the summer 2022 European heat waves in a mixed temperate deciduous broadleaf forest, located in the French Fontainebleau-Barbeau station. Continuous measurements of carbon dioxide (CO_2) and energy exchanges, SIF, F_{yieldLIF} , and ancillary environmental variables were acquired. We investigated how heat-wave induced high atmospheric dryness, measured as Vapor Pressure Deficit, affected canopy chlorophyll fluorescence (both SIF and F_{yieldLIF}) and GPP, as well as their relationships. At the half-hourly scale, our results revealed a decrease of the correlation between SIF and GPP (R^2 decreased from 0.49 to 0.17) at high atmospheric dryness. In contrast, the correlation between F_{yieldLIF} and GPP increased significantly under high atmospheric dryness (R^2 increased from 0.07 to 0.43). However, at the daily scale, the correlations between SIF and GPP and between F_{yieldLIF} and GPP showed an overall increase compared to the half-hourly scale, suggesting a time-scale-dependent response of these relationships to atmospheric dryness. This study also highlighted F_{yieldLIF} 's advantage in detecting plant responses

Abbreviations: ϕ_F , the quantum yield of SIF; ϕ_k , the ratio between SIFy and F_{yieldLIF} ; ϕ_p , the photosynthetic light use efficiency of the canopy; I_{LED} , the irradiance of the LED pulse; f_{APAR} , the fraction of photosynthetically active radiation (PAR) absorbed by the canopy; f_{APARchl} , the fraction of PAR absorbed by the chlorophyll; f_{LAPARchl} , the fraction of the LED pulse absorbed by the chlorophyll; f_{esc} , the fraction of all chlorophyll fluorescence photons escaping from the canopy after re-absorption and multiple scattering within the canopy; f_{escL} , the fraction of all chlorophyll fluorescence photons induced by the LED that escape from the canopy; 3FLD, the three-band Fraunhofer Line Discrimination; a , the slope of the light-response curve at low light intensity; A_{max} , the maximal rate of photosynthesis; APAR, Absorbed PAR; CV, Coefficients of Variation; ChlF, Chlorophyll Fluorescence; DC, Dark Current; DN, Digital Numbers; DOY, Day-Of-Year; EC, Eddy Covariance; FOV, Field Of View; FWHM, Full Width at Half Maximum; F_{yieldLIF} , apparent chlorophyll fluorescence yield measured by LIF; GPP, Gross Primary Production; GPPy, apparent quantum yield of GPP, calculated as GPP/PAR ; HAD, High Atmospheric Dryness; ICOS, Integrated Carbon Observation System; IT, Integration Time; k , a constant that combines the effects of I_{LED} , f_{LAPARchl} and f_{esc} ; k_p , the effective rate constant of photochemistry; k_{PSII} , the maximum intrinsic rate constant of photochemistry; k_F , the rate constant of fluorescence; k_D , rate constant of non-radiative thermal dissipation by means of constitutive regulated mechanisms; k_{NPQ} , rate constant of non-radiative thermal dissipation by means of physiological regulated mechanisms; LAI, Leaf Area Index; LED, Light Emitting Diode; LIF, LED-Induced chlorophyll Fluorescence; LUE, Light Use Efficiency; mNDI705, modified red-edge Normalized Difference Index; NAD, No Atmospheric Dryness; NDVI, Normalized Difference Vegetation Index; NPQ, Non-Photochemical Quenching; PAM, Pulse Amplitude Modulation; PAR, Photosynthetically Active Radiation in the visible light spectrum (400–700 nm); $\text{PAR}_{\text{diffuse}}$, diffuse radiation measured in the visible light spectrum (400–700 nm); $\text{PAR}_{\text{reflected}}$, total radiation reflected by the canopy in the visible light spectrum (400–700 nm); $\text{PAR}_{\text{transmitted}}$, total radiation in the visible light spectrum (400–700 nm) that penetrates beneath the canopy and reaches the understory; $\text{PAR}_{\text{total}}$, total radiation measured in the visible light spectrum (400–700 nm); PQ, Photochemical Quenching; q_L , the fraction of open and functional photosynthetic reaction centers of PSII; R_{eco} , ecosystem respiration; REW, Relative Extractable Water; SIF, Sun-Induced chlorophyll Fluorescence; SIFy, apparent quantum yield of SIF, calculated as SIF/PAR ; SWC, Soil Water Content; SWHC, Soil Water Holding Capacity; T_a , air temperature; VPD, Vapor Pressure Deficit; VZA, Viewing Zenith Angle.

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to high atmospheric dryness, and emphasized the potential of canopy-level active chlorophyll fluorescence for assessing the chlorophyll fluorescence-photosynthesis relationship under extreme climatic conditions.

1. Introduction

Gross Primary Production (GPP) is a key carbon flux in the global carbon cycle, quantifying carbon fixation by terrestrial ecosystems (Beer et al., 2010). Both decrease in soil moisture and increase in atmospheric water demand can negatively affect GPP (Novick et al., 2016; Reichstein et al., 2013; Sulman et al., 2016). These effects on GPP are all the more important that the frequency and severity of extreme climate events are projected to increase in the future (Lee et al., 2023). Atmospheric demand for water is directly related to atmospheric dryness, measured as Vapor Pressure Deficit (VPD). Similar to soil water deficit induced stress, high VPD affects both leaf stomatal conductance and ecosystem evapotranspiration, thereby profoundly influencing vegetation productivity (Novick et al., 2016). Under high VPD conditions, the stomata of leaves close to prevent excessive water loss (McAdam and Brodribb, 2015). High atmospheric dryness has been found to limit leaf stomatal conductance and evapotranspiration to a greater extent (>70 %) than soil water deficit induced moisture stress in various biomes, including forest ecosystems, emphasizing the importance of atmospheric drought in carbon and water fluxes across all ecosystems (Novick et al., 2016).

Remote sensing of Sun-Induced chlorophyll Fluorescence (SIF) has emerged as a promising tool to estimate GPP across various ecosystems (Mohammed et al., 2019), primarily because of its mechanistic connection to the photosynthetic machinery and its responsiveness to changes in Absorbed Photosynthetically Active Radiation (APAR) (Porcar-Castell et al., 2014). Previous studies have demonstrated that SIF is closely related to GPP at different scales: local (site) (Dechant et al., 2020; Goulas et al., 2017; Li et al., 2020; Miao et al., 2018; Yang et al., 2018; Yang et al., 2015), regional (Guanter et al., 2014; Zhang et al., 2018), and global (Frankenberg et al., 2011; Guanter et al., 2012; Joiner et al., 2011; Pickering et al., 2022; Song et al., 2021). The measured SIF signal at canopy scale arises from complex interactions involving light absorption, chlorophyll fluorescence (ChlF) emission and re-absorption, and light-scattering processes within the canopy. Consequently, the relationship between SIF and GPP is influenced by several confounding factors, including solar radiation, leaf-level energy partitioning, leaf biochemical properties, canopy structure, and abiotic conditions. Among these, APAR represents the primary driver of the SIF-GPP relationship (Dechant et al., 2020; Miao et al., 2018; Yang et al., 2018). In addition, biochemical and morphological changes in plants, such as a decrease in leaf chlorophyll and carotenoid contents or leaf scrolling due to increased water loss under stress, can alter the optical properties of the canopy. These changes affect scattering and re-absorption pathways, ultimately influencing the amount of ChlF photons that escape the canopy and are detected by the SIF sensors (Dechant et al., 2020; Hwang et al., 2023; Xu et al., 2021). Importantly, under environmental stress conditions—such as high VPD or drought—the relationship between SIF and GPP can weaken or become nonlinear (Martini et al., 2022; Wohlfahrt et al., 2018; Wieneke et al., 2024), complicating the direct use of SIF as a reliable proxy for GPP (Porcar-Castell et al., 2014). This SIF-GPP relationship decoupling under stress is largely driven by physiological processes such as reduced stomatal conductance and increased Non-Photochemical Quenching (NPQ), a mechanism that plants use to dissipate excess absorbed light energy, which reduces ChlF emission and complicates SIF interpretation under stress (Martini et al., 2022; Wohlfahrt et al., 2018; Yi et al., 2024). Under such conditions, stomatal closure reduces CO₂ uptake and thus GPP, while absorbed light energy may still be re-emitted as fluorescence or dissipated through NPQ, causing a divergence between SIF and photosynthetic carbon fixation (Martini et al., 2022). Thus, observed SIF-GPP relationships carry inherent uncertainty, particularly under dynamic

environmental conditions.

Currently, most studies addressing the influence of abiotic stress on photosynthesis and ChlF have focused on three distinct observational scales: satellite-based approaches using SIF at regional to global scales (Liu et al., 2020; Fu et al., 2022); tower-based studies using SIF at site scale (Wohlfahrt et al., 2018; Wieneke et al., 2018, 2024; Yi et al., 2024; Balde et al., 2024) and leaf-level investigations not using SIF to measure ChlF but measuring it through Pulse Amplitude Modulation (PAM) fluorometry (Magney et al., 2017; Martini et al., 2022). While each scale offers valuable insights, they differ in spatial resolution, measurement principles, and sensitivity to physiological versus structural drivers:

- i) Satellite-derived SIF data offer substantial advantages for large-scale ecosystem monitoring. However, these data are often limited in spatial and temporal resolution and can be influenced by canopy structural variations and viewing geometry, which make it difficult to cope with the SIF-GPP relationship decoupling (Wieneke et al., 2024).
- ii) Tower-based SIF measurements provide high temporal resolution and stable observation geometry, enabling detailed studies of canopy-level physiological dynamics and the monitoring of responses to rapidly changing environmental conditions (Yang et al., 2015; Magney et al., 2019; Yi et al., 2024). However, the complexity of SIF signals makes it challenging to accurately interpret the relationship between SIF and GPP during environmental stress.
- iii) The PAM technique, associated with the saturating light pulses method, allows for direct measurement of ChlF yield (Φ_F) at the leaf scale (Schreiber et al., 1986). According to the lake model, the fraction of open and functional photosynthetic reaction centers of PSII (q_L) can be expressed by the ratio of the effective rate constant of photochemistry (k_P) and the maximum intrinsic rate constant of photochemistry (k_{PSII}) (Laverge and Trissl, 1995; Kramer et al., 2004). Therefore, the quantum yield of fluorescence emission of PSII can be expressed as $\Phi_F = k_F / (k_D + k_F + k_{NPQ} + q_L k_{PSII})$. k_F is the rate constant of fluorescence. k_D and k_{NPQ} are the rate constants of non-radiative thermal dissipation by means of constitutive and physiological regulated mechanisms, respectively. In this model, both k_{NPQ} and q_L vary in response to the acclimation of photosynthesis, while k_F is assumed to remain constant in physiological processes (Butler and Kitajima, 1975; Clegg, 2004) and k_D is invariable by definition (i.e. any variation is embedded in k_{NPQ}). As a consequence, Φ_F is directly linked to the acclimation of photosynthesis, and serves as a direct proxy of physiological functioning, particularly for capturing stress-induced adjustments in photosynthesis (Porcar-Castell et al., 2014). Thus, the PAM technique has been widely used for a long time at leaf scale (or below) in studies evaluating vegetation and photosynthesis responses to environmental factors (Baker, 2008; Magney et al., 2017; Martini et al., 2022). However, the applicability of commercial PAM techniques at the canopy scale is not possible (Ounis et al., 2001). These setups are inherently designed for monitoring ChlF yield at leaf scale, the measurement of which requires saturation light pulses and dark adaptation.

To overcome these limitations associated with fluorescence measurement techniques, recent advances have introduced active ChlF measurements—specifically Laser- or Light Emitting Diodes (LED)-Induced Fluorescence (LIF)—as a promising tools for canopy-level monitoring (Ounis et al., 2001; Balde et al., 2024; Loayza et al., 2023;

Moya et al., 2019; Ounis et al., 2016). LIF techniques address several key challenges in remote ChlF monitoring. Designed for canopy-scale applications, LIF can not use saturating light pulses and can operate effectively at several meters from the foliage. Its controlled excitation light source reduces the influence of radiative confounders such as varying sunlight and canopy structure. Moreover, LIF overcomes the spatial and operational limitations of leaf-level PAM systems, enabling high-frequency, physiologically meaningful measurements at canopy scale in natural field conditions. Importantly, the motivation for developing remote active ChlF techniques mainly stems from the inherent limitations of SIF, particularly its sensitivity to canopy structure and ambient radiation, which can complicate its interpretation at the canopy scale (Miao et al., 2018; Dechant et al., 2020). Unlike SIF, which depends on fluctuating sunlight and changing sun–canopy–sensor geometry, actively measured ChlF relies on the use of controlled artificial excitation light sources at constant intensity (e.g., LEDs or LASERS) and fixed canopy-sensor geometry, providing measurements at the canopy scale of the variability of the apparent ChlF yield (Moya et al., 2019; Balde et al., 2024; Flexas et al., 2002; Loayza et al., 2023), which is directly proportional to Φ_F . Thus, active ChlF measurements can more directly capture physiological responses, notably the rapid adjustments in NPQ that occur during stress events (Balde et al., 2024; Moya et al., 2019, 2023). For instance, Rosema et al. (1998) combined measurements of LIF and CO₂ exchange and found that the fluorescence yield rose fast after sunrise, but declined below the nighttime fluorescence under high radiation and high temperature conditions. They attributed this extremely strong quenching of fluorescence to photosystem deactivation. Flexas et al. (2002) found that the ratio of steady state chlorophyll fluorescence (LIF signal measured by FIPAM system) normalized to dark-adapted intrinsic fluorescence inversely correlated with NPQ and positively correlated with CO₂ assimilation under strong illumination, providing a good method for early detection of water stress for C3 plants.

This study aims to investigate how atmospheric dryness—elevated VPD conditions during heat waves—affects the relationship between ChlF signals and GPP. To this end, we integrated LIF measurements with passive SIF measurements. We refer to the LIF signal as F_{yieldLIF} to emphasize that, in our configuration (constant excitation light intensity and illumination-viewing geometry), it is a measure of the apparent ChlF yield. Our study was conducted in a mixed temperate deciduous broadleaf forest in the north of France. A 35-m-high flux tower has been used to measure gas and energy exchanges, SIF, F_{yieldLIF} , and ancillary environmental variables. To better disentangle the environmental and physiological drivers of ChlF–photosynthesis relationships, our analysis follows a stepwise approach. First, we examine the raw relationships among SIF, GPP, and F_{yieldLIF} under different atmospheric dryness conditions to characterize their general responses. Second, to reduce the confounding influence of radiation, we normalize SIF and GPP by the incident Photosynthetically Active Radiation (PAR), obtaining SIFy and GPPy, which better highlight their physiological component. This enables a more direct comparison with F_{yieldLIF} , which more directly reflects physiological regulation. Finally, to further investigate the mechanistic underpinning of ChlF changes, we introduced, in our analysis, an estimate of the maximum CO₂ assimilation rate (A_{max}) at the canopy scale under saturating irradiance conditions, using a light-response photosynthesis model based on GPP and PAR measurements. This allowed us to have a representative parameter of the plant's maximum photosynthetic potential that is completely independent of the PAR, which is not the case of GPP and even of GPPy. This tiered framework provides a more complete understanding of the decoupling between SIF and GPP under atmospheric stress.

Focusing on the 2022 West European heatwaves, we address three specific research questions: (1) How does atmospheric dryness affect the relationships among SIF, GPP, and F_{yieldLIF} ? (2) To what extent can normalization by radiation (SIFy and GPPy) clarify physiological versus radiative controls on the ChlF–GPP relationships? And (3) can F_{yieldLIF}

and/or SIFy effectively capture photosynthetic capacity limitations under stress, as reflected in A_{max}?

2. Materials and methods

2.1. Site description

The study site, Fontainebleau-Barbeau forest site (FR-Fon, 48°28'26" N, 2°46'57" E, <https://barbeau.ese.cnrs.fr>), is located 53 km southeast of Paris, France. It is a mixed temperate deciduous broadleaf forest, in which 79 % of the basal area are sessile oaks (*Quercus petraea* (Matt.) Liebl.) and 18 % of the basal area are hornbeam (*Carpinus betulus* L.) occupying the understory (Maysonnave et al., 2022). Tree species such as *Pinus sylvestris* L., *Sorbus torminalis* (L.) Crantz, *Corylus avellana* L., and *Mespilus germanica* L. are sparsely distributed throughout the stand, comprising less than 3 % of the total basal area (Delpierre et al., 2016).

FR-Fon is a fairly productive stand, with the dominant species averaging about 25 m in height (Balde et al., 2024). Using the litter collection method, the average stand leaf area index (LAI) measured from 2012 to 2018 is 5.8 m² m⁻², with values ranging from 4.6 to 6.8 m² m⁻² (Soudani et al., 2021). Long-term (1980–2010) mean annual temperature and precipitation are 11.2 °C and 677 mm, respectively (Delpierre et al., 2016).

An Eddy Covariance (EC) flux observation system has been installed on a 35-m high tower at the site since 2005 to collect energy, water vapor and CO₂ fluxes (Delpierre et al., 2016). FR-Fon is one of the French sites belonging to the European ICOS (Integrated Carbon Observation System) research infrastructure. Various proximal sensors for high spectral resolution light measurements and micrometeorological sensors are also installed on the tower and around.

2.2. Passive fluorescence measurements: SIF

Passive fluorescence, namely SIF, was measured using the SIF3 instrument, which is a laboratory-made automated equipment (Balde et al., 2024). SIF3 is equipped with a high-spectral resolution spectrometer (HR1-T model, ASEQ instruments, Vancouver, Canada) with a spectral-range of 658 to 800 nm and a ~ 0.3 nm full width at half maximum (FWHM) resolution. It also includes a broadband spectrometer (LR1-T model, ASEQ instruments, Vancouver, Canada) with a spectral-range of 400 to 1000 nm and a ~ 1.5 nm FWHM resolution. The main components of the SIF3 system (Fig. 1) are: two spectrometers, a computer for system control (LattePanda V1, LattePanda Shanghai, China, and two Arduino microcontrollers), two optical shutters and their controllers, two bare optical fibers, a reference panel with a drive motor, and several sensors for measuring PAR, inside temperatures and relative humidity. For measurement stability and reducing noise and dark current (DC), the system is enclosed in a dry and thermostatic box (19 ± 0.61 °C).

A sequential measurement of SIF3 consists of four steps. First, the downwelling radiance of sunlight is measured using a servomotor-driven reference panel (PMR10P1, Thorlabs, Maisons-Laffitte, France) with the HR1-T and LR1-T spectrometers. Second, the reference panel is rotated 90 degrees so that the optical fibers face the forest canopy. Third, the upwelling radiance reflected by the canopy is measured with both spectrometers. Fourth, the reference panel is rotated 90 degrees back so that the optical fibers face the reference panel again.

During each measurement of the target canopy or the reference, each spectrometer undergoes three sub-steps. First, the integration time (IT) is automatically optimized for each measurement. Second, the digital number (DN) values are recorded by the spectrometer to get the spectra. Third, the shutters are closed and the DN values are recorded with the same IT to get the dark noise to be subtracted to the spectra. The field of view (FOV) of the optical fibers are 25°, ensuring an approximate 6 m² footprint on the canopy at a fiber-to-canopy distance of around 6 m (Fig. 1). A detailed description of SIF3 is reported in Balde et al. (2024).

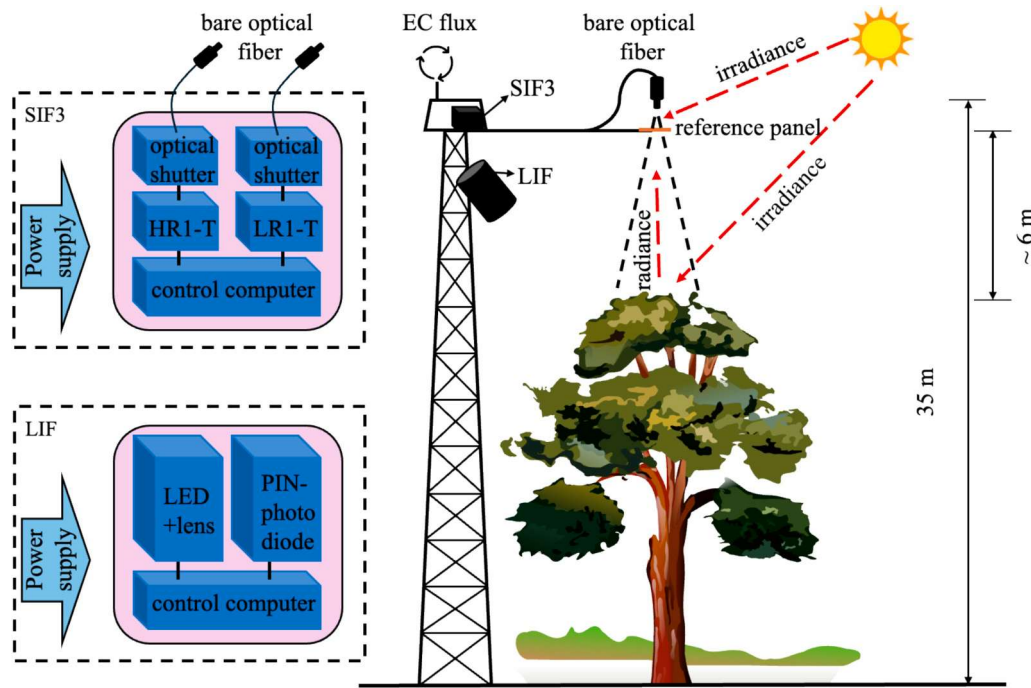


Fig. 1. The schematic diagram of the two instruments (SIF3 and LIF) and of their installation at the Barbeau forest site.

The HR1-T spectrometer was employed to measure SIF, which was retrieved at the O₂-A band using the three-band Fraunhofer Line Discrimination (3FLD) algorithm (Meroni et al., 2009; Balde et al., 2024).

2.3. Active fluorescence measurements: F_{yieldLIF}

Active fluorescence measurements, namely apparent ChlF yield (F_{yieldLIF}), was recorded using the LIF instrument. This instrument has been developed by the Laboratoire de Météorologie Dynamique (LMD, École Polytechnique, France). It is a similar version of the instrument described by Moya et al. (2019). However, the LIF uses a 6-W-modulated blue array LED (ENFIS Ltd., Swansea, UK) with a 5-μs pulse duration, a peak-wavelength at 455 nm and FWHM of 25 nm. A Fresnel-lens (diameter 180 mm) was used to collimate the excitation light. The detection module of the LIF is also based on a Fresnel-lens with the same diameter. A PIN-photodiode (10 × 10 mm², S3590, Hamamatsu Photonic, Japan) with a set of optical filters in front and mounted on a laboratory-made (LMD) amplifier extracts the LED-induced fluorescence signal (F_{yieldLIF}) from the ambient light. The optical filter set combines a high-pass interferential filter with a 400 nm cut-off wavelength to block UV light, a high-pass interferential filter with a 650 nm cut-off wavelength to block the excitation light, and a 3 mm thick RG9 filter (Schott, Germany) to isolate the far-red fluorescence emission above 725 nm. The LIF instrument was mounted next to the SIF3 one, at the top of the 35-m tower, with a smaller optical footprint than that of SIF3 on the forest canopy. The FOV of LIF is checked using an onboard camera (RLC-520 A, Reolink, Hong-Kong). We targeted LIF at the top-of-canopy within the FOV of SIF3 with a viewing zenith angle (VZA) of 30°, resulting in a 0.4 m² FOV (approximately 100 mrad). A detailed description of LIF is reported in Balde et al. (2024).

2.4. Eddy Covariance gas fluxes and environmental variables measurements

Carbon, water, and energy exchange fluxes between the forest and the atmosphere were acquired on the top of the 35-m tower at FR-Fon site. The primary flux measurement instrument consisted of a Li7500

open-path and a Li7200 enclosed-path infrared gas analyser (Li-Cor Inc., Lincoln, Nebraska, USA), associated with a R3-50 and a HS-50 three-dimensional sonic anemometer (Gill Instruments Ltd., Lymington, Hampshire, UK), respectively (Maysonnave et al., 2022). Half-hourly fluxes of CO₂ and H₂O were derived with EddyPro software (v7.0.6, Li-cor Inc., Lincoln, Nebraska, USA). The additional enclosed-path gas analyser Li7200 and sonic anemometer HS-50 were used to gap fill the main time series of fluxes data. The derived fluxes underwent quality control, gap filling, and were partitioned into GPP and ecosystem respiration (R_{eco}) using the night-time algorithm (Delpierre et al., 2016; Reichstein et al., 2005). Air temperature (T_a) and relative humidity used to calculate the VPD were recorded using a HMP155Ax6 thermohygrometer (Vaisala Group., Helsinki, Finland) from bottom to top of the tower. Total incident PAR above the canopy (PAR), total PAR reflected by the canopy ($\text{PAR}_{\text{reflected}}$), understory PAR ($\text{PAR}_{\text{transmitted}}$) were measured at high frequency (1-min interval) by three identical sensors (PQS1 PAR Quantum Sensor (OTT Hydromet (formerly Kipp&Zonen), The Netherlands)). The fraction of PAR absorbed by the canopy (f_{APAR}) was derived as follows:

$$f_{\text{APAR}} = \frac{\text{PAR} - \text{PAR}_{\text{reflected}} - \text{PAR}_{\text{transmitted}}}{\text{PAR}} \quad (1)$$

In addition, diffuse ($\text{PAR}_{\text{diffuse}}$), and total radiation ($\text{PAR}_{\text{total}}$) were measured using a BF5 sunshine sensor (Delta-T Devices Ltd. UK). The diffuse fraction of radiation ($\text{PAR}_{\text{diffuse}}/\text{PAR}_{\text{total}}$) was computed to represent the diffuse radiation conditions in this study. Other environmental variables were synchronously collected and processed every half an hour, including precipitation (ARG100 rain gauge, EML, North Shields, UK) and soil water content (SWC) (Enviroscanx4, Sentek Tech., Stepney, Australia).

2.5. High atmospheric dryness and no atmospheric dryness

Time intervals (always one or several entire days) of High Atmospheric Dryness (HAD) conditions and No Atmospheric Dryness (NAD) conditions were carefully extracted from the entire growing season (day-of-year (DOY) ranged from 104 to 260) according to extreme air temperature and VPD variations. Two explicit criteria were used together to

define the HAD periods: (1) a continuous increase in Ta and VPD, culminating in a VPD peak, and (2) a daily maximum VPD exceeding 3.0 kPa. At last, five periods were selected as HAD conditions, namely DOY 168, 193–194, 198–199, 215, and 221–225 (11 days, Fig. 3, red shaded stripes). To minimize the influence of SWC variability, we selected NAD data temporally close to each HAD interval, ensuring similar SWC levels between HAD and NAD data. We selected two consecutive days immediately following the HAD period with no rainfall and confirmed that the average VPD remained below 1.0 kPa, indicating very low atmospheric dryness. Finally, four periods were selected out: DOY 170–171, 202–203, 217–218, and 230–231 (8 days, Fig. 3, blue shaded stripes). Moreover, our study period spans from DOY 150 to DOY 254—including 80 effective days used for the ALL DATA analysis (grey stripes in Fig. 3)—which fully encompasses the duration for which F_{yieldLIF} data were available.

In addition, to evaluate the differences in environmental variables between HAD and NAD periods and assess their statistical significance, we first applied Shapiro–Wilk tests to assess the normality of each variable. Given that most variables did not meet the assumption of normality, we subsequently used non-parametric Mann–Whitney U tests to compare the two periods.

2.6. Phenological variations

In order to assess potential variations in canopy structure and chlorophyll content, reflectance-based vegetation indices along with the f_{APARchl} were used. The Normalized Difference Vegetation Index (NDVI; Tucker, 1979) and the modified red-edge Normalized Difference Index (mNDI₇₀₅; Datt, 1999) are widely recognized as indicators of canopy structural properties and chlorophyll content, respectively. Their relevance to these canopy properties have been previously validated at the Barbeau forest site (Hmimina et al., 2014). These indices were calculated using the following formulas:

$$\text{NDVI} = \frac{\rho_{\text{nir}} - \rho_{\text{red}}}{\rho_{\text{nir}} + \rho_{\text{red}}} \quad (2)$$

$$\text{mNDI}_{705} = \frac{\rho_{750} - \rho_{705}}{\rho_{750} + \rho_{705} - 2 \times \rho_{445}} \quad (3)$$

where ρ_{nir} and ρ_{red} represent the averaged canopy reflectance at 780–800 nm and 670–680 nm, respectively. ρ_{445} , ρ_{705} and ρ_{750} represent the canopy reflectance integrated over a 25 nm waveband centred at 445, 705 and 750 nm, respectively.

2.7. Hypotheses and data analysis

The basic equations for canopy GPP, SIF, F_{yieldLIF} in terms of its mechanistic components were given as Eqs. (4a)–(4c).

$$\text{GPP} = \text{PAR} \times f_{\text{APARchl}} \times \phi_P \quad (4a)$$

$$\text{SIF} = \text{PAR} \times f_{\text{APARchl}} \times f_{\text{esc}} \times \phi_F \quad (4b)$$

$$F_{\text{yieldLIF}} = I_{\text{LED}} \times f_{\text{LAPARchl}} \times f_{\text{Lesc}} \times \phi_F \quad (4c)$$

where f_{APARchl} is the fraction of PAR absorbed by the chlorophyll in the canopy (Zhang et al., 2014). ϕ_P is the photosynthetic light use efficiency of leaves in the canopy, namely the quantum yield of photosynthesis. ϕ_F is the quantum yield of ChlF of leaves in the canopy and f_{esc} is the fraction of emitted SIF that escapes from the canopy (Guanter et al., 2014; Zeng et al., 2019). Similarly, I_{LED} represents the irradiance of the LED pulse, f_{LAPARchl} and f_{Lesc} represent the fraction of the LED pulse absorbed by the chlorophyll throughout the canopy and the fraction of all ChlF photons induced by the LED that escape from the canopy. To reduce the confounding effects of radiation and better isolate the physiological signal, we normalize SIF and GPP by the incident PAR,

resulting in SIF_y and GPP_y. This normalization (Eqs. (5a), (5b)) facilitates a more meaningful comparison with F_{yieldLIF} , which is not directly dependent on ambient light conditions (i.e. PAR), cf. Eq. (4c).

$$\text{GPP}_y = \frac{\text{GPP}}{\text{PAR}} = f_{\text{APARchl}} \times \phi_P \quad (5a)$$

$$\text{SIF}_y = \frac{\text{SIF}}{\text{PAR}} = f_{\text{APARchl}} \times f_{\text{esc}} \times \phi_F \quad (5b)$$

The f_{APARchl} and f_{esc} may vary with canopy structure (e.g. leaf angle) and chlorophyll content, as well as illumination geometry (e.g. sun angle and diffuse radiation fraction). Thus, the variations of f_{APARchl} and f_{esc} can be considered as a source of uncertainty for estimation of ϕ_P and ϕ_F using GPP_y and SIF_y. However, given the fixed intensity of the LED excitation source (i.e., I_{LED} is constant), the fixed LIF instrument to canopy geometry and the stable canopy, f_{LAPARchl} and f_{Lesc} can be regarded as constant throughout the study period. Thus, Eq. (4c) can thus be simplified to Eq. (6) (Fig. 2), where k is a constant that combines the effects of I_{LED} , f_{LAPARchl} and f_{Lesc} .

$$F_{\text{yieldLIF}} = k \times \phi_F \quad (6)$$

Then SIF_y can be expressed as:

$$\text{SIF}_y = \frac{(f_{\text{APARchl}} \times f_{\text{esc}})}{k} \times F_{\text{yieldLIF}} = \phi_k \times F_{\text{yieldLIF}} \quad (7)$$

ϕ_k is the ratio between SIF_y and F_{yieldLIF} , which represents the confounding effect due to the canopy structure, f_{APARchl} and f_{esc} , as defined in Balde et al. (2024).

Because GPP_y still depends on PAR, since the relationship between the two is not linear, and in order to completely remove the influence of PAR variations on GPP and further investigate the mechanisms underlying fluorescence changes under stress conditions, we incorporated A_{max} —the maximum photosynthetic rate—into our analysis. This allowed us to evaluate whether F_{yieldLIF} or SIF_y can more effectively track stress-induced limitations in photosynthetic capacity. A_{max} was derived using a photosynthetic light-response curve fitting model (Baly, 1935). The photosynthetic light-response curve model is expressed as Eq. (8):

$$\text{GPP} = \frac{\alpha \times \text{PAR} \times A_{\text{max}}}{\alpha \times \text{PAR} + A_{\text{max}}} \quad (8)$$

where α is the slope of the light-response curve at low light intensity. A_{max} and α were estimated using a least-squares method. A moving window of 5 days was selected in order to alleviate the influence of diurnal variations of GPP and PAR and improve the robustness and significance of the fitting model. For instance, the photosynthetic light-response fitting model of DOY 172 was conducted using half-hourly data from DOY 170, 171, 172, 173, and 174. In addition, specific days with particular abiotic conditions were selected to minimize the influence of diffuse radiation on analysis of differences between F_{yieldLIF} and SIF_y in detecting plant responses to high atmospheric dryness. Based on thresholds on the diffuse ratio of incident radiation (Alton, 2008; Li et al., 2020) and on the VPD (Fig. S1), three specific conditions were identified: (1) cloudy and low VPD ($\text{PAR}_{\text{diffuse}}/\text{PAR}_{\text{total}} > 0.6$ and $\text{VPD} < 1$ kPa), (2) clear sky and medium VPD ($\text{PAR}_{\text{diffuse}}/\text{PAR}_{\text{total}} < 0.3$ and 1 kPa $< \text{VPD} < 2$ kPa), and (3) clear sky and high VPD ($\text{PAR}_{\text{diffuse}}/\text{PAR}_{\text{total}} < 0.3$ and $\text{VPD} > 2$ kPa).

The main objective of this study is to disentangle how atmospheric dryness, particularly elevated VPD during heat waves, alters the relationships between chlorophyll fluorescence and photosynthesis at the canopy scale. Specifically, we aim to:

1. Assess whether the traditionally strong correlation between SIF and GPP weakens under high VPD, reflecting the increasing role of NPQ in decoupling fluorescence from photosynthesis.

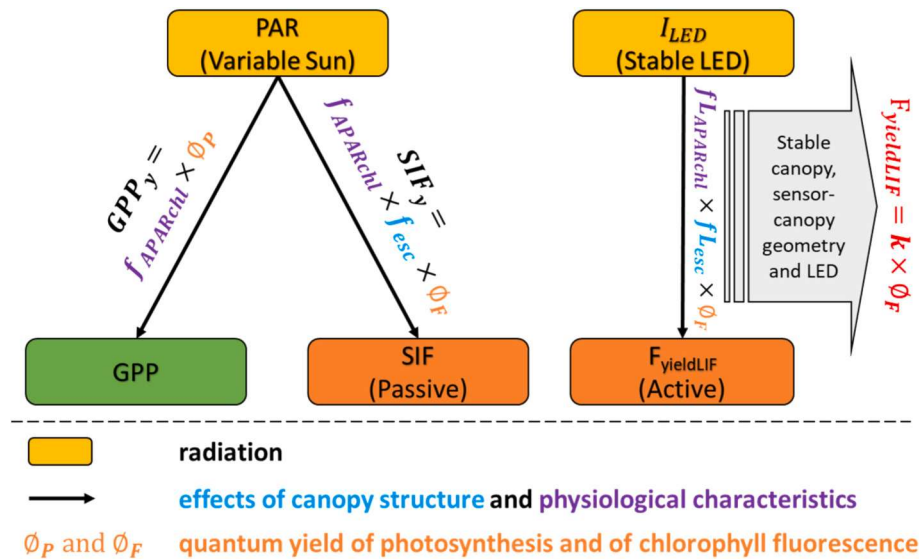


Fig. 2. Overview of the conceptual meaning of GPP, SIF, F_{yieldLIF} and relevant variables. All terms are given at the canopy scale. f_{APARchl} is the fraction of absorbed PAR by the chlorophyll in the canopy. ϕ_P is the photosynthetic light use efficiency of leaves in the canopy (quantum yield of photosynthesis). ϕ_F is the quantum yield of ChlF of leaves in the canopy and f_{esc} is the fraction of emitted SIF that escapes from the canopy. I_{LED} represents the irradiance of the LED pulse, f_{LAPARchl} represents the fraction of the LED pulse absorbed by the chlorophyll throughout the canopy, and f_{Lesc} represents the fraction of all ChlF photons induced by the LED that escape from the canopy. Grey arrows represent stable canopy, fixed LIF sensor-canopy geometry, and constant LED intensity during the study period, indicating constant f_{LAPARchl} and f_{Lesc} .

- Examine whether canopy-level active fluorescence (F_{yieldLIF}), by directly capturing ϕ_F , provides a more robust proxy of GPPy than SIFy, particularly under stress conditions.
- Evaluate the extent to which F_{yieldLIF} and SIFy track photosynthetic capacity (A_{max}), and test the hypothesis that F_{yieldLIF} more sensitively detects stress-induced declines in A_{max} , thereby offering greater mechanistic insight into vegetation responses.

In this study, measurements were analyzed from April to mid-September 2022. SIF and F_{yieldLIF} data were averaged at half-hour intervals from 7:00 to 18:00 UTC each day, aligned with the half-hour EC flux data. All data collected this way were used for half-hourly analysis, while daily mean values were calculated for daily analysis. The coefficient of determination (R^2) and the p -value were used to evaluate the strength and the significance of the relationships between variables. SIF retrieval and photosynthetic light-response curve fitting were carried out with Matlab R2021a (MathWorks, Inc., USA). Statistical analyses and visualizations were performed using Python 3.9.6 (Python Software Foundation, USA).

3. Results

3.1. Environmental differences, soil water availability, and phenological stability

We found that environmental conditions significantly differed between the HAD and NAD periods (Fig. S2A), with PAR, Ta, and VPD all showing higher values under HAD conditions ($p < 0.05$). Regarding SWC, we compared its values between HAD and NAD periods only at the daily scale, since substantial intra-day variation in SWC is not expected. The results showed no significant difference in SWC between HAD and NAD conditions (Fig. S2B). The minimum SWC observed during the measurement period was around $0.26 \text{ cm}^3/\text{cm}^3$ (Fig. S2B). The temporal dynamics of NDVI, mNDI₇₀₅, and f_{APAR} at both half-hourly and daily scales (Fig. S3) were analyzed to assess potential phenological changes during the study period. All three indices showed stable trends, with Coefficients of Variation (CV) below or equal to 0.03 for both half hourly and daily scales.

3.2. Seasonal and diurnal variations of SIF, F_{yieldLIF} , GPP and environmental variables

The deciduous forest canopy of FR-Fon exhibited noticeable seasonal variations in GPP (Fig. 3f) and SIF (Fig. 3g) due to changes in PAR and plant phenology. Specifically, both GPP and SIF reached their highest values in the early growing season (mid-June) when the canopy nearly achieved its maximum development (Fig. 3f & g). They remained relatively high when PAR was stable and high but decreased significantly during periods of low light intensity until mid-July (Fig. 3a, f & g). Finally, they gradually declined for the remainder of the season due to decreasing PAR (Fig. 3a, f & g). SWC decreased throughout the growing season, with only occasional increases following precipitation events (Fig. 3c & d). VPD showed similar variations to Ta (Fig. 3e and b). F_{yieldLIF} data, collected from the beginning of June, showed a generally decreasing trend over the season (Fig. 3h). A relatively stable NDVI was observed during the entire observation period after the canopy was closed and so during the HAD and NAD periods (Fig. 3h).

Diurnal patterns of GPP and SIF corresponded well to the pattern of PAR under NAD conditions but not for GPP under HAD conditions (Fig. 4). Under NAD conditions, GPP exhibited a unimodal diurnal pattern, increasing in the morning, peaking around noon, and gradually decreasing in the afternoon (Fig. 4e). However, under HAD conditions, GPP showed an advanced peak around 8:30 am (UTC) compared to PAR and SIF (Fig. 4e). SIF exhibited similar depressions in the morning under both HAD and NAD conditions (Fig. 4f). Meanwhile, VPD reached its maximum for the day in the late afternoon (around 4:00 pm) under both HAD and NAD conditions, with significantly higher values under HAD (Fig. 4c). During NAD, F_{yieldLIF} remained relatively stable. However, during HAD, it continuously decreased from 7:00 am, reaching its minimum around 4:00 pm, and then stabilized (Fig. 4g). Diurnal variations of SWC were not observed. There was only a non-significant difference in mean values between HAD and NAD (Fig. 4b). Regarding the apparent yield of SIF and GPP, represented as SIFy and GPPy, there were obvious fluctuations in SIFy (Fig. 4d) compared to the variation of GPPy under both HAD and NAD conditions (Fig. 4h). SIFy values were relatively lower under HAD conditions compared to NAD conditions, which was consistent with GPPy (Fig. 4d and h).

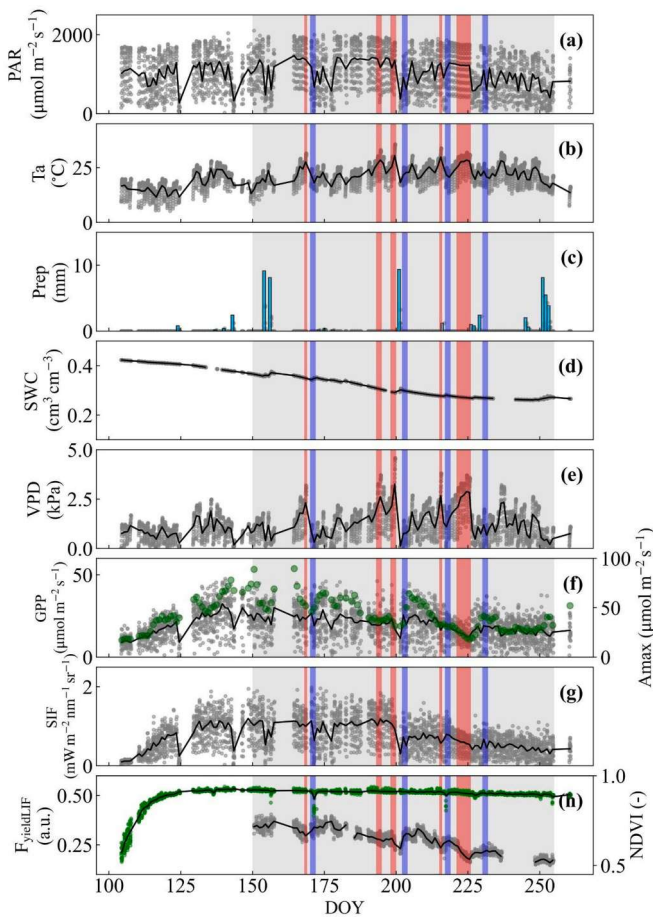


Fig. 3. Seasonal variations of (a) Photosynthetically Active Radiation (PAR), (b) air temperature (Ta), (c) precipitation (Prep), (d) Soil Water Content (SWC), (e) Vapor Pressure Deficit (VPD), (f) Gross Primary Productivity (GPP, represented in grey) and the maximal rate of photosynthesis (Amax, represented in green), (g) Sun-Induced chlorophyll Fluorescence (SIF), and (h) apparent ChlF yield (F_{yieldLIF} , represented in grey) and Normalized Difference Vegetation Index (NDVI, represented in green). Grey (or green) dots and black lines in each panel represent half-hour data (from 7:00 to 18:00 UTC) and daily mean data, respectively. The blue bars in (c) represent the accumulated precipitation for each day. The red, blue, and grey stripes indicate periods of High Atmospheric Dryness (HAD), No Atmospheric Dryness (NAD), and the whole study period (ALL DATA), respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3.3. Responses of SIF, F_{yieldLIF} and GPP to changing VPD

The influence of VPD on SIF, GPP, and F_{yieldLIF} varied at different temporal scales as shown in Fig. 5. At the half-hourly scale, the relationship between SIF and VPD is not monotonic. A bell-shaped curve, positive up to a certain threshold and decreasing thereafter, was observed. In contrast, GPP and F_{yieldLIF} showed a slight decreasing trend with increasing VPD, depicting a negative correlation with VPD (Fig. 5). At the daily scale, the aforementioned correlations remained consistent except for the relationship between SIF and VPD under HAD conditions (Fig. 5). Under HAD conditions, a negative correlation was observed for SIF and VPD at the daily scale (Fig. 5a). This suggests that at a lower time resolution, the effect of diurnal variations is minimized, revealing a negative effect of VPD on SIF under HAD conditions.

3.4. Relationships among PAR, SIF, F_{yieldLIF} and GPP

We examined the correlations between SIF and PAR, GPP and SIF, F_{yieldLIF} and SIF, and F_{yieldLIF} and GPP under HAD, NAD, and ALL DATA

conditions at two different time resolutions, the half-hourly scale (Fig. 6) and the daily scale (Fig. 7). We applied non-linear regressions for the relationships between SIF and PAR, and GPP and SIF due to their known saturation behavior (Zhang et al., 2016; Wang et al., 2023; Kim et al., 2021; Martini et al., 2022). In contrast, linear regressions were used for F_{yieldLIF} and SIF, and GPP and F_{yieldLIF} since F_{yieldLIF} is light-independent and the point plots exhibited approximately linear trends without saturation. Generally, positive correlations were observed between these variables, except for the correlations between F_{yieldLIF} and SIF and between F_{yieldLIF} and GPP under NAD conditions, which showed no specific patterns (Fig. 6g and h). The effect of atmospheric dryness on these relationships was significant. Specifically, the highest correlation between SIF and PAR was found under NAD conditions ($R^2 = 0.71$, Fig. 6e), while the lowest correlation was under HAD conditions ($R^2 = 0.45$, Fig. 6a). The correlation was intermediate when ALL DATA were considered ($R^2 = 0.67$, Fig. 6i). Similar differences in correlation were found for GPP and SIF under HAD ($R^2 = 0.17$, Fig. 6b), NAD ($R^2 = 0.49$, Fig. 6f), and ALL DATA conditions ($R^2 = 0.40$, Fig. 6j). The correlations between F_{yieldLIF} and SIF and between F_{yieldLIF} and GPP were relatively lower than those between SIF and PAR and between GPP and SIF. However, a slight but significant relationship was observed between F_{yieldLIF} and SIF ($R^2 = 0.17$, Fig. 6c) under HAD condition. A relationship was observed between F_{yieldLIF} and GPP ($R^2 = 0.43$, Fig. 6d) under HAD condition. These relationships did not hold under NAD conditions (Fig. 6g and h).

Significant differences were found when upscaling from half-hourly to daily scale as shown in Fig. 7. The correlations between F_{yieldLIF} and SIF and between F_{yieldLIF} and GPP under HAD conditions improved markedly, with R^2 increasing from 0.17 to 0.78 (Figs. 6c and 7c) and from 0.43 to 0.90 (Figs. 6d and 7d), respectively. Similar improvements were observed for the ALL DATA condition, with R^2 increasing from 0.17 to 0.50 (Figs. 6k and 7k) and from 0.21 to 0.65 (Figs. 6l and 7l), respectively. A non-linear relationship was observed between GPP and SIF, whereas the relationship between SIF and PAR appeared to be more linear. The other correlations in Fig. 7 were not significant.

3.5. Relationships among SIFy, GPPy, F_{yieldLIF} and Amax

Correlations among GPPy, SIFy and F_{yieldLIF} , under different atmospheric dryness conditions were further analyzed at both the half-hourly scale and the daily scale (Figs. 8 and 9). We applied linear regressions for the relationships among GPPy, SIFy, and F_{yieldLIF} since GPPy and SIFy are already normalized by incident light (PAR), and no obvious saturation pattern was observed. At the half-hourly scale, GPPy showed no obvious correlation with SIFy under both HAD and NAD conditions ($R^2 < 0.1$, Fig. 8a, e). However, a weak correlation was observed between GPPy and F_{yieldLIF} under HAD conditions ($R^2 = 0.34$, Fig. 8c). At the daily scale, both the GPPy-SIFy and GPPy- F_{yieldLIF} relationships exhibited a stronger correlation under HAD conditions, reaching $R^2 = 0.74$ (Fig. 8b, d).

In addition, after standardization of GPP by PAR, a slight decrease in the correlation between F_{yieldLIF} and GPP was observed under HAD conditions at both the half-hourly scale (R^2 decreased from 0.43 to 0.34, Figs. 6d and 8c) and the daily scale (R^2 decreased from 0.90 to 0.74, Figs. 7d and 8d). In contrast, when SIF is standardized using PAR, a slight increase in the correlation between F_{yieldLIF} and SIF under HAD conditions was observed at the half-hourly scale (R^2 increased from 0.17 to 0.35, Figs. 6c and 9a), whereas a slight decrease was observed at the daily scale (R^2 decreased from 0.78 to 0.66, Figs. 7c and 9b). Similar trends in SIF correlations were also observed under NAD conditions and when analyzing ALL DATA conditions.

To investigate the differences between F_{yieldLIF} and SIFy in detecting plant responses to high atmospheric dryness, a photosynthetic light-response curve is fitted to data to derive Amax and α (Eq. (8)). The robustness of the fitting model is demonstrated in Fig. S4, showing a minimum and average R^2 value of 0.67 and 0.83, respectively, as well as

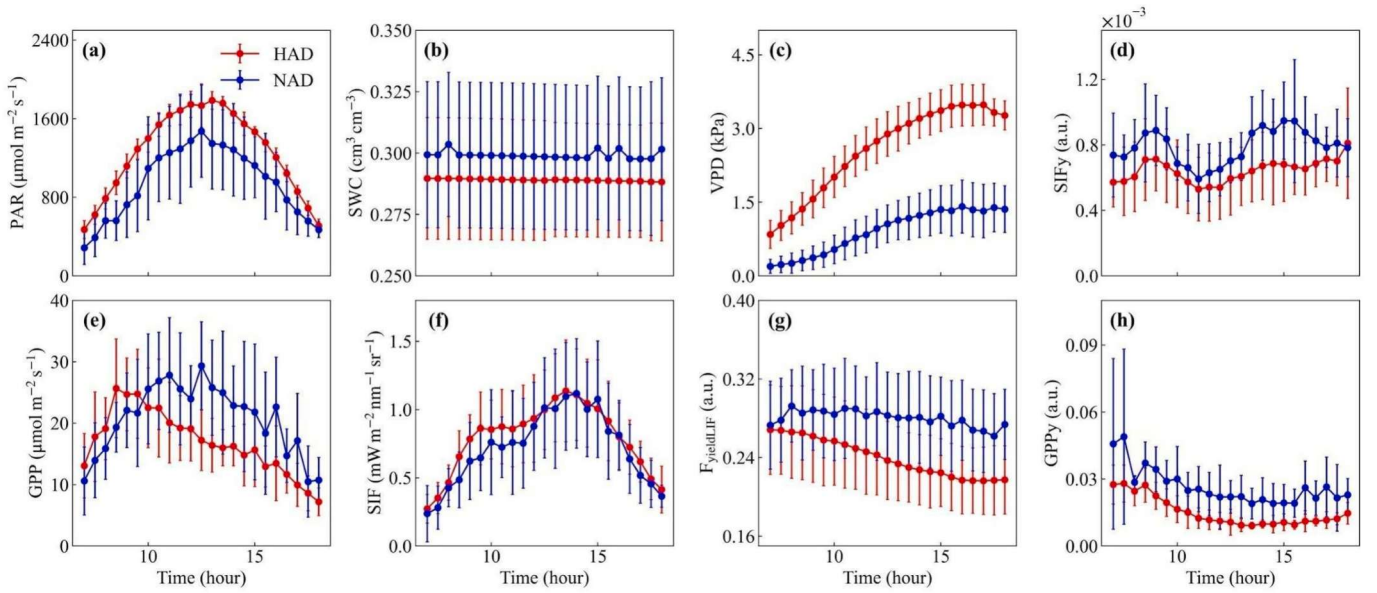


Fig. 4. Diurnal variations (from 7:00 to 18:00 UTC) of (a) PAR, (b) SWC, (c) VPD, (d) apparent SIF yield (SIFy = SIF/PAR), (e) GPP, (f) SIF, (g) F_{yieldLIF} , and (h) apparent GPP yield (GPPy = GPP/PAR). The red and blue dots represent mean values of data at each half-hour interval during periods of HAD and NAD, respectively. Error bars represent standard deviations. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

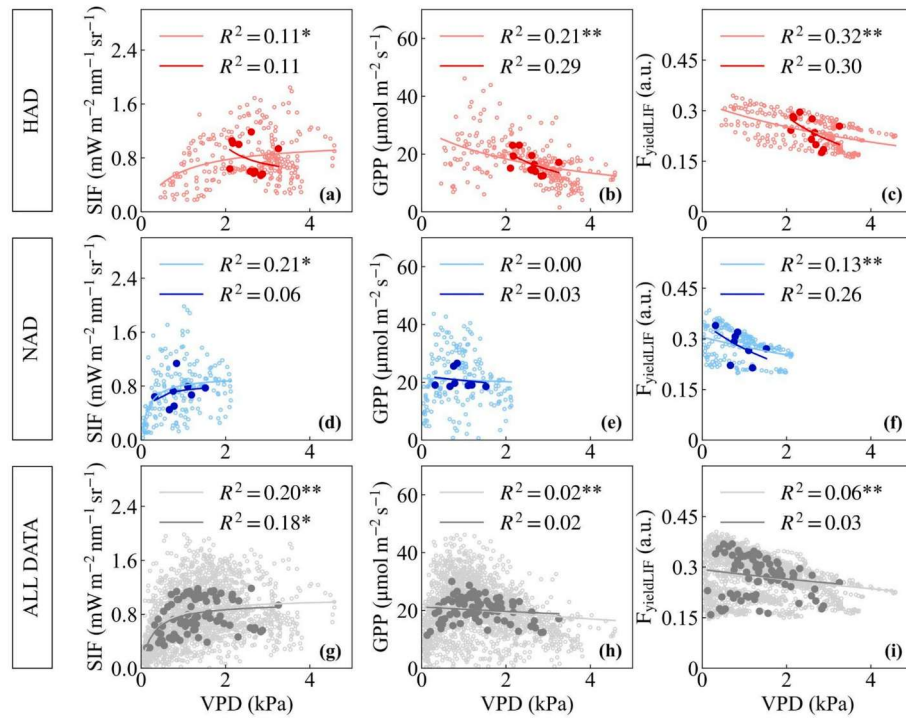


Fig. 5. Responses of SIF (a, d and g), GPP (b, e and h) and F_{yieldLIF} (c, f and i) to changing VPD at the half-hourly scale (hollow and light-colored circles) and daily scale (solid and darker circles). Red circles indicate data from periods of HAD and blue circles indicate data from periods of NAD. Grey circles represent data from the whole growing season (ALL DATA). Each line represents the non-linear regression. R^2 is the coefficient of determination (* for $p < 0.05$, ** for $p < 0.001$). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

a maximum and average RMSE of 6.67 and $4.56 \mu\text{mol m}^{-2} \text{s}^{-2}$, respectively. The correlations between Amax and F_{yieldLIF} , as well as between Amax and SIFy, under three specific conditions are presented in Fig. 10. Under cloudy and low VPD conditions, a slightly higher R^2 was observed for the correlation between Amax and F_{yieldLIF} ($R^2 = 0.61$, Fig. 10a) compared to that between Amax and SIFy ($R^2 = 0.55$, Fig. 10b). However, under clear sky and medium VPD conditions, a substantial difference was observed, with R^2 increasing from 0.19

(Amax and SIFy) to 0.50 (Amax and F_{yieldLIF}). A similar trend was observed under clear sky and high VPD conditions, where R^2 increased from 0.56 (Amax and SIFy) to 0.85 (Amax and F_{yieldLIF}). The highest correlation was observed between Amax and F_{yieldLIF} under clear sky and high VPD conditions ($R^2 = 0.85$, Fig. 10a). These results demonstrate a significantly stronger relationship between Amax and F_{yieldLIF} compared to Amax and SIFy, highlighting the advantages of F_{yieldLIF} in monitoring photosynthesis, particularly under conditions of high atmospheric

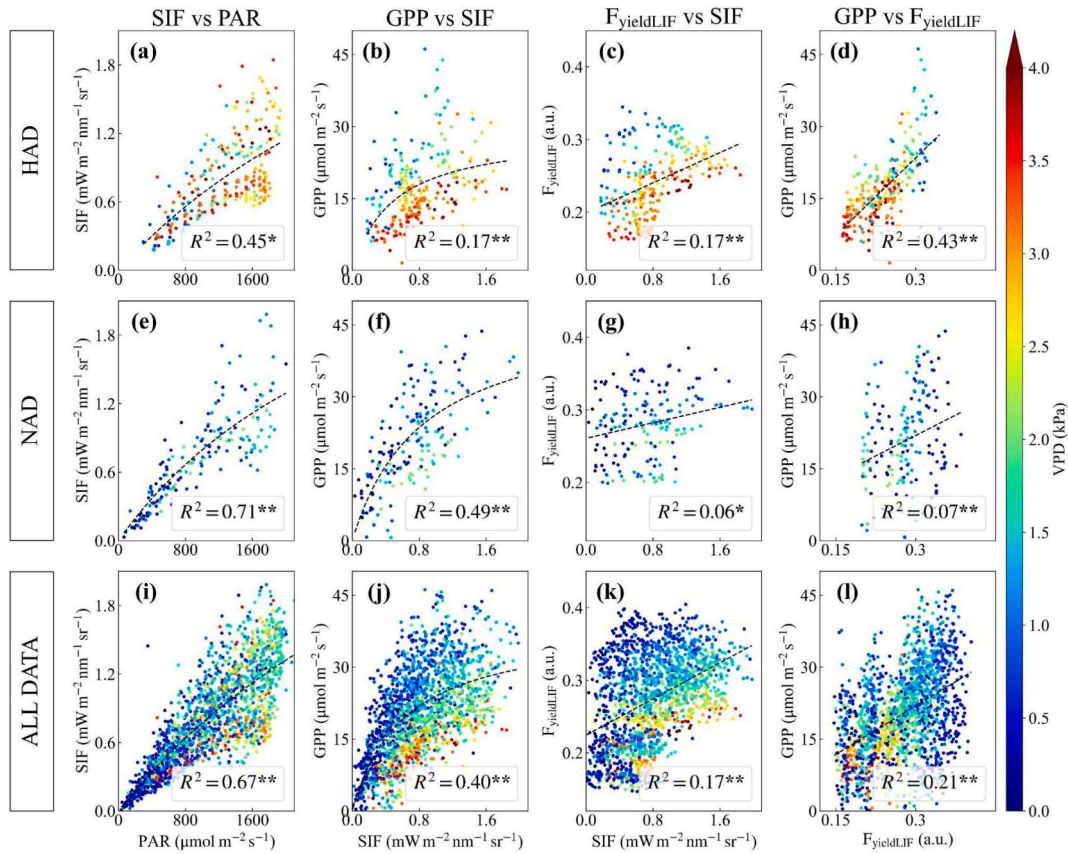


Fig. 6. Correlations between (a, e and i) SIF and PAR, (b, f and j) GPP and SIF, (c, g and k) F_{yieldLIF} and SIF and (d, h and l) F_{yieldLIF} and GPP for different conditions, HAD, NAD and ALL DATA, at the half-hourly scale with VPD values as a color scale. The dashed black line represents the non-linear or linear regression. R^2 is the coefficient of determination (* for $p < 0.05$, ** for $p < 0.001$).

dryness.

4. Discussion

Previous studies have underlined the importance of understanding the relationships between photosynthesis and chlorophyll fluorescence at canopy scale under extreme stress conditions, which is crucial for effectively leveraging proximal and remote sensing measurements of SIF in carbon cycle research (Martini et al., 2022; van der Tol et al., 2014). Our study investigated the effects of atmospheric dryness on canopy chlorophyll fluorescence, GPP as well as their relationships in a deciduous forest during the summer 2022 heat waves in the Northern of France. Specifically, we analyzed two ways of measuring chlorophyll fluorescence (i.e., active way, F_{yieldLIF} , and passive way, SIF) at different temporal scales (i.e., half-hourly and daily) in relation to photosynthesis under heat waves conditions. Our results showed that the R^2 of the relationship between SIF and GPP decreased with atmospheric dryness stress at the half-hourly scale, while it was improving with atmospheric dryness stress for the relationship between F_{yieldLIF} and GPP. Our findings revealed the difference between SIF and F_{yieldLIF} in detecting atmospheric dryness effects on GPP. Active fluorescence measurements F_{yieldLIF} , representing robust fluorescence yield information, showed more precise responses to plant heat stress than SIF.

4.1. Influences of environmental differences, soil water availability, and phenological stability

The significant differences in environmental conditions, combined with similar SWC levels between the HAD and NAD periods (Fig. S2), provide statistical support for the robustness of our classification criteria

(Section 2.5). The absence of significant differences in SWC further indicates that soil moisture remained relatively stable across both periods and was unlikely to be a limiting factor. In addition, the stable temporal dynamics of NDVI, mNDI705, and fAPAR (Fig. S3), with no apparent trends or abrupt shifts, confirm that canopy structure, chlorophyll content, and light absorption capacity did not undergo substantial phenological changes during the study period.

Soil moisture plays a critical role in evaluating the impacts of heat waves. Summer heat waves enhance evapotranspiration from both soil and vegetation, and when this increased atmospheric demand is not matched by sufficient soil water availability, it can result in concurrent drought stress (Rennenberg et al., 2006). Previous studies have demonstrated that both elevated VPD and low soil moisture significantly constrain plant photosynthesis (Wang et al., 2024; Qiu et al., 2023; Rennenberg et al., 2006). However, disentangling the individual effects of high VPD and low soil moisture remains challenging due to their often concurrent occurrence and interactive influences on plant physiological responses (Fu et al., 2022; Liu et al., 2020). In our study, however, soil water limitation was unlikely to be a stressor during the 2022 heatwave periods. The estimated Soil Water Holding Capacity (SWHC) based on the analysis of SWC measurements at the Barbeau forest site is approximately 390 mm within the upper 300 cm of soil (Maysonnave et al., 2022). According to Granier et al. (1999), water stress is assumed to occur when the Relative Extractable Water (REW) falls below 0.4, corresponding to about 156 mm of available water. In our study, the minimum SWC observed during the measurement period was around $0.26 \text{ cm}^3/\text{cm}^3$ in the upper 150 cm soil profile (Figs. 3 and S2B), which corresponds to approximately 260 mm of water. This value is well above the stress threshold, indicating that soil moisture was sufficient and unlikely to have limited plant functioning. For this reason we based our

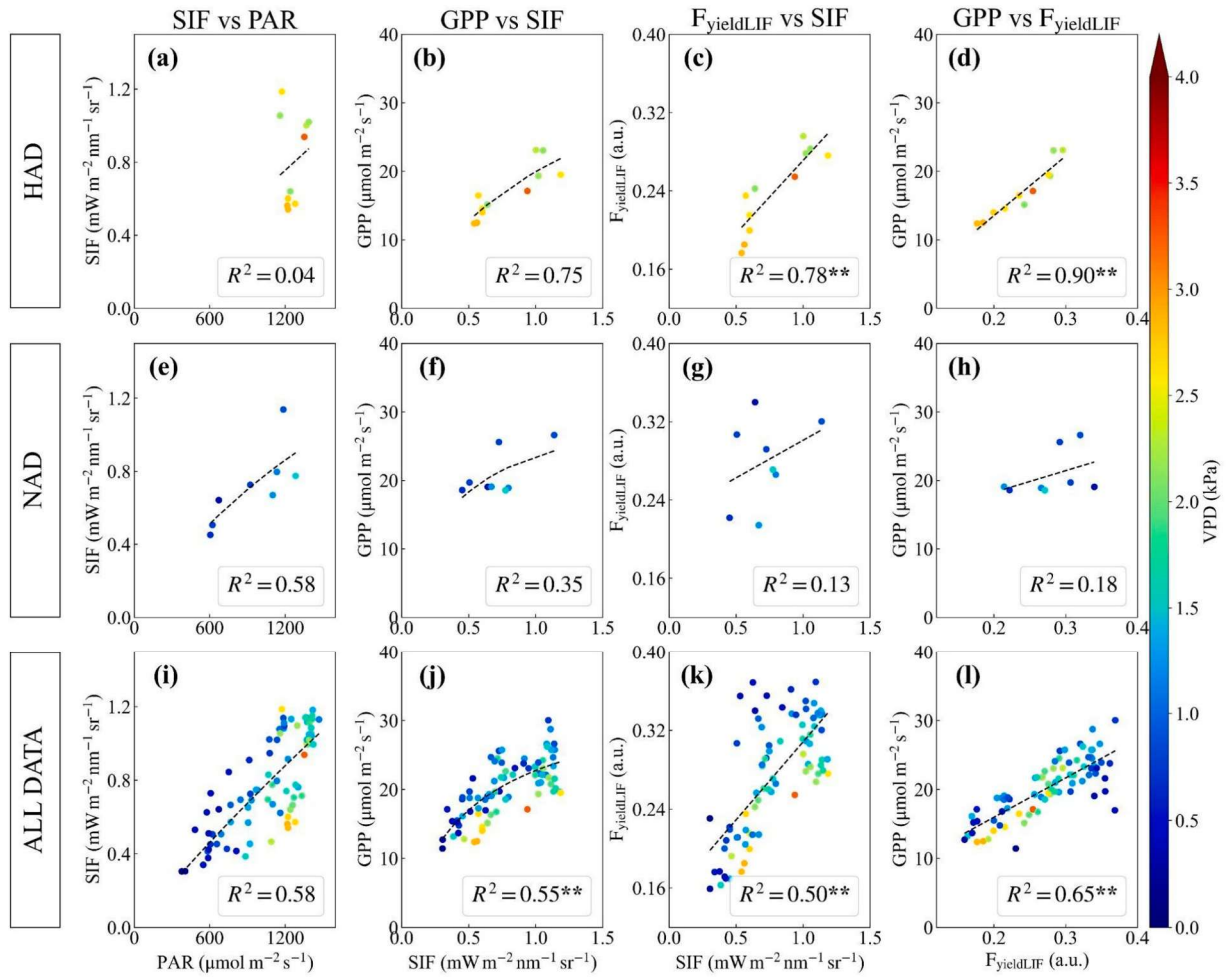


Fig. 7. Correlations between (a, e and i) SIF and PAR, (b, f and j) GPP and SIF, (c, g and k) F_{yieldLIF} and SIF and (d, h and l) F_{yieldLIF} and GPP for different conditions, HAD, NAD and ALL DATA, at the daily scale with VPD values as a color scale. The dashed black line represents the non-linear or linear regression. R^2 is the coefficient of determination (* for $p < 0.05$, ** for $p < 0.001$).

analysis on the assumption that the heat waves did not induce soil water deficit but lead to a clear atmospheric dryness (i.e., elevated VPD), which in this case would be the primary driver of the observed changes in ChlF and photosynthesis.

4.2. Effects of high atmospheric dryness on relationships between SIF and PAR, and SIF and GPP

The positive correlations between SIF and PAR demonstrated in our study are consistent with previous findings in various terrestrial ecosystems (Dechant et al., 2020; Goulas et al., 2017; Miao et al., 2018; Yang et al., 2018; Yang et al., 2015). This consistency can be attributed to the informational content of SIF, which includes the incoming solar radiations (PAR), the canopy structure (f_{esc}), and the modulation of photosynthesis (f_{APARchl} and Φ_F). The considerably stronger linear relationships between SIF and absorbed PAR (APAR, equal to $\text{PAR} \times f_{\text{APARchl}}$) than between either SIF and GPP or APAR and GPP indicate the role of APAR as the main driver of SIF (Dechant et al., 2020; Wieneke et al., 2018; Yang et al., 2018). Furthermore, the importance of the canopy structure components in SIF has also been confirmed in crop ecosystems (Dechant et al., 2020). In this study, the data were all acquired during the main growing season, characterized by fully expended crowns and minimal changes in canopy structure and chlorophyll content (Fig. S3).

The relationship between SIF and PAR changes with atmospheric dryness. A higher correlation was observed between SIF and PAR under

NAD conditions compared to HAD conditions. Under HAD conditions, plants have to dissipate a higher excess of absorbed light energy as heat through the photoprotective mechanism of NPQ, thereby preventing the formation of harmful reactive oxygen species and protecting the photosynthetic machinery from damage (Demmig-Adams et al., 2014; Ghosh et al., 2023; Murakami et al., 2024). Additionally, plants can regulate stomatal conductance to maximize carbon gain while reducing water loss in response to high VPD (Grossiord et al., 2020). These physiological modulations, which are more pronounced under HAD conditions, affect the quantum efficiency of SIF (Φ_F), though these changes in Φ_F are crucial to understand and interpret SIF under atmospheric dryness stress. This is directly shown in Fig. 9a and b, where significant relationships were observed between SIF and the chlorophyll fluorescence yield F_{yieldLIF} at the half-hourly scale and the daily scale, respectively. Our findings confirmed that SIF (namely SIFy) contains physiological information beyond structural and radiative components. This is particularly highlighted in our results during short-term periods with relatively stable APAR but reduced SIF due to atmospheric dryness stress (Fig. 3g), challenging previous studies that suggested the correlation between SIF and GPP is mainly determined by the canopy structure and radiation component of SIF (Dechant et al., 2020).

The nonlinear relationship between SIF and GPP in our results is consistent with findings in a temperate forest in the US (Yi et al., 2024), although the R^2 values (0.40 and 0.20 for the half-hourly and daily scales, respectively) of the nonlinear regressions in Yi et al., 2024 were lower compared to our results (0.46 and 0.66 for the half-hourly (Fig. 6j)

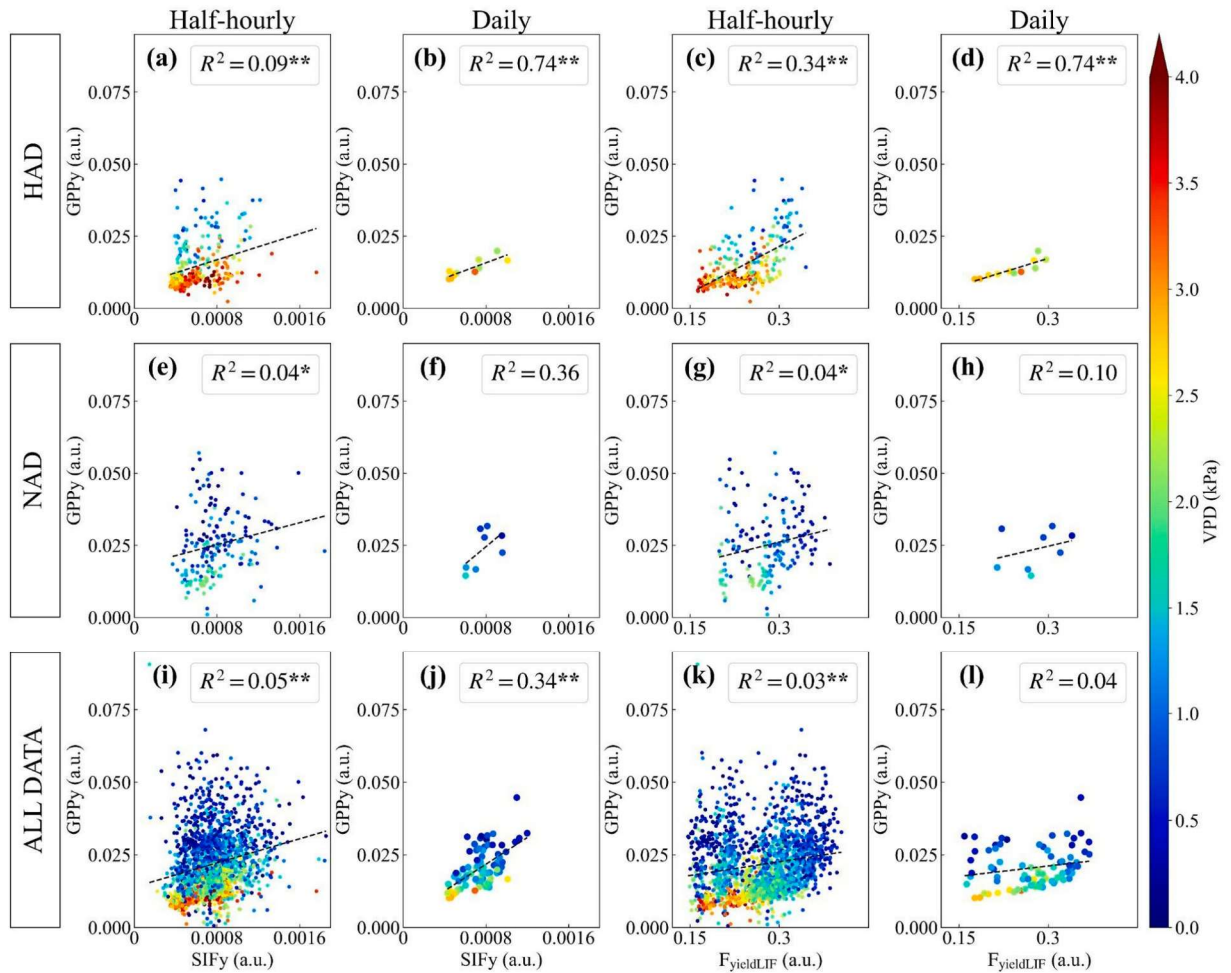


Fig. 8. Correlations between GPPy and SIFy at half-hourly (a, e and i) and daily scale (b, f and j), between GPPy and F_{yieldLIF} at half-hourly (c, g and k) and daily scale (d, h and l), under different atmospheric dryness conditions with VPD values as a color scale. The dashed black line represents the linear regression. R² is the coefficient of determination (* for $p < 0.05$, ** for $p < 0.001$).

and daily (Fig. 7j) scales, respectively). The nonlinear correlation of SIF and GPP under high atmospheric dryness conditions could be attributed to NPQ (Wieneke et al., 2024), which is the predominant dissipation pathway of excess absorbed light during heat waves. This was also confirmed in an evergreen broadleaved forest during the 2018 European heat wave (Martini et al., 2022), where leaf-level NPQ was measured using the active PAM fluorescence technique. However, a diagonal mirror of the relationship between SIF and GPP was observed when comparing our results to those of Martini et al. (2022). Differences in SIF (SIF measured by the sensors versus total SIF emitted from the canopy) and plant functional types (deciduous and evergreen) may account for this discrepancy. Leaf chlorophyll absorbs light energy, which can then be used in photochemistry, or emitted as fluorescence (captured by sensors at the top of the canopy as SIF), or dissipated as heat through NPQ (Kitajima and Butler, 1975). The partitioning of absorbed energy by plants between NPQ, photosynthesis and fluorescence is complex as it depends on numerous parameters and thus its influence on the relationship between SIF and GPP, is complex. Our results showed that the correlation between SIF and GPP diminishes, with R² decreasing from 0.49 to 0.17 at half-hourly scale when transitioning from NAD to HAD conditions (Fig. 6f and b). This suggests that the half-hourly scale relationship between SIF and GPP is mainly driven by APAR, and that NPQ acts as a confounding factor and degrades this relationship in HAD conditions. These results highlight the need for integrating active (both canopy and leaf level) and passive fluorescence measurements, along with modeling, to elucidate the partitioning of energy between NPQ,

fluorescence, and photochemistry, and understand how this affects the relationship between SIF and GPP (Magney et al., 2017; Martini et al., 2022; Porcar-Castell et al., 2014).

4.3. Effects of high atmospheric dryness on diurnal dynamics in SIF, GPP, and F_{yieldLIF}

Our study revealed differences in diurnal variations of GPP, F_{yieldLIF}, and SIF under different atmospheric dryness conditions (Fig. 4). Under HAD conditions, GPP tends to reach its maximum in advance (8:30 am instead of around noon in NAD conditions), which is likely caused by stomatal closure in response to elevated VPD. However, this advance is inconsistent with published findings (Yi et al., 2024). Yi et al. (2024) observed a diurnal pattern similar to PAR, with a peak around noon, from April to November throughout the entire growing season. The primary reason for this discrepancy with Yi et al. (2024) results is that the monthly mean diurnal patterns of GPP in Yi et al.'s study included data measured under both low VPD and high VPD conditions. The influence of high VPD on GPP was not evident after averaging with GPP under low VPD, which accounted for the majority of the measured data (Yi et al., 2024).

F_{yieldLIF} was observed to consistently decrease from the morning on (Fig. 4g), while SIFy exhibited fluctuating variations (Fig. 4d) under HAD conditions. This indicates a weak correlation between diurnal (half-hourly scale) F_{yieldLIF} and SIFy, which was confirmed in a previous study (Balde et al., 2024). The potential reason for this weak correlation

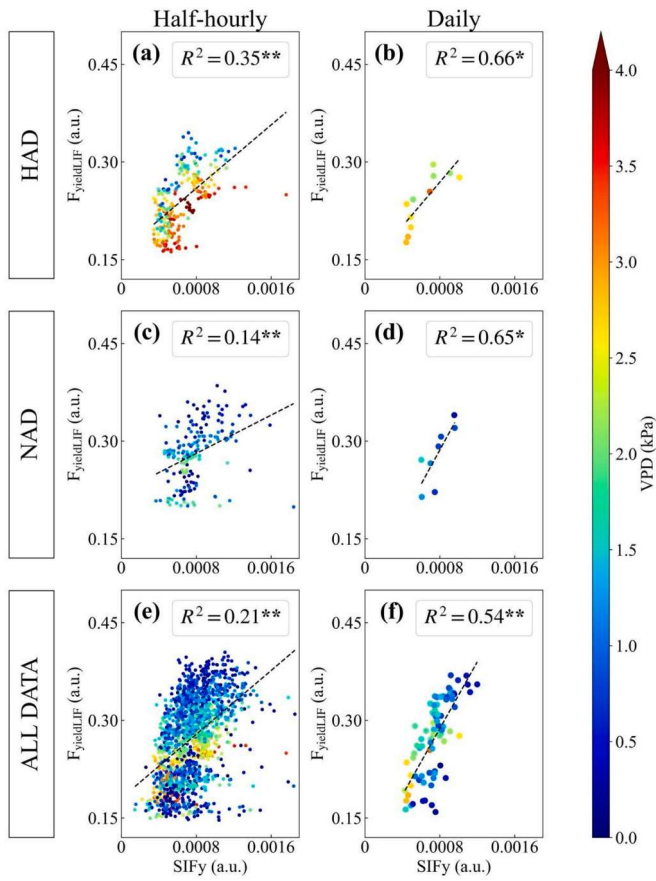


Fig. 9. Correlations between $F_{yieldLIF}$ and $SIFy$ at half-hourly (a, c, and e) and daily scale (b, d, and f) under different atmospheric dryness conditions with VPD values as a color scale. The dashed black line represents the linear regression. R^2 is the coefficient of determination (* for $p < 0.05$, ** for $p < 0.001$).

is the inclusion of additional information from $f_{APARchl}$ in $SIFy$ (Eq. (5b)). Previous studies have demonstrated that f_{esc} is highly responsive to changes in leaf area index (Fournier et al., 2012; Yang and van der Tol, 2018), leaf inclination angle (Du et al., 2017; Migliavacca et al., 2017; Zeng et al., 2019), as well as leaf clumping (Zeng et al., 2019). In this study, the observed NDVI, mNDI705, and $fAPAR$ (Fig. S3) suggest that vegetation structure and chlorophyll content remained stable over the relatively short period analyzed. However, it is important to note that even subtle changes in canopy architecture reacting to heat

waves—such as leaf angle distribution—can influence f_{esc} . Therefore, the potential impact of f_{esc} variability on $SIFy$ cannot be entirely neglected in our interpretation. However, during the entire growing season period, a significant correlation ($R^2 = 0.35$, Fig. 9a) was observed between $F_{yieldLIF}$ and $SIFy$ at the half-hourly scale. At the daily scale, a stronger correlation ($R^2 = 0.66$, Fig. 9d) was evident. This suggests that the influence of $f_{APARchl}$ is mitigated to some extent, especially at the daily scale, resulting in a strong correlation between $F_{yieldLIF}$ and $SIFy$. Additionally, we found that both $SIFy$ and GPPy values were relatively lower under HAD conditions compared to NAD conditions (Fig. 4d and h). Our results are consistent with findings in an evergreen forest (Martini et al., 2022), where diurnal ϕ_P ($GPPy/f_{APARchl}$) and ϕ_F ($SIFy/(f_{APARchl} \times f_{esc})$) showed lower values under heat wave conditions compared to pre-heat wave conditions.

4.4. The strong correlation between $F_{yieldLIF}$ and GPP under HAD conditions

$F_{yieldLIF}$ is presumably influenced solely by the physiological functioning of vegetation due to the constant intensity of the LED used to induce it and the fixed geometry. As no significant phenological changes occurred during the study period, $F_{yieldLIF}$ was assumed to be a relative assessment of the ChlF quantum yield ϕ_F (Balde et al., 2024). A significant influence of HAD on the relationship between $F_{yieldLIF}$ and GPP was observed. Our results demonstrated an improvement in the relationship between $F_{yieldLIF}$ and GPP for HAD conditions compared to NAD conditions (Fig. 6d and h), with R^2 increasing from 0.07 to 0.43 at the half-hourly scale, indicating the capability of $F_{yieldLIF}$ to capture high-temporal-resolution variations in photosynthesis under HAD conditions. An even more pronounced improvement was found at the daily scale, with R^2 increasing from 0.18 to 0.90 (Fig. 7h and d). This suggests that, after mitigating the effects of high-temporal variability, the relationship between $F_{yieldLIF}$ and GPP becomes even more robust at the daily scale under the extreme heat stress. Indeed, the temporal aggregation from half-hourly to daily scale reduces the influence of short-term variability—such as changes in solar angle, cloud cover, and within-canopy light heterogeneity—primarily on GPP. These environmental fluctuations can introduce variability in GPP at fine temporal resolutions, thereby obscuring their relationships with $F_{yieldLIF}$. At the daily scale, such fluctuations are averaged out, allowing the underlying physiological relationship between $F_{yieldLIF}$ and GPP to emerge more clearly. This is similar with recent findings showing improved SIF–GPP relationships at coarser temporal scales (Magney et al., 2019; Zhang et al., 2018). SIF is influenced by both ϕ_F and multiple radiative and structural confounding factors, including $f_{APARchl}$ and f_{esc} that fluctuate with sun angle and canopy heterogeneity. Furthermore, SIF retrieval is subject to additional uncertainties arising from algorithmic

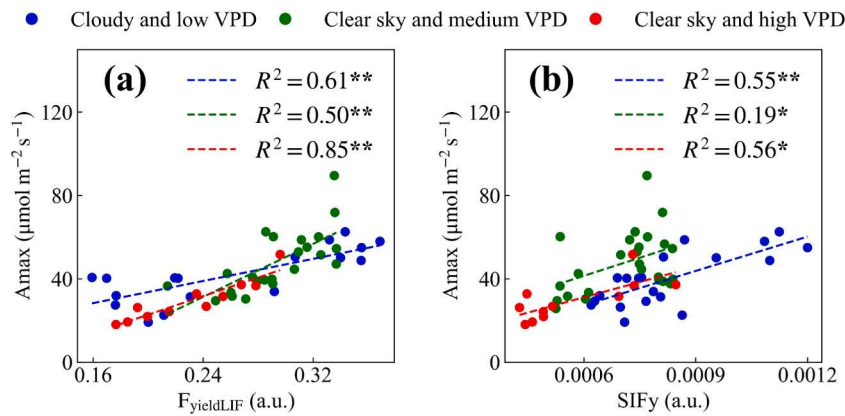


Fig. 10. Correlations between $Amax$ and $F_{yieldLIF}$ (a) and $Amax$ and $SIFy$ (b) under three specific conditions. Each dashed line represents the linear regression. R^2 is the coefficient of determination (* for $p < 0.05$, ** for $p < 0.001$).

assumptions, such as treating the canopy as a Lambertian surface (Meroni et al., 2009; Sabater et al., 2018), which is not true for complex forest structures. These factors introduce “noise” into the SIF–GPP relationship, especially at high temporal resolution. In addition, these results reveal a strong correlation between Φ_F and photosynthesis, which contrasts with previous studies that primarily demonstrated a relatively weak correlation between Φ_F and light use efficiency (LUE) (Dechant et al., 2020; Li et al., 2020; Miao et al., 2018; Yang et al., 2018; Yang et al., 2015). A similar improvement was observed between F_{yieldLIF} and SIF at both temporal scales (Fig. 6c and g at the half-hourly scale and Fig. 7c and g at the daily scale), partially explaining the strong relationship between SIF and GPP (Figs. 6f, 7b).

The strong correlation between F_{yieldLIF} and GPP under HAD condition ($R^2 = 0.43$ at the half-hourly scale, Fig. 6d; $R^2 = 0.90$ at the daily scale, Fig. 7d) can largely be attributed to the strong correlation between F_{yieldLIF} and GPPy ($R^2 = 0.34$ at the half-hourly scale, Fig. 8c; $R^2 = 0.74$ at the daily scale, Fig. 8d) after standardization of GPP by PAR. Under HAD conditions, GPP is primarily determined by the biochemical rate of photosynthesis rather than by incident radiation. This suggests that, under such circumstances, Φ_P is closely related to F_{yieldLIF} , especially when the influence of f_{APARchl} is mitigated at the daily scale. The primary reason is that F_{yieldLIF} serves as an effective assessment of Amax, which is closely related to the photosynthetic rate, particularly under conditions of high atmospheric dryness (Fig. 10). The significant and strong relationship between Amax and F_{yieldLIF} underscores the advantages of F_{yieldLIF} in capturing plant photosynthetic responses to elevated atmospheric dryness. Consequently, our results demonstrate that F_{yieldLIF} can serve as a “proxy” for Φ_P under HAD conditions in forests with relatively stable canopy structures.

The observed improvement in the correlations between ChlF signal and GPP at the daily scale between NAD and HAD conditions, especially for F_{yieldLIF} , can be explained, at least partly, by physiological mechanisms. The ChlF yield is directly modulated by the balance between photochemical quenching (PQ) and NPQ processes. During periods of HAD, stomatal closure limits CO_2 uptake and reduces photochemical efficiency, triggering rapid NPQ activation to dissipate excess excitation energy as heat (Grossiord et al., 2020; Porcar-Castell et al., 2014). This leads to a strong decline in apparent ChlF yield, which is directly captured by F_{yieldLIF} . SIF also captures this stress induced decline in apparent ChlF yield, but it is often partially or totally masked by structural and radiative effects at the canopy scale. Indeed, as said before SIF represents the ChlF fluorescence signal modulated by canopy structure and illumination-viewing geometry, while F_{yieldLIF} quantifies directly the apparent ChlF yield.

4.5. Comparison between F_{yieldLIF} and SIF as proxies of plant physiology

While SIF maintained stronger correlations with GPP (than F_{yieldLIF}) at the half-hourly scale under ALL DATA conditions (Fig. 6j), this outcome partly reflects their shared sensitivity to incoming radiation and canopy structural effects. In contrast, F_{yieldLIF} is directly linked to the physiological regulation of photosynthesis. By separating the effects of light and physiology through light-response curve analysis, we showed that F_{yieldLIF} maintained stronger and more consistent correlations with Amax than SIFy, across a range of conditions, including sunny versus cloudy days and high versus low VPD periods (Fig. 10). This suggests that the advantage of F_{yieldLIF} is not restricted to extreme stress events, but rather reflects its intrinsic mechanistic sensitivity to photosynthetic capacity.

This stronger and more robust correlation between F_{yieldLIF} and Amax compared to the one between SIFy and Amax, particularly under high VPD conditions (Fig. 10), can be mechanistically explained by the fact that F_{yieldLIF} is directly proportional to the Φ_F , which is a physiological proxy of the regulation of photosynthetic energy partitioning (Flexas et al., 2002). In contrast, SIFy additionally depends on structural and radiative transfer components such as f_{APARchl} and f_{esc} (as shown in

Eq. (7)), which are sensitive to canopy geometry, sun–shade dynamics, and illumination conditions. These confounding factors explain why the correlation between Amax and SIFy is weaker, while F_{yieldLIF} provides a more direct assessment of photosynthetic regulation. The higher correlation between F_{yieldLIF} and Amax under high VPD conditions further supports this mechanistic interpretation. From a broader perspective, these results suggest that active ChlF has the potential to complement passive SIF in ecosystem monitoring by offering a more direct link to plant physiological functioning, particularly under environmental stress. Importantly, by combining both active and passive ChlF measurements, we gain complementary insights: SIF provides integrative information useful for large-scale applications, while F_{yieldLIF} provides mechanistic clarity at the canopy scale, which is very useful for validation and, more generally, for the accurate interpretation of the SIF signal. Future studies could build upon these findings by coupling ChlF measurements with process-based modeling of NPQ and radiative transfer to further separate structural and physiological components. This would not only strengthen the mechanistic interpretation of SIF–GPP relationships but also help assess the potential scalability of active ChlF approaches to broader observational networks.

5. Conclusions

Our study evaluated the utility of tower-based passive (SIF) and active (F_{yieldLIF}) chlorophyll fluorescence measurements for detecting plant responses to high atmospheric dryness. The present study demonstrates that i) the relationship between SIF and PAR changes with atmospheric dryness stress; ii) the correlation between SIF and GPP decreases with atmospheric dryness stress; iii) the relationship between F_{yieldLIF} and GPP improves significantly with atmospheric dryness stress; and iv) F_{yieldLIF} showed stronger relationship to the maximal rate of photosynthesis Amax than SIFy, particularly under conditions of high atmospheric dryness. These findings highlight the advantages of F_{yieldLIF} in detecting plant responses to high atmospheric dryness, indicating its potential for monitoring the response of ChlF and photochemistry to extreme climatic events and for the study of the relationship between SIF and GPP. F_{yieldLIF} can pave the way for using canopy-level ChlF to monitor photosynthesis under projected climatic events characterized by higher frequency and intensity of heat waves. Considering these findings, we emphasize the importance of further research to investigate the internal mechanisms of plant responses to heat waves by integrating leaf-level active fluorescence with canopy-level passive and active fluorescence measurements. Additionally, modeling efforts that couple both leaf and canopy levels, as well as passive and active ChlF measurements, are required to provide valuable insights for practical applications and to enhance our understanding of plant responses to environmental stressors.

CRedit authorship contribution statement

Zhaohui Li: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Formal analysis, Data curation, Conceptualization. **Gabriel Hmimina:** Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Gwendal Latouche:** Writing – review & editing, Writing – original draft, Supervision, Investigation, Conceptualization. **Daniel Berveiller:** Writing – review & editing, Writing – original draft, Investigation, Conceptualization. **Abderrahmane Ounis:** Writing – review & editing, Writing – original draft, Investigation, Conceptualization. **Yves Goulas:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. **Kamel Soudani:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used ChatGPT in order to improve language and readability. After using ChatGPT, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.rse.2025.115148>.

Data availability

Data will be made available on request.

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Supplementary Information

Atmospheric dryness effects on canopy chlorophyll fluorescence and Gross Primary Production (GPP) in a deciduous forest during heat waves

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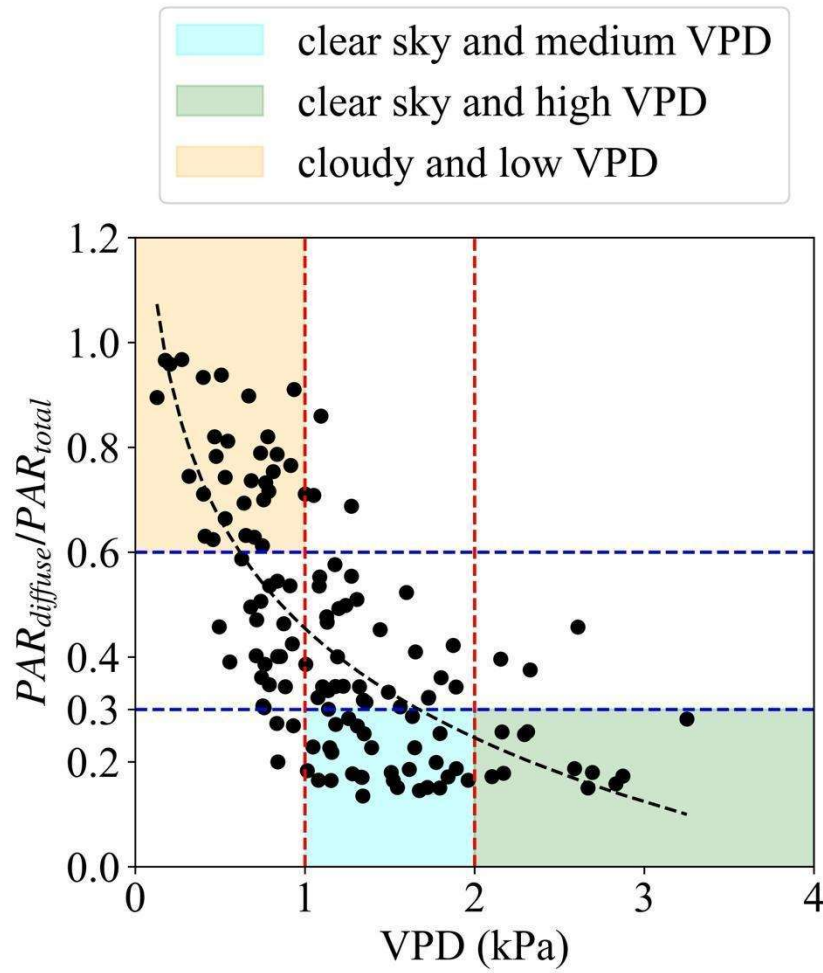


Figure S1 Scatter plot of daily mean VPD and daily mean diffuse ratio of incident radiation ($PAR_{diffuse}/PAR_{total}$), with the black dashed line representing the fitted regression. Specific conditions were identified as follows: cyan color shadow represents clear sky and medium VPD ($PAR_{diffuse}/PAR_{total} < 0.3$ and $1 \text{ kPa} < VPD < 2 \text{ kPa}$), green color shadow represents clear sky and high VPD ($PAR_{diffuse}/PAR_{total} < 0.3$ and $VPD > 2 \text{ kPa}$), and orange color shadow represents cloudy and low VPD ($PAR_{diffuse}/PAR_{total} > 0.6$ and $VPD < 1 \text{ kPa}$).

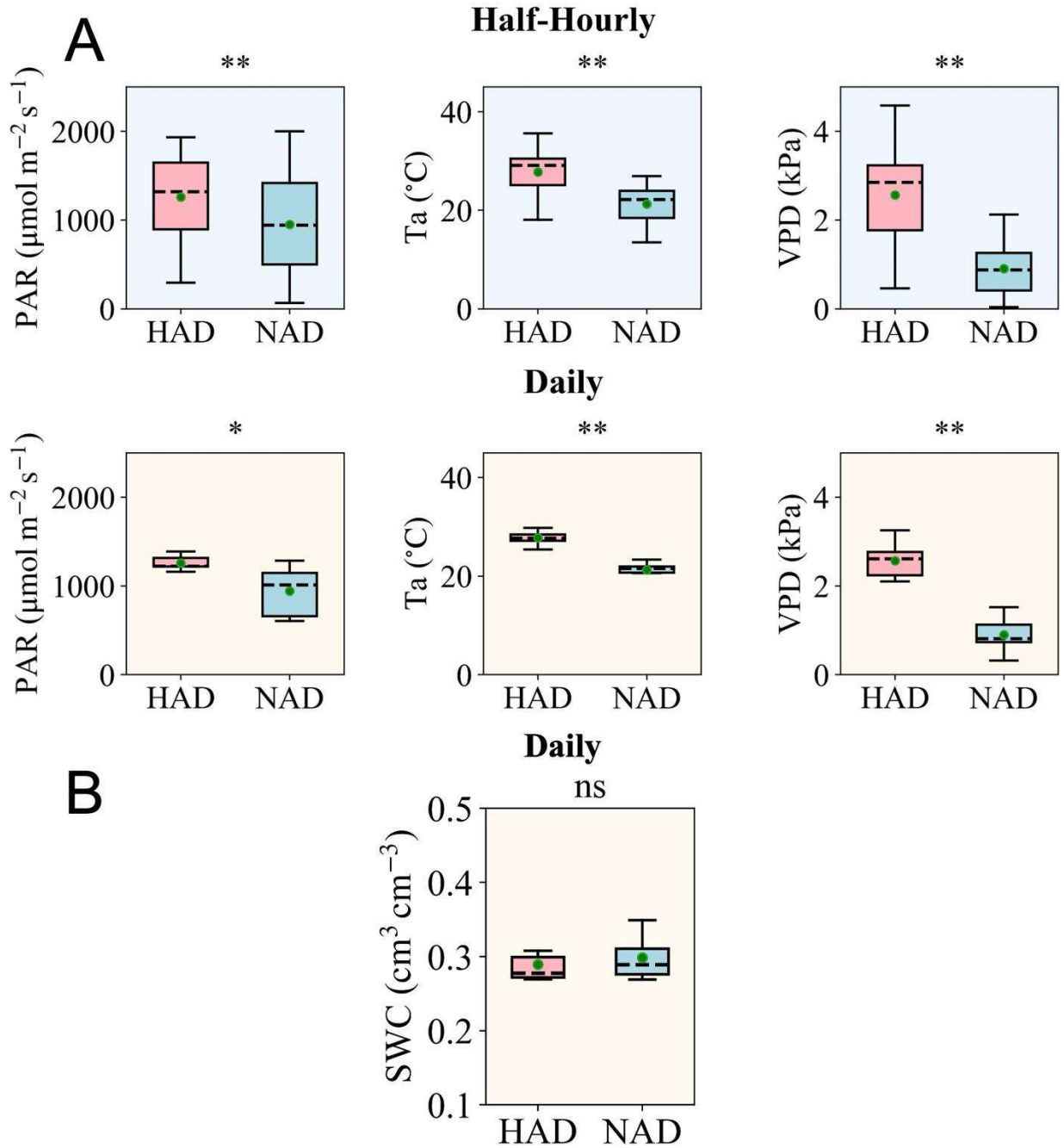


Figure S2 Boxplots comparing environmental variables between HAD and NAD periods at half-hourly (top row) and daily (bottom row) time scales (A) and boxplots comparing SWC between HAD and NAD periods at the daily scale (B). The variables include: Photosynthetically Active Radiation (PAR), air temperature (T_a), and Vapor Pressure Deficit (VPD). Boxes show the interquartile range with the median (dashed horizontal line), whiskers indicate the 5th and 95th percentiles, and green dots represent the mean values. Statistical significance of differences between HAD and NAD periods was assessed using the Mann–Whitney U test. Significance levels: ** $p < 0.001$, * $p < 0.05$, ns: not significant.

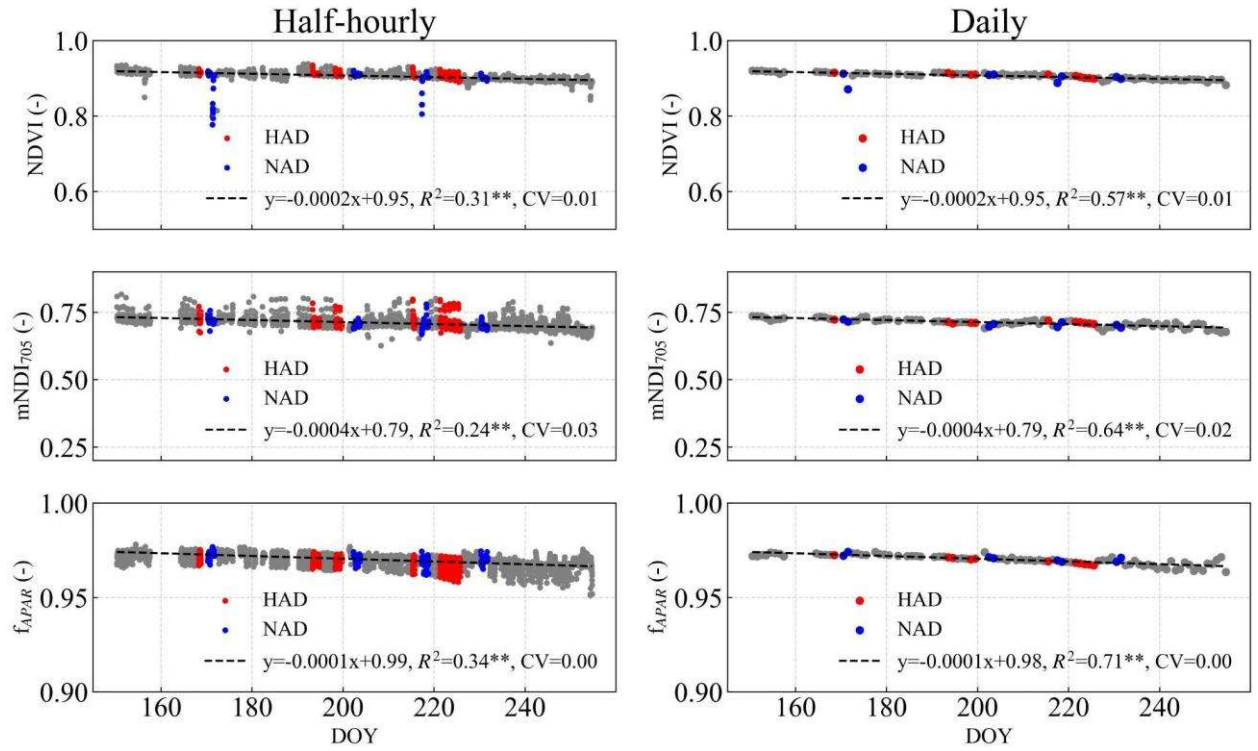


Figure S3 Vegetation indices: NDVI, mNDI₇₀₅ and f_{APAR} at half-hourly (left column) and daily (right column) time scales during the study period. All dots (grey, red and blue) represent ALL DATA, in which red and blue dots indicate data collected during periods of High Atmospheric Dryness (HAD) and No Atmospheric Dryness (NAD), respectively. The black dashed line is the linear regression between each variable and DOY for ALL DATA. R^2 is the coefficient of determination (** $p < 0.001$, * $p < 0.05$, ns: not significant). CV is the Coefficient of Variation.

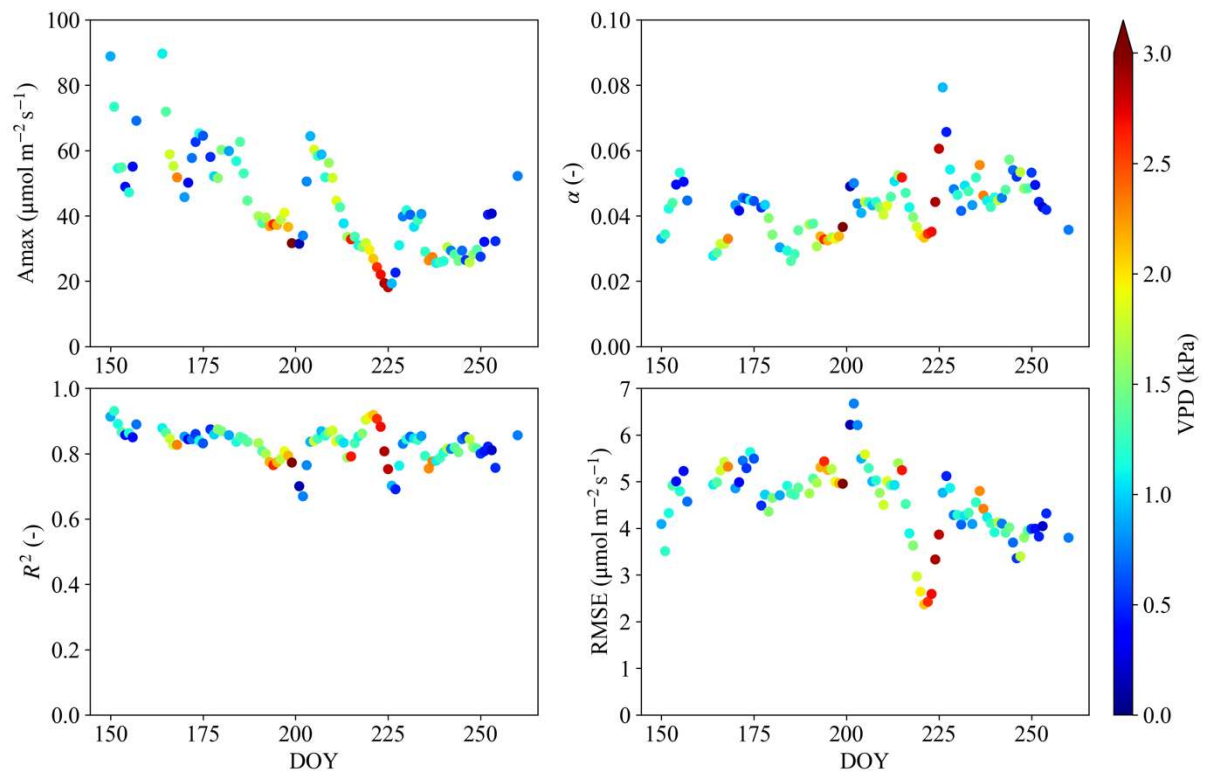


Figure S4 The A_{max} and α of the photosynthetic light-response curve for each day during the growing season. R^2 and RMSE are the coefficient of determination and the Root Mean Square Error of the curve fitting, respectively