

Accounting for Changes in Radiation Improves the Ability of SIF to Track Water Stress-Induced Losses in Summer GPP in a Temperate Deciduous Forest

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Abstract

As global observations of solar-induced chlorophyll fluorescence (SIF) have become available from multiple satellite platforms, SIF is increasingly used as a proxy for photosynthetic activity and ecosystem productivity. Because the relationship between SIF and gross primary productivity (GPP) depends on a variety of factors including ecosystem type and environmental conditions, it is necessary to study SIF observations across various spatiotemporal scales and ecosystems. To explore how SIF signals relate to productivity over a temperate deciduous forest, we deployed a PhotoSpec spectrometer system at the University of Michigan Biological Station AmeriFlux site (US-UMB) in the northern Lower Peninsula of Michigan during the 2018 and 2019 growing seasons. The PhotoSpec system consisted of two narrowband spectrometers, for the retrieval of SIF in the red (680-686 nm) and far-red (745-758 nm) regions of the electromagnetic spectrum, and a broadband spectrometer for the assessment of vegetation indices. We found that SIF correlated with GPP across diurnal and seasonal cycles, but that SIF irradiances were more strongly related to downwelling radiation than GPP. However, while this dependence of SIF on radiation obscured drought signals in SIF itself, we demonstrate that a SIF response to severe drought was apparent as a decrease in relative SIF. These results highlight the potential of SIF for detecting stress-induced losses in forest productivity. Additionally, we found that the red:far-red SIF ratio did not exhibit a response to drought stress, but was largely driven by seasonal and interannual changes in canopy structure, as well as by synoptic changes in downwelling radiation.

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1 **Accounting for Changes in Radiation Improves the Ability of SIF to Track Water**
2 **Stress-Induced Losses in Summer GPP in a Temperate Deciduous Forest**

3
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14 **Key Points:**

- 15 • Solar-induced chlorophyll fluorescence above a temperate deciduous forest is more
16 strongly tied to radiation than to productivity.
- 17 • Relative solar-induced fluorescence signals provide the strongest proxy for water stress-
18 induced summer losses in productivity.
- 19 • The ratio of red to far-red solar-induced fluorescence is sensitive to phenological changes
20 in canopy structure and downwelling radiation.

21 **Abstract**

22 As global observations of solar-induced chlorophyll fluorescence (SIF) have become available
23 from multiple satellite platforms, SIF is increasingly used as a proxy for photosynthetic activity
24 and ecosystem productivity. Because the relationship between SIF and gross primary
25 productivity (GPP) depends on a variety of factors including ecosystem type and environmental
26 conditions, it is necessary to study SIF observations across various spatiotemporal scales and
27 ecosystems. To explore how SIF signals relate to productivity over a temperate deciduous forest,
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29 AmeriFlux site (US-UMB) in the northern Lower Peninsula of Michigan during the 2018 and
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31 the retrieval of SIF in the red (680-686 nm) and far-red (745-758 nm) regions of the
32 electromagnetic spectrum, and a broadband spectrometer for the assessment of vegetation
33 indices. We found that SIF correlated with GPP across diurnal and seasonal cycles, but that SIF
34 irradiances were more strongly related to downwelling radiation than GPP. However, while this
35 dependence of SIF on radiation obscured drought signals in SIF itself, we demonstrate that a SIF
36 response to severe drought was apparent as a decrease in relative SIF. These results highlight the
37 potential of SIF for detecting stress-induced losses in forest productivity. Additionally, we found
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39 by seasonal and interannual changes in canopy structure, as well as by synoptic changes in
40 downwelling radiation.

41 **Plain Language Summary**

42 Satellite measurements of solar-induced chlorophyll fluorescence (SIF), a faint light signal
43 emitted from vegetation during photosynthesis, are increasingly being used to estimate
44 ecosystem productivity and carbon uptake. To accurately do so requires a robust understanding
45 of how the relationship between SIF and plant productivity changes over time, in response to
46 environmental stressors, and across different ecosystems. To better understand SIF signals and
47 how they relate to carbon uptake over a temperate deciduous forest, we used a high-precision
48 spectrometer system to observe SIF signals at an AmeriFlux site (US-UMB) in the northern
49 Lower Peninsula of Michigan. While the shared dependence of SIF and ecosystem productivity
50 on sunlight lead to strong daily and seasonal correlations, we found that SIF signals were more
51 closely tied to the amount of incoming sunlight than to ecosystem productivity. Despite the
52 stronger dependence of SIF on sunlight, we show that drought conditions lead to a lower SIF
53 relative to the total light signal. Lastly, we show that the observation of SIF at multiple
54 wavelengths may provide additional information on seasonal and interannual changes in canopy
55 structure. Our results demonstrate the value and limitations in using SIF to assess carbon
56 dynamics over temperate deciduous forest ecosystems.

57 **1 Introduction**

58 Global ecosystems currently provide a sink for roughly one quarter of anthropogenic
59 carbon emissions (Friedlingstein et al., 2022), and the climate-driven variations in this carbon
60 sink therefore have significant implications for long-term changes in climate. Direct
61 quantification of net and gross ecosystem productivity at regional to global scales is elusive,
62 however, given the spatial heterogeneity of the global land surface and the sparse nature of direct
63 observations of land-atmosphere carbon exchange, and contributes significant uncertainty to the
64 global carbon budget (Friedlingstein et al., 2022; le Quéré et al., 2018).

65 The unique challenges involved in quantifying the biospheric carbon sink at the global
 66 scale underscore the need for satellite-based observations that allow for the inference of
 67 ecosystem productivity across a variety of ecosystems and spatiotemporal scales. Traditionally,
 68 optical indices such as the normalized difference vegetation index (NDVI) have been used to
 69 quantify ecosystem productivity (Tucker, 1979). These signals represent the ‘greenness’ of
 70 vegetation which relates to the amount of light absorbed by vegetation, and empirically correlate
 71 with productivity across spatial gradients. However, vegetation indices lack a direct mechanistic
 72 relation with the short-term variations of photosynthetic rates, and thus require ancillary
 73 meteorological data to account for environmental stressors and to estimate light use efficiency
 74 (LUE), which is the efficiency at which sunlight is used to drive photochemistry and carbon
 75 fixation (Running et al., 2004). Additionally, vegetation indices can be vulnerable to saturation
 76 effects (X. Yang et al., 2015) or influenced by factors unrelated to vegetation, such as snow
 77 cover (Beck et al., 2006).

78 Solar-induced chlorophyll fluorescence (SIF) is a newer space-based proxy for terrestrial
 79 photosynthesis (Frankenberg, Butz, et al., 2011). As leaves absorb solar photons for use in
 80 photosynthesis, photons not used for photochemistry are either dissipated as heat via non-
 81 photochemical quenching (NPQ) or are fluoresced back to the environment as SIF. SIF,
 82 therefore, is directly related to activity of the photosynthetic machinery, as it represents an
 83 emission of red and far-red photons from the photosystems. Satellite observations of far-red SIF
 84 have been shown to scale with spatial and seasonal patterns of gross primary productivity (GPP;
 85 Frankenberg, Fisher, et al., 2011; Sun et al., 2017), indicating a potential for SIF as a direct
 86 proxy of carbon uptake through photosynthesis. There has been a recent proliferation of satellite-
 87 based observations of far-red SIF (Frankenberg et al., 2014; Joiner et al., 2013; Köhler et al.,
 88 2018) and, more recently, red SIF (Köhler et al., 2020; Wolanin et al., 2015). Quantitative
 89 assessments of SIF signals across a range of ecosystems and spatial and temporal scales are
 90 needed to inform the interpretation of these data.

91 The strong relationship between SIF and GPP stems in part from a shared dependence on
 92 solar radiation (Magney et al., 2020). Top-of-canopy SIF can be expressed as:

$$93 \quad \text{SIF} = \text{PAR} \times \text{fPAR} \times \text{SIF}_{\text{yield}} \times f_{\text{esc}} \quad (1)$$

94 (Zeng et al., 2019) where fluorescence yield ($\text{SIF}_{\text{yield}}$) represents the efficiency at which the
 95 photosystems emit photons, photosynthetically active radiation (PAR) indicates downwelling
 96 radiation available for photosynthesis, and fPAR indicates the fraction of PAR absorbed by the
 97 canopy, which depends primarily on green leaf area, chlorophyll content, and canopy structure.
 98 The fluorescence escape ratio (f_{esc}) represents the fraction of total emitted fluorescence that
 99 escapes the top of canopy and can be detected remotely, rather than being deflected or
 100 reabsorbed by leaves deeper within the canopy (Dechant et al., 2020; Zeng et al., 2019).
 101 Similarly, GPP can be expressed as the product of PAR, fPAR, and LUE (X. Yang et al., 2015):

$$102 \quad \text{GPP} = \text{PAR} \times \text{fPAR} \times \text{LUE} \quad (2)$$

103 As LUE is the most difficult component of GPP to estimate using remote sensing and is
 104 traditionally inferred from models (Gitelson & Gamon, 2015; Monteith, 1977), there is much
 105 interest in characterizing its relationship with SIF (and $\text{SIF}_{\text{yield}}$, or the rate at which absorbed
 106 photons are fluoresced as SIF). X. Yang et al. (2015) showed that SIF contained some
 107 information about LUE over a temperate deciduous forest, by dividing tower-based SIF by total

108 absorbed PAR to reveal a weak correlation between LUE and SIF_{yield}, although this relationship
109 was weaker than the correlation between far-red SIF and GPP.

110 Magney, Bowling, et al. (2019) and Pierrat et al. (2022) further showed a strong
111 relationship between SIF and GPP in northern evergreen forests under minimal changes in
112 canopy structure and absorbed PAR, when more traditional observations such as NDVI, which
113 are closely tied to changes in chlorophyll content, did not capture seasonal productivity
114 dynamics. The demonstrated seasonality in SIF, even when greenness remains constant, suggests
115 that the SIF signal is sensitive to seasonal changes in photoprotective pigments and LUE, and
116 therefore provides a more robust proxy of GPP than greenness alone.

117 Despite the strong correlations reported between SIF and GPP at seasonal and diurnal
118 timescales, uncertainties remain in the mechanistic relationship between SIF and GPP (Ryu et
119 al., 2019), and in how that relationship changes across different ecosystems and spatiotemporal
120 scales. Several studies have found that SIF over cropland is more closely tied to absorbed PAR
121 (APAR) than to GPP (Miao et al., 2018; K. Yang et al., 2018; Yazbeck et al., 2021), and Zeng et
122 al. (2019) broadly demonstrated that SIF is strongly influenced by canopy structure and changes
123 in f_{esc} . SIF is also dependent on the fluorescence yield of the photosystems. Furthermore, while
124 GPP is sensitive to ecosystem stress through changes in LUE, it is not understood how
125 fluorescence yield, and therefore observed SIF, responds to stress-induced changes. It is
126 therefore unclear how closely the SIF response to environmental stressors mirrors changes in
127 GPP. Several satellite-based studies have used SIF to observe the impacts of moderate to severe
128 drought (Li et al., 2020; Song et al., 2018; Yoshida et al., 2015); nonetheless, observations of SIF
129 tend to be less sensitive to interannual variability in GPP during summer and may not show the
130 impacts of mild stress (Butterfield et al., 2020). Furthermore, Yazbeck et al. (2021) demonstrated
131 that SIF did not reliably capture daily-scale reductions in GPP due to water stress at multiple flux
132 tower sites. Wohlfahrt et al. (2018) showed that local scale observations of SIF over a
133 Mediterranean pine forest decoupled from GPP under environmental stress and suggested that
134 much of the strong correlation between SIF and GPP in this ecosystem was driven by a shared
135 dependence on APAR, calling into question the detectability of stress-induced changes in GPP
136 from SIF observations. However, they also noted an increase in the red:far-red SIF ratio aligning
137 with peak stress conditions. The differing behaviors of red and far-red SIF signals during an
138 ecosystem stress event warrant further investigations into what can be learned from simultaneous
139 observations of SIF at both red and far-red wavelengths.

140 To assess the relationship between SIF and GPP and their responses to environmental
141 variables and stressors, we deployed a tower-based PhotoSpec spectrometer system (Grossmann
142 et al., 2018) above a temperate deciduous forest within the footprint of the US-UMB flux tower
143 at the University of Michigan Biological Station. We present results from two years of growing-
144 season observations, during which we collected red and far-red SIF observations at a high
145 temporal frequency (~20 s), providing an opportunity to quantify diurnal and intraseasonal
146 variation in the SIF signal. Our goals were to: 1) explore the dependence of SIF on downwelling
147 PAR and test how this dependence influenced the ability of SIF to track intraseasonal changes in
148 GPP; 2) characterize the relationship between SIF and GPP and test how it changed over the
149 course of the growing season and during periods of water stress; and 3) explore the behavior of
150 the red:far-red SIF ratio and assess its response to changes in environmental conditions.

151 2 Data and Methods

152 2.1 Study Location at University of Michigan Biological Station

153 We obtained data at the University of Michigan Biological Station site within a
154 deciduous broadleaf forest composed primarily of aspen, oak, maple, beech, and some
155 understory pine, with a canopy height of approximately 22 m. The forest age is roughly one
156 century as widespread fires burned much of the region in the early twentieth century. The site is
157 characterized by sandy soil, with rapid percolation of rainfall to deep soil layers. This location
158 was chosen in part because it is a well-studied forest ecosystem, with long-standing eddy
159 covariance-based observations of water and carbon fluxes (Frasson et al., 2015; Gough et al.,
160 2013, 2022), canopy structure (Fotis et al., 2018), soil moisture (He et al., 2014), and sap flow
161 and tree hydrology (Aron et al., 2019; Matheny et al., 2014, 2017).

162 2.2 PhotoSpec Tower-Based Observations

163 We built and deployed a PhotoSpec spectrometer system (Grossmann et al., 2018) at the
164 US-UMB tower during the 2018 and 2019 growing seasons (Butterfield et al., 2022). The
165 PhotoSpec system consisted of two narrowband spectrometers (QEPro, Ocean Optics Inc.): one
166 with a wavelength range of 670-732 nm and a resolution of 0.074 nm/pixel, 0.3 nm full width
167 half maximum (FWHM), for measuring SIF in the red region of the spectrum, and a second
168 QEPro (729-784 nm, 0.067 nm/pixel, 0.3 nm FWHM) optimized for measuring SIF in the far-
169 red. An additional broadband spectrometer (Flame, Ocean Optics Inc.; 177-874 nm, 0.382
170 nm/pixel, 1.2 nm FWHM) permitted the calculation of vegetation indices, such as NDVI, from
171 the measured spectra. A 2-D scanning telescope was mounted on the US-UMB tower at a height
172 of 45 m and could point at various locations in the canopy using a narrow field of view (about
173 0.7°). Light from the canopy was thus directed through a fiber optic cable, and subsequently
174 split as input to the three spectrometers.

175 We acquired automated observations in three azimuthal directions: 60° east of south, due
176 south, and 60° west of south. For each azimuth angle, we acquired data along an elevation
177 transect by scanning from 90° (nadir) to 45° below the horizon. For each individual location
178 along the transects, we optimized the exposure times for the spectrometers to maintain consistent
179 detector signal level. Multiple exposures were then integrated together into 20 s measurements
180 before moving the telescope to the next location. Observations were collected when the solar
181 elevation angle was > 10° and solar reference spectra were collected at least every 10
182 measurements using an upward-facing diffuser disk. To ensure that observations included green
183 vegetation and were of sufficiently high quality, data were further filtered to only include
184 retrievals where NDVI was > 0.2, red and far-red SIF retrieval errors were < 0.1 mW m⁻² sr⁻¹
185 nm⁻¹, and SIF irradiances were calculated to be between -0.1 and 10 mW m⁻² sr⁻¹ nm⁻¹ and
186 between -2 and 20% of the total light signal. These filters resulted in the removal of ~12% of
187 collected data. A full cycle through the three azimuth angles took approximately 90 minutes;
188 therefore, after removing outlier data, we used 90-minute averages for sub-daily comparisons.

189 The uncertainty of each 90-minute period was calculated as the standard deviation of included
190 observations.

191 SIF irradiances were calculated from the QEPro spectra for both the red (680-686 nm)
192 and far-red (745-758 nm) regions of the electromagnetic spectrum using a physical retrieval
193 based on the infilling of solar Fraunhofer lines (Grossmann et al., 2018). To isolate SIF signals
194 from their dependence on PAR, we calculated relative SIF by dividing the observed SIF
195 irradiance by the total reflected and fluoresced irradiance at the respective wavelength to
196 represent SIF as a percentage of the total light signal. We calculated NDVI, the photochemical
197 reflectance index (PRI), which is sensitive to de-epoxidation of xanthophyll cycle pigments and
198 light use efficiency (Gamon et al., 2001), and a chlorophyll index (Chlorophyll_{RS}; Magney,
199 Frankenberg, et al., 2019; Datt, 1999) using spectra from the broadband Flame spectrometer
200 (Text S1). While our site did not include direct observations of fPAR, we assume a rough
201 proportionality between NDVI and fPAR (Running et al., 2004) from which we inferred the
202 qualitative seasonal behavior of fPAR (i.e., we assumed that seasonal changes in fPAR tracked
203 seasonal changes in NDVI).

204 The SIF observations were radiometrically calibrated using a second broadband Flame
205 spectrometer with a cosine corrector (CC-3-UV-S, Ocean Optics Inc.) that was calibrated using
206 radiometric standard lamp (HL-3-P-CAL, Ocean Optics Inc.). We recorded simultaneous
207 measurements alongside the PhotoSpec instrument with the second Flame spectrometer using a
208 reflective calibration disk (Spectralon Diffuse Reflectance Standard, Labsphere Inc.) at least
209 once per growing season whenever any adjustments were made to the optical components.
210 Between the 2018 and 2019 growing seasons, radiometric calibration coefficients remained
211 within 2.5 and 1% for red and far-red SIF retrievals, respectively. Wavelength calibrations were
212 done using a Mercury-Argon lamp (HG-1, Ocean Optics Inc.).

213 2.3 AmeriFlux and Meteorological Data

214 For this study, we compared PhotoSpec SIF data with ecosystem flux observations from
215 the AmeriFlux tower (46 m above ground), from which CO₂ and H₂O flux data have been
216 observed since 1999 (Gough et al., 2022). Eddy covariance (EC) flux observations of Net
217 Ecosystem Exchange (NEE) were partitioned into estimates of ecosystem respiration (RE) and
218 GPP, from which we used the processed half-hourly estimates of GPP from April 2018 through
219 November 2019. We used the data from 2007-2019 for a baseline comparison with a multi-year
220 mean. In addition to GPP flux data, we used coincident meteorological observations from the
221 same AmeriFlux dataset. These included air temperature, precipitation, vapor pressure deficit
222 (VPD), volumetric soil water content (SWC) at a depth of 30 cm, and downwelling PAR. Data
223 for the site was obtained through the AmeriFlux database (AmeriFlux site ID: US-UMB; Gough
224 et al., 2022). More details about the data processing approach for this site are described by
225 Gough et al. (2013).

226 Flux data were processed by the site team following the standard EC processing protocol
227 (Rebmann et al., 2012). Flux data during periods of low turbulent mixing were filtered using the
228 u^* -filter threshold approach, with the threshold values calculated seasonally following
229 Reichstein et al. (2005). Filtered nighttime NEE observations were assumed to represent RE, and
230 seasonal nighttime RE observations were then used to train an automated neural network model

231 (ANN; see Morin et al., 2014) to infer daytime RE using time of day, air temperature, vapor
232 pressure deficit, soil temperature, and soil moisture as inputs (Lasslop et al., 2010). For all ANN
233 models, 50% of the data were used for training, 25% for evaluation and 25% for validation of the
234 ensemble's goodness of fit. The ensemble mean of the best-performing 10% of 1000 ANN
235 models was used to predict RE during the day, and during nighttime observation gaps. GPP was
236 assumed to be zero during winters and overnight, and daytime GPP during the growing season
237 was calculated as the difference between observed NEE and modelled RE. ANN models with a
238 setup similar to the one used for RE were used to model GPP and gapfill missing daytime
239 observations during the growing season. The GPP ANN models used air temperature, incoming
240 PAR, relative humidity, vapor pressure deficit, sensible and latent heat fluxes, and soil moisture
241 as input variables.

242 We aggregated the half-hourly AmeriFlux data to 90-minute and daily values for each
243 variable either by simple summation (precipitation) or averaging (other variables). As NDVI
244 (and therefore fPAR) was generally constant between leaf out and senescence, we calculated an
245 LUE proxy as GPP/PAR (Gitelson & Gamon, 2015). Seasonal estimates for species-specific
246 maximal leaf area index (LAI) at the site were measured using samples collected with leaf litter
247 traps.

248 2.4 Satellite Observations of SIF from OCO-2

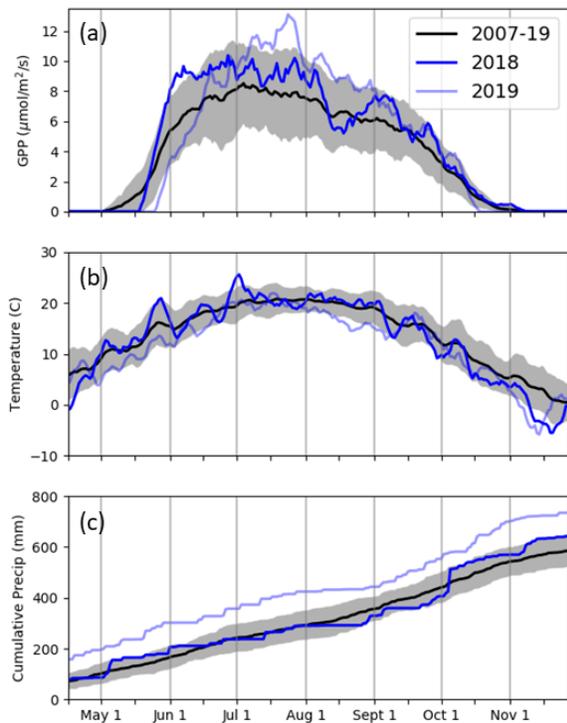
249 We compared satellite-based observations of SIF from the Orbiting Carbon
250 Observatory-2 (OCO-2; Science Team et al., 2017; Yu et al., 2019) with our tower-based
251 PhotoSpec observations. OCO-2 is a polar orbiting satellite with a local overpass time of
252 1:30pm. SIF was retrieved from OCO-2 spectra at 757 nm and 771 nm using a non-linear least-
253 squares approach to evaluate the infilling of solar Fraunhofer lines (Sun et al., 2018). We
254 averaged OCO-2 SIF retrievals at 757 nm (which was within our far-red fitting window of 745-
255 758 nm) that fell within a one-degree grid cell centered at US-UMB. Individual soundings were
256 converted to daily-averages using a clear-sky PAR proxy, which uses the cosine of the solar
257 zenith angle to account for diurnal variability in the SIF signal. We subsequently calculated a
258 single mean and standard deviation of OCO-2 observations for each day with available overpass
259 data, resulting in nine individual data points throughout the 2018 and 2019 growing seasons. We
260 then tested the linear correlation of these data with corresponding daily means observed using the
261 PhotoSpec instrument.

262 3 Results

263 3.1 Climatological Context for 2018-2019 Growing Seasons

264 The 2018 and 2019 growing seasons were both more productive than the 2007-2019
265 mean based on eddy covariance GPP data (Figure 1a). In 2018, growing season onset was
266 delayed by about a week relative to the multi-year mean, but GPP increased rapidly ($\sim 0.5 \mu\text{mol}$
267 $\text{m}^{-2} \text{s}^{-1} \text{day}^{-1}$) throughout the second half of May during a period with above average
268 temperatures (Figure 1a-b). GPP reached a seasonal peak value of about $10 \mu\text{mol m}^{-2} \text{s}^{-1}$ in late
269 June, roughly 25% higher than the multi-year mean, and remained higher than average until mid-
270 August. In 2019, onset of the growing season occurred even later, following the multi-year mean
271 by about 2 weeks, due to very wet and cold spring conditions (Figure 1b-c). GPP subsequently

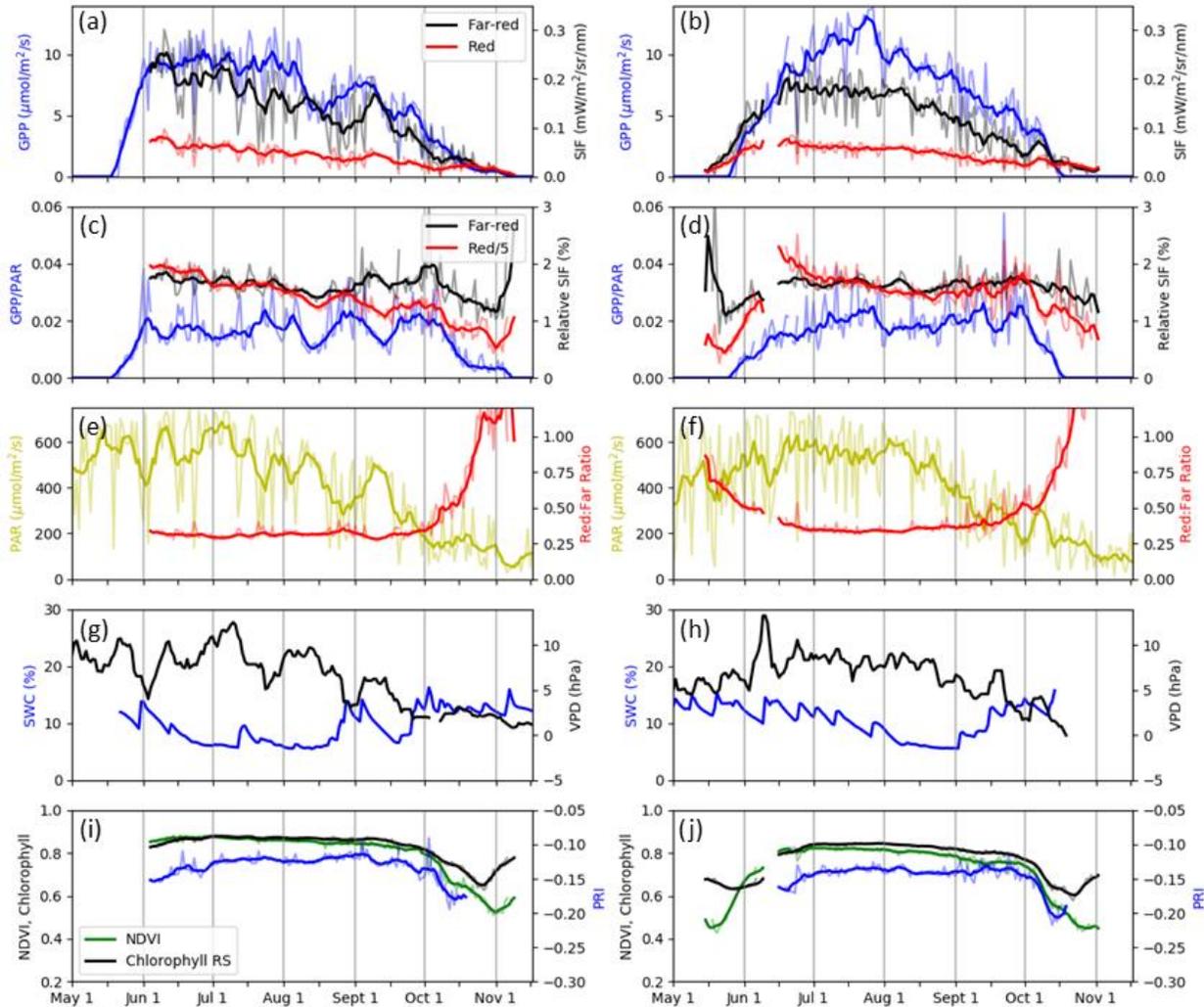
272 reached a peak value of $> 12 \mu\text{mol m}^{-2} \text{s}^{-1} \text{day}^{-1}$ in late July, 50% higher than the multi-year
 273 mean, and remained nearly a standard deviation higher than average until September (Figure 1a).



274
 275 **Figure 1.** Observations of GPP (a), temperature (b), and cumulative precipitation (c) at US-UMB during
 276 the 2018 (dark blue) and 2019 (light blue) growing seasons. The 2007-2019 multi-year mean for each
 277 panel is included as a black line, with shading representing ± 1 standard deviation. GPP and temperature
 278 are plotted as 7-day running means.

279 Both 2018 and 2019 experienced water stress-induced declines in GPP during late
 280 summer that occurred with moderate to severe drought conditions as classified by the U. S.
 281 Drought Monitor (USDM; Svoboda et al., 2002; accessed via <http://droughtmonitor.unl.edu>).
 282 The USDM classification showed a severe drought in mid-August 2018 that followed a series of
 283 three dry spells in early June, early July, and August (Figure 1c). While the first of these dry
 284 periods did not lead to dry soil moisture conditions, the cumulative influence of the two later dry
 285 periods led to soil water content falling to $\sim 5\%$ and coincided with local maxima in VPD
 286 upwards of 9 hPa (Figure 2g). GPP levels were relatively robust during the first period of dry
 287 soil conditions from late June through July 11, but during the second dry period from late July
 288 through August 18, productivity ultimately declined by about 30%, to levels below the multi-
 289 year mean. Towards the end of August, GPP recovered back to about 20% above the
 290 climatological mean. GPP may be increasingly sensitive to dry soil conditions over the growing
 291 season due to the fact that the soil matric potential can continue to increase even as SWC
 292 asymptotes to a lower limit (Köcher et al., 2009; Lascano et al., 2007). The soil matric potential
 293 reflects soil hydraulic tension, which at higher values indicates greater resistance to vegetation
 294 taking up water through their roots. Late summer declines in GPP occur roughly every other year
 295 at the US-UMB site and are not always tied to an obvious drought signal (Figure S1). While
 296 2019 was not characterized by any periods of severe drought stress, GPP observations did

297 decrease in late July from about 50% to only 20% above the climatological mean (Figure 1a).
 298 This decline in productivity coincided with decreasing SWC (Figure 2h) and little accumulated
 299 precipitation (Figure 1c), but also with cooler temperatures (Figure 1b) and only a slight increase
 300 in VPD (Figure 2h).



301 **Figure 2.** Growing season time series of GPP and SIF irradiance (a, b), GPP/PAR and relative SIF (c, d),
 302 photosynthetically active radiation (PAR) and the red:far-red SIF ratio (e, f), soil water content (SWC)
 303 and vapor pressure deficit (VPD (g, h), and NDVI, Chlorophyll_{RS}, and PRI (i, j) during 2018 (left) and
 304 2019 (right). With the exception of SWC and VPD, bold lines represent the 7-day running mean of daily-
 305 averaged data (thin lines).
 306

307 3.2 Characteristics of Red and Far-red SIF Signals

308 Far-red SIF observations during 2018 and 2019 generally followed a seasonal cycle
 309 similar to that of GPP (Figure 2a-b). Both SIF and GPP reached peak levels in early summer and
 310 steadily declined throughout late summer and fall. The red SIF signal followed a similar pattern
 311 but exhibited relatively higher values in early spring and fall (Figure 2a-b), illustrated by higher
 312 red:far-red SIF ratios during the shoulder seasons (Figure 2e-f) corresponding with low NDVI
 313 and Chlorophyll_{RS} values (Figure 2i-j). This contrast between red and far-red SIF seasonality

314 results from top-of-canopy red SIF observations being more sensitive to canopy structure and
 315 chlorophyll content (Magney, Frankenberg, et al., 2019), since a smaller fraction of total emitted
 316 SIF is scattered or reabsorbed by the canopy during the springtime when the canopy is not yet
 317 fully developed or as chlorophyll content decreases in fall. This dependence is also evident in
 318 lower red:far-red SIF ratios in 2018, concurring with differences in other observations including
 319 NDVI (maximum value of 0.88 in 2018 and 0.84 in 2019) and LAI, where measurements using
 320 leaf litter traps showed almost a 20% reduction in 2019 compared to 2018 (4.38 in 2018 versus
 321 3.64 in 2019; Table 1). The lower red:far-red SIF ratio in 2018, when LAI was high, corroborates
 322 the hypothesis that a denser canopy limits top-of-canopy red fluorescence. Taken together, these
 323 differences in the behavior of SIF at different wavelengths suggested that far-red SIF better
 324 reflected the seasonal cycle of productivity in a temperate deciduous forest, and that red SIF was
 325 more sensitive than far-red SIF to seasonal, and potentially interannual, changes in canopy
 326 structure and chlorophyll concentration.

327

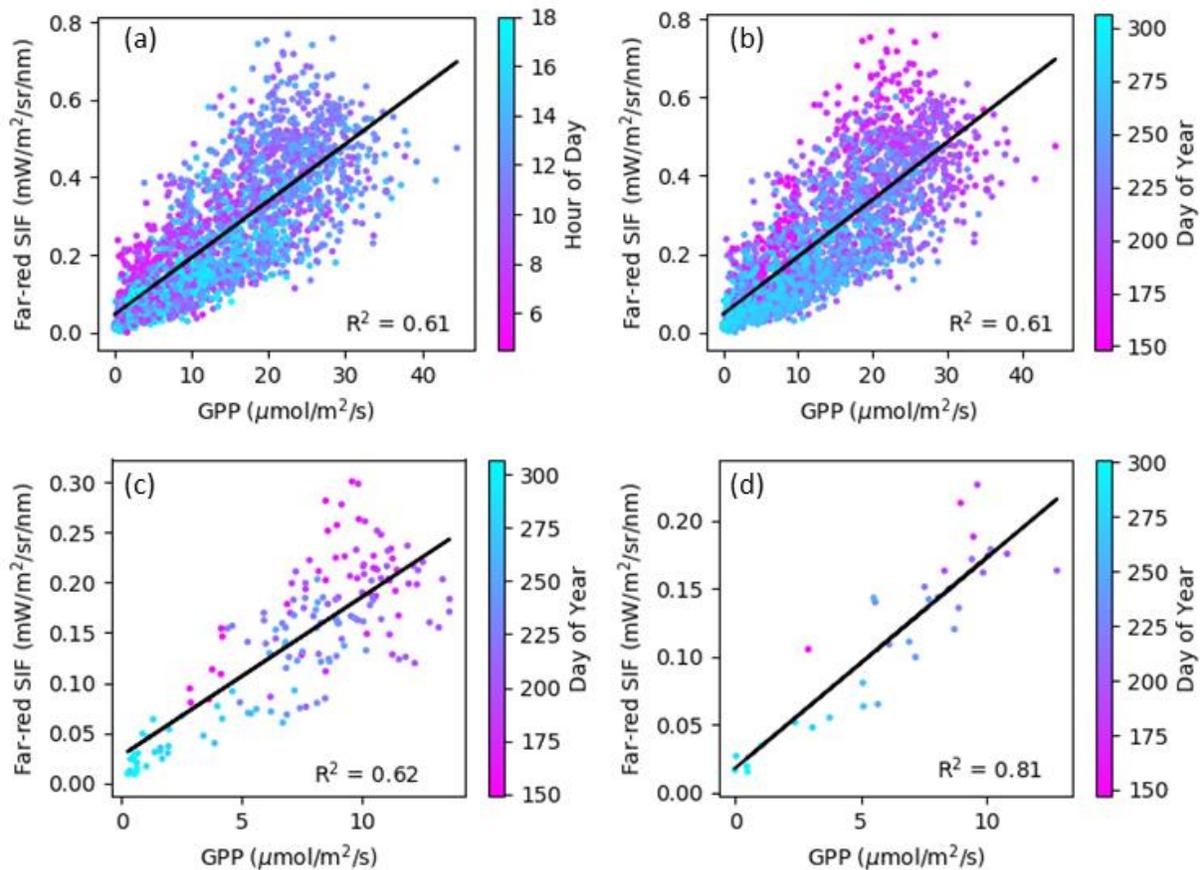
328 **Table 1.** Species-specific leaf area index (LAI) values as observed at the US-UMB AmeriFlux site for
 329 2018 and 2019 using leaf litter traps.

330

Species	2018 LAI	2019 LAI
Bigtooth aspen (<i>Populus grandidentata</i>)	1.286	0.981
Red maple (<i>Acer rubrum</i>)	0.891	0.730
American beech (<i>Fagus grandifolia</i>)	0.292	0.281
Red oak (<i>Quercus rubra</i>)	1.073	0.878
Paper birch (<i>Betula papyrifera</i>)	0.238	0.178
White pine (<i>Pinus strobus</i>)	0.587	0.578
Red pine (<i>Pinus resinosa</i>)	0.008	0.011
Total	4.375	3.636

331 We calculated correlations between SIF and GPP with data aggregated to 90-minute,
 332 daily, and weekly timescales (Figure 3). For far-red SIF, weekly-aggregated data had the highest
 333 correlation with GPP ($R^2 = 0.81$), while 90-minute- and daily-aggregated data had R^2 values of
 334 0.61 and 0.62, respectively. The correlations between GPP and red SIF were weaker (R^2 values

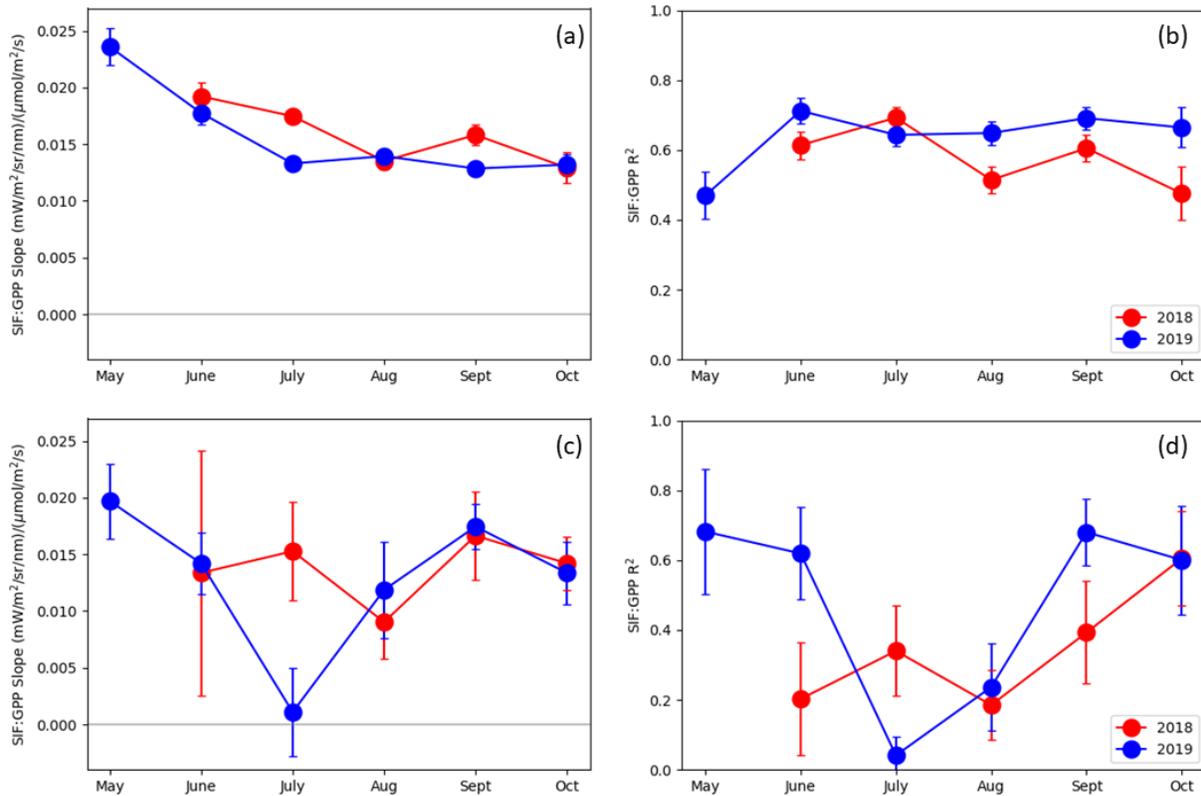
335 of 0.56, 0.54, and 0.72 for 90-minute, daily, and weekly timescales; Figure S2). Over the
 336 growing season, weekly values of far-red SIF span the range from near zero during the early and
 337 late growing season, to $0.2 \text{ mW m}^{-2} \text{ sr}^{-1} \text{ nm}^{-1}$ during peak growing season in July (Figure 3d).
 338 Daily values during the month of July, in contrast, have a standard deviation of $\sim 0.05 \text{ mW m}^{-2}$
 339 $\text{sr}^{-1} \text{ nm}^{-1}$ and reach as high as $0.3 \text{ mW m}^{-2} \text{ sr}^{-1} \text{ nm}^{-1}$ (Figure 3c), suggesting that cloud-driven
 340 variability in PAR may be a significant driver in far-red SIF variability while GPP in this
 341 ecosystem may be less sensitive to day-to-day variability in light availability.



342
 343 **Figure 3.** Correlation between far-red SIF and GPP, temporally aggregated to 90-minute (a, b), daily (c),
 344 and weekly (d) resolutions. Color bars indicate hour of day (a) or day of year (b-d).

345 To investigate how seasonal changes influence the relationship between GPP and far-red
 346 SIF we fit linear correlations to data within individual months for 2018 and 2019 (Figure 4). We
 347 quantified uncertainties both on slopes and R^2 values using a bootstrapping approach in which
 348 we sampled the monthly data with replacement. Results for daily-averaged data confirmed that
 349 GPP and far-red SIF are best correlated during spring and fall, when seasonal phenological
 350 changes in the deciduous forest result in a large dynamic range in fPAR (using NDVI as a
 351 proxy). Shared dependence on fPAR between SIF and GPP thus lead to stronger correlations
 352 during these months (Figure 4d; discussed in more detail in section 4.1). Correlations between
 353 90-minute data showed that the inclusion of diurnal variations led to consistently stronger
 354 correlations throughout the summer (Figure 4b). The resulting slopes from the linear fits of daily
 355 data exhibited large uncertainties and do not exhibit obvious changes over the course of the
 356 growing season (Figure 4c). Linear fits of 90-minute data were better constrained to the origin by

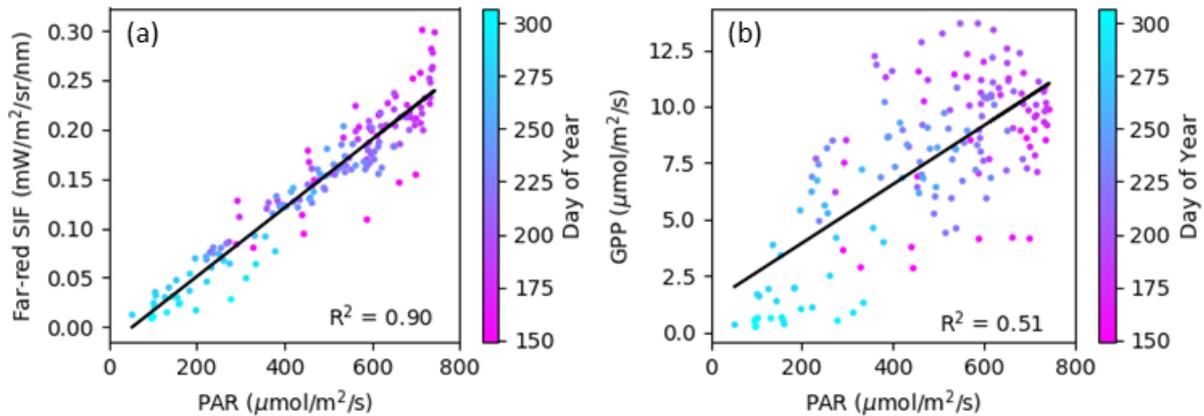
357 including near-zero values in morning and evening, resulting in more precise slopes (Figure 4a).
 358 These results showed that the far-red SIF:GPP slope was highest during the spring and declined
 359 over the course of the growing season (Figure 4a; further discussed in Section 4.2).



360
 361 **Figure 4.** Slopes and R^2 values from monthly linear regressions of 90-minute- (a, b) and daily-averaged
 362 (c, d) far-red SIF with GPP. Data from 2018 are in red, while 2019 data are in blue. Error bars represent
 363 the standard deviations of results from a bootstrapping method used to test the robustness of the linear
 364 regressions.

365 While both SIF and GPP depend on PAR (Equation 1 and 2), SIF was more tightly
 366 coupled to downwelling PAR than was GPP at our site (Figure 5). Without direct observations of
 367 fPAR, we assumed that fPAR was near constant under peak growing season conditions when
 368 NDVI was stable (see Running et al., 2004; Figure 2i-j), and that the relationship during summer
 369 between SIF and PAR were therefore indicative of the relationship between SIF and APAR. The
 370 close dependence of SIF on radiation was illustrated by shared temporal patterns of SIF and PAR
 371 throughout summer (Figure 2a-b, e-f), and by a strong correlation between daily-aggregated far-
 372 red and red SIF with PAR ($R^2 = 0.90$, Figure 5a, S3). GPP and PAR exhibited a much weaker
 373 correlation ($R^2 = 0.51$; Figure 5b). Monthly correlations of far-red SIF and GPP with PAR
 374 confirmed that GPP exhibits a weaker relationship with downwelling PAR than SIF (Figure S4b,
 375 d). Monthly correlations also showed that the relationship between SIF and PAR was weakest
 376 during spring and fall (Figure S4d) when variations in NDVI (and fPAR), due to rapid changes
 377 in the canopy (i.e. leaf-out and senescence), cause APAR to deviate qualitatively from PAR.
 378 Lower NDVI (and fPAR) during spring and fall also led to lower values of SIF and GPP relative

379 to PAR (Figure S4a, c), as a smaller fraction of downwelling radiation is absorbed by vegetation
 380 during these periods.



381
 382 **Figure 5.** Correlation between daily-averaged far-red SIF (a) and GPP (b) with photosynthetically active
 383 radiation (PAR). Color bars are weighted by day of year.

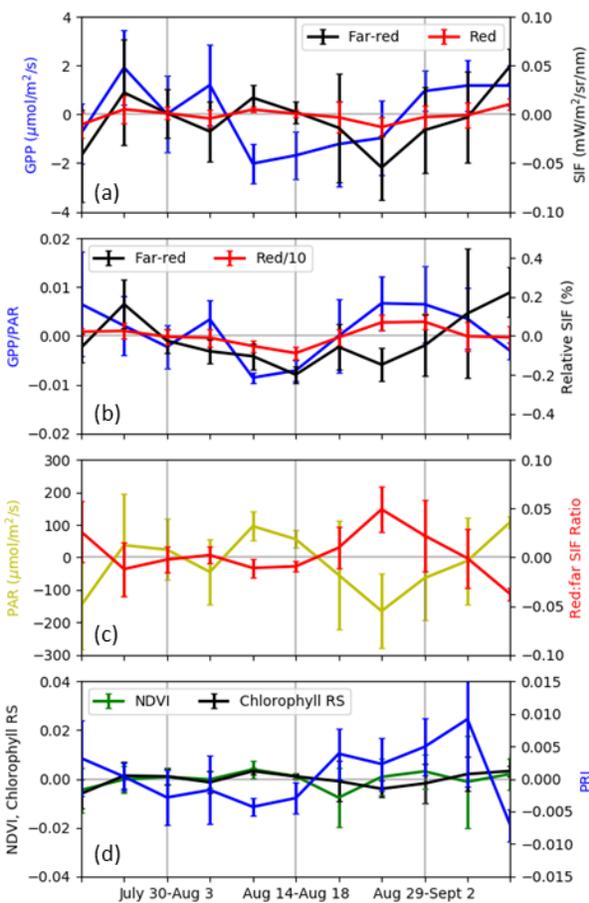
384 We calculated relative SIF, or SIF as a fraction of the total light signal, in order to
 385 decouple the SIF signal from its dependence on PAR (Figure 2c-d). During peak summer
 386 conditions, relative far-red SIF typically was just under 2% of total observed light, while relative
 387 red SIF was 5-10%. Red and far-red relative SIF exhibited lower values during early spring and
 388 late fall, when the ecosystem absorbs less downwelling radiation for photosynthesis. We
 389 calculated an LUE proxy as GPP divided by PAR and found that relative far-red and especially
 390 red SIF visually track intraseasonal patterns in LUE (Figure 2c-d), notably during the August
 391 2018 severe drought. Relative red SIF shares a similar seasonal pattern with GPP/PAR, leading
 392 to a stronger correlation between daily-aggregated data ($R^2 = 0.34$; Figure S5b), while the
 393 correlation between relative far-red SIF and GPP/PAR is weaker ($R^2 = 0.07$; Figure S5a).

394 3.3 Detectability of Mid-summer Ecosystem Stress

395 While there were clear stress-induced decreases in GPP inferred from eddy covariance in
 396 August 2018 (Figure 2a; Section 3.1) coinciding with severe drought as classified by USDM
 397 (Svoboda et al., 2002; accessed via <http://droughtmonitor.unl.edu>), these intraseasonal stress
 398 dynamics were not obvious in remote sensing observations of SIF irradiances from PhotoSpec.
 399 Variations in red and far-red SIF irradiances followed synoptic-scale patterns in downwelling
 400 PAR (Figure 2a-b, e-f) rather than changes in GPP. Only relative red and far-red SIF values
 401 showed a notable change coinciding with the mid-summer drought, which dipped to a local
 402 minimum in mid-August (Figure 2c). Optical vegetation indices, including NDVI,
 403 Chlorophyll_{RS}, and PRI, remained constant over the course of the growing season (Figure 2i-j),
 404 indicating limited changes in chlorophyll and carotenoid pigments within the canopy.

405 To further investigate potential influences of drought stress on canopy SIF, we linearly
 406 detrended peak growing season observations (between July 15 and September 15, 2018) to
 407 distinguish intraseasonal variability from seasonal trends. We then calculated 5-day binned
 408 averages of observed data over the course of the August 2018 drought (Figure 6), and calculated
 409 correlation coefficients between detrended GPP and other variables over this period using both

410 daily and 5-day binned data (Table 2). GPP first experienced a decline around August 10 and
 411 recovers roughly 20 days later, but the far-red and red SIF irradiances exhibited higher (instead
 412 of lower) values over these 20 days (Figure 6a). The higher SIF irradiances during a cloud- and
 413 precipitation-free period was consistent with the strong relationship with PAR demonstrated
 414 above, however relative red and far-red SIF signals were more sensitive to ecosystem stress and
 415 saw local minimum values during the second 5-day period of the drought (August 14-18; Figure
 416 6b). Relative far-red SIF was the only variable to show a statistically significant ($p < 0.01$)
 417 correlation with GPP at both daily and 5-day temporal scales, but did not exhibit significant
 418 correlations with GPP/PAR, our LUE proxy, at daily ($R = -0.17$) or 5-day ($R = 0.08$) scales.
 419 Relative red SIF, however, showed a strong correlation with GPP/PAR at both daily ($R = 0.69$)
 420 and 5-day ($R = 0.87$) temporal scales. In contrast to Wohlfahrt et al. (2018), our observations did
 421 not show a strong red:far-red SIF ratio response to drought-induced stress (Figure 6a, c;
 422 discussed further in Section 4.3), but instead the detrended daily SIF ratio was strongly
 423 anticorrelated ($R^2 = 0.79$) with PAR. Diurnal stress-induced effects were also not seen in the 90-
 424 minute-aggregated observations of the red:far-red SIF ratio (Figure S6). We note that there was
 425 a delayed increase in PRI following the drought by ~ 10 days (Figure 6), which may indicate an
 426 increase in carotenoid pigments resulting from the drought period; however, we did not observe
 427 any corresponding changes in Chlorophyll_{RS} (Figure 6d).



428
 429 **Figure 6.** Five-day binned and detrended data showing GPP and SIF irradiances (a), GPP/PAR and
 430 relative SIF (b), the red:far-red SIF ratio and PAR (c), and NDVI, Chlorophyll_{RS}, and PRI (d) during
 431 drought conditions in August 2018. Error bars represent the standard deviation of each five-day bin.

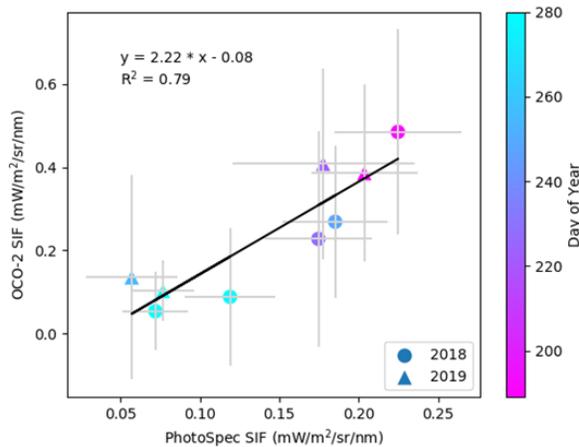
432 **Table 2.** R-values resulting from linear fits between detrended GPP and other variables between July 15
 433 and September 15, 2018 for both daily and 5-day binned observations. Values in bold indicate statistically
 434 significant fits ($p < 0.01$).
 435

	Daily GPP	5-day binned GPP
Far-red SIF	0.51	0.31
Red SIF	0.51	0.29
Relative Far-red SIF	0.56	0.76
Relative Red SIF	0.20	0.43
Red:Far-red SIF Ratio	-0.41	-0.27
PAR	0.39	0.10
NDVI	0.15	0.12
Chlorophyll _{RS}	0.37	0.17
PRI	0.05	0.15

436 3.4 Comparison with Space-based SIF from OCO-2

437 The ultimate goal of our tower-based SIF observations is to improve the interpretation of
 438 space-based, global SIF observations. We compared daily averages of far-red SIF observations
 439 from PhotoSpec with mean estimates of daily-averaged SIF from the OCO-2 satellite (Figure 7).
 440 The OCO-2 satellite observations were well correlated with our tower observations ($R^2 = 0.79$)
 441 showing that both sets of observations captured proportionally similar patterns in the SIF signal.
 442 However, the slope between the two datasets of 2.2 ± 0.4 , reflected that the raw SIF irradiance
 443 measured by OCO-2 was twice that measured by PhotoSpec. The lower irradiance values
 444 observed by our PhotoSpec instrument likely resulted from including observations with larger
 445 incident angles between solar and viewing directions, due to including elevation angles up to 45°
 446 below horizon in the calculation of daily-averaged SIF, as well as deploying the telescope on the
 447 south side of the tower. Thus, our tower-based observations included a greater fraction of shaded
 448 vegetation because illumination and viewing angles were often from opposing cardinal
 449 directions. These differences highlight that, while tower- and space-based platforms capture
 450 similar relative patterns in SIF signals, more comprehensive comparisons between SIF
 451 observations require a more complex study of viewing and illumination angle sensitivities in top-
 452 of-canopy SIF observations.

453



454
 455 **Figure 7.** Correlation plot and linear fit results between far-red SIF observations from PhotoSpec and the
 456 OCO-2 satellite. OCO-2 data includes soundings within a one-degree gridcell centered at US-UMB. Each
 457 sounding was multiplied by a daily correction factor, which uses a clear-sky proxy to account for diurnal
 458 changes in the SIF signal. Means were calculated from soundings across individual days, and error bars
 459 represent the standard deviation of included observations. Mean daily values from OCO-2 were then
 460 correlated with the daily-average SIF signal seen from the PhotoSpec instrument, where uncertainties
 461 were propagated from the standard deviation of 20 s observations included in every sub-daily 90-minute
 462 average. Circles indicate data from 2018 and triangles indicate 2019. The color bar is weighted by day of
 463 year.

464 4 Discussion

465 4.1 Dependence of SIF and GPP on PAR

466 While our results align with several studies that suggest that high correlations between
 467 SIF and GPP primarily result from a shared dependence on absorbed radiation or APAR
 468 (Wohlfahrt et al., 2018; K. Yang et al., 2018), our findings also support many studies that have
 469 demonstrated that GPP can be estimated from SIF observations from either satellite (Guanter et
 470 al., 2012; Sun et al., 2017) or tower (Magney, Bowling, et al., 2019; Pierrat et al., 2022; X. Yang
 471 et al., 2015). That the linear relationship between SIF and GPP is largely driven by APAR is
 472 illustrated by stronger correlations between daily-averaged GPP with far-red SIF during spring
 473 and fall months (Figure 4) when canopy changes drive large swings in fPAR. The strong
 474 dependence of SIF on APAR also likely explains why correlations between far-red SIF and GPP
 475 were stronger for weekly-averaged data (which are sensitive to seasonal light variability, but
 476 average away changes driven by clouds and weather) than for daily-averaged data (which reflect
 477 both seasonal and cloud/weather-driven variations in light; Figure 3). However, the decrease in
 478 relative SIF values during the August 2018 drought (Figure 2a, c) demonstrate that SIF signals,
 479 when normalized by light levels, may reflect changes in productivity that are independent from
 480 APAR. This was confirmed by shared intraseasonal patterns between GPP/PAR, an LUE proxy,
 481 and relative SIF (Figure 2c, d), and the strong correlation between detrended GPP/PAR and
 482 relative red SIF during the August 2018 drought. These findings echo X. Yang et al. (2015) who

483 also showed that SIF provided information related to LUE above another temperate deciduous
484 location at Harvard Forest (US-Ha1).

485 We showed that SIF is more closely tied to APAR than to GPP at our site through the fact
486 that daily-averaged SIF data were more strongly correlated with downwelling PAR ($R^2 = 0.90$;
487 Figure 5a), which was roughly proportional to APAR during peak summer conditions with near-
488 constant NDVI, than it was with GPP ($R^2 = 0.61$; Figure 3b). Given that the correlation between
489 GPP and PAR was significantly weaker ($R^2 = 0.51$; Figure 5b), these results demonstrate the
490 challenges in using direct SIF observations to detect changes in LUE as they may not be an
491 effective indicator of synoptic-scale changes in productivity under mid-season conditions where
492 canopy structure and fPAR remain relatively stable. These results contrast with the findings of X.
493 Yang et al. (2015) who found only slightly weaker correlations between SIF and GPP than
494 between SIF and APAR at US-Ha1. US-Ha1 is, however, more radiation-limited than is US-
495 UMB (Wozniak et al., 2020), which would explain a closer coupling between variations in
496 radiation and GPP at their site. Our results are in line with those of K. Yang et al. (2018), who
497 found that SIF is a better indicator of APAR than of GPP albeit over a rice paddy. The different
498 relationships among SIF, GPP, and PAR in these three studies indicate that SIF-derived
499 estimates of productivity may not be free from the need for additional inputs, such as
500 meteorological conditions that may signal ecosystem stress (as have been used for NDVI-derived
501 estimates of GPP; see Running et al., 2004), but also that the necessity of these additional inputs
502 is likely influenced by whether ecosystem productivity is limited by water, temperature, or
503 radiation. At our site, we showed that relative far-red SIF responded to water stress and served as
504 a better proxy than SIF irradiances for seasonally detrended GPP during severe drought, however
505 this was only the case under water-limited conditions. Furthermore, as relative far-red SIF
506 tracked productivity only during drought conditions where SIF and PAR were decoupled from
507 GPP, we could not derive a simple regression model that combined absolute and relative SIF
508 observations to reflect both stressed and non-stressed conditions. Future studies should
509 investigate the necessity of using ancillary data or relative SIF to model GPP from space-based
510 SIF observations across ecosystems comprised of various plant types and also characterized by
511 various productivity limiting factors.

512 4.2 Relationship between SIF and Ecosystem Productivity

513 One key finding from this study is the variable relationship between far-red SIF and GPP
514 over the course of the growing season, with the linear slope between 90-minute far-red SIF and
515 GPP decreasing over the course of the growing season (Figure 4a). While a seasonally changing
516 relationship between SIF and productivity has been noted in previous studies (e.g. K. Yang et al.,
517 2018), these studies occurred over cropland where such changes could be attributed to structural
518 changes among different phenological stages. While we see the most drastic changes in spring
519 when there is rapid structural change, we show that the SIF:GPP relationship above a temperate
520 deciduous forest continues to evolve after the emergence of a well-developed canopy when
521 changes in canopy structure are minimal. The higher SIF:GPP slope in spring suggests that
522 assuming constant proportionality may lead to an overestimate of productivity in springtime, or
523 an underestimate in fall, when converting SIF to GPP based on an annual mean slope. Butterfield
524 et al. (2020) showed that interannual variability in satellite-based SIF observations is higher in
525 spring and is in better agreement with optical vegetation indices, whereas IAV in fall SIF is
526 small and only weakly correlated with other remote sensing products. The seasonal decline in the

527 SIF:GPP relationship could partly explain this phenomenon since it suggests that late-season
528 observations are characterized by a lower signal (and thus a lower signal-to-noise ratio) than are
529 spring data, potentially obscuring IAV. The decrease in the SIF:GPP slope as the growing season
530 progresses (Figure 4a) may be due to leaf age effects that impart subtle changes in the canopy.
531 Specifically, if leaves wilt or shrivel as they age due to progressive water stress, absorption of
532 PAR may shift slightly deeper into the canopy where f_{esc} is lower, thus leading to lower top-of-
533 canopy SIF. In the future, observations of leaf area and angle distribution over the course of the
534 growing season, in combination with canopy radiative transfer modeling, may help to further
535 elucidate the drivers of seasonal changes in the SIF:GPP slope.

536 The challenges of using SIF to estimate productivity under stable canopy conditions were
537 further illustrated by the limited response of red or far-red SIF irradiances to summer declines in
538 GPP. When GPP declined in response to drought conditions in August 2018, SIF signals
539 continued to reflect changes in radiation. Wohlfahrt et al. (2018) similarly found that SIF signals
540 in a Mediterranean pine forest exhibited poor correlation with GPP during a heat wave, although
541 their data indicated that that top-of-canopy SIF signals eventually declined in response to losses
542 in productivity. Marrs et al. (2020) also found that SIF signals in individual deciduous species
543 did not exhibit an immediate response to induced water stress. Yet, we found that relative far-red
544 SIF tracks stress-induced changes in GPP more effectively than SIF irradiances and various
545 vegetation indices over both daily and 5-day timescales, and that relative red SIF consistently
546 mirrored synoptic-scale changes in GPP/PAR, indicating that SIF observations do capture
547 changes in GPP and LUE when isolated from their dependence on PAR. While PAR levels in
548 Wohlfahrt et al. (2018) were largely consistent from day to day, indicating that SIF irradiances
549 should have been roughly proportional to relative SIF, we note the differences in timescale
550 between our two studies (i.e., the heatwave in their study occurred over a period of 8 days while
551 our observations captured the effects of longer-term, cumulative drought stress).

552 4.3 Applications of the Red:Far-red SIF Ratio

553 Our results show that the red:far-red SIF ratio is sensitive to changes in downwelling
554 PAR as well as canopy structure at both seasonal and interannual scales. Similar to Magney,
555 Frankenberg, et al. (2019), we saw considerably higher red:far-red ratios during early spring
556 canopy development, and in late fall as canopy chlorophyll content dropped, and as lower leaf
557 area and decreased chlorophyll content lead to decreased reabsorption of red SIF by the canopy.
558 The red:far-red SIF ratio showed significant differences between 2018 and 2019, with 2018
559 ratios being slightly lower than in 2019. These year-to-year differences in the red:far-red SIF
560 ratio are very likely explained by 2018 having greater NDVI and LAI values (see section 3.2), in
561 turn leading to variations in the canopy escape ratio for red fluorescence on interannual
562 timescales. However, we also showed that the red:far-red SIF ratio is highly correlated with
563 downwelling PAR (Figure 6c), suggesting that it is also dependent on light conditions that are
564 independent of canopy traits. These results highlight the value in simultaneous retrievals of SIF
565 at multiple wavelengths, which are becoming increasingly available from satellites such as
566 TROPOMI (Köhler et al., 2020), but also demonstrate that the interpretation of SIF observations

567 at multiple wavelengths must be cognizant of differences in sensitivity to ecosystem and
568 environmental changes on synoptic, seasonal, and interannual timescales.

569 Our results highlight the difficulty in leveraging the red:far-red SIF ratio to detect
570 ecosystem stress. Magney, Frankenberg, et al. (2019) showed that stressed conditions lead to a
571 lower red:far-red ratio at the leaf level, but that these leaf-level changes in NPQ were not
572 noticeable in canopy-level measurements. In contrast, Wohlfahrt et al. (2018) observed an
573 increase in the red:far-red ratio coinciding with a heat wave, and hypothesized that the
574 contrasting response of SIF at different wavelengths may have been due to a decrease in
575 chlorophyll content leading to less reabsorption of red fluorescence. Our results generally
576 corroborated Magney, Frankenberg, et al. (2019; see their Figure 7b, our Figure S6), and showed
577 that while the red:far-red SIF ratio at canopy-scale does reflect seasonal and interannual changes
578 in canopy structure, it is also influenced by changes in downwelling PAR (Figure 6c). Thus,
579 further studies into the response of the red:far-red SIF ratio to environmental stress would require
580 a detailed analysis of both the influence of phenological changes in canopy structure as well as
581 incoming light conditions on top-of-canopy SIF observations. These analyses necessitate that
582 observations be made at high temporal frequency since year-to-year or even month-to-month
583 changes are primarily driven by changes in canopy structure that are independent from
584 environmental stress, as well as the incorporation of canopy radiative transfer modeling.

585 **5 Conclusions**

586 We deployed a PhotoSpec system with two high spectral resolution spectrometers to measure red
587 and far-red SIF to a deciduous forest in northern Michigan. Results from the first two years of
588 data acquisition showed that SIF signals over a temperate deciduous forest are more strongly
589 related to radiation than to photosynthetic productivity. While a shared dependence on PAR did
590 result in a significant correlation between SIF and GPP, the slope of this linear relationship
591 gradually decreased over the course of the growing season, indicating that temporal changes in
592 the far-red SIF:GPP ratio should be considered when using SIF to assess ecosystem productivity.

593 Our study demonstrates challenges in using SIF irradiances to detect short-term stress-induced
594 declines in ecosystem productivity. Nonetheless, we show that observations of relative SIF may
595 be a more reliable indicator of ecosystem stress, indicating that SIF signals do respond to stress-
596 induced changes in productivity and track changes in LUE after accounting for changes in solar
597 radiation. Additionally, we show that the red:far-red SIF ratio is sensitive to seasonal and
598 interannual changes in canopy structure. Our results point to the need for coordinated multi-scale
599 studies on the relationship between SIF and photosynthesis including at the leaf and canopy
600 level, especially under conditions of environmental stress.

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606 the University of Michigan, for their assistance with the construction of the PhotoSpec
607 instrument.

608 **Open Research**

609 SIF and other PhotoSpec data are available at <https://doi.org/10.7302/sx8c-y281>. AmeriFlux
610 environmental and eddy flux data are available at <https://doi.org/10.17190/AMF/1246107>.
611 OCO-2 SIF data are available at <https://doi.org/10.5067/XO2LBBNPO010>.

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Supporting Information for

Accounting for Changes in Radiation Improves the Ability of SIF to Track Water Stress-Induced Losses in Summer GPP in a Temperate Deciduous Forest

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Contents of this file

Text S1

Figures S1 to S6

Introduction

The supporting information include additional methods and results that are relevant but not critical to the conclusions of the paper. Contents include:

- a brief explanation and list of equations used to calculate vegetation indices included in the study;
- several figures that present supplemental information using similar methods as described in the main manuscript.

Text S1. Equations for calculating vegetation indices

The normalized difference vegetation index (NDVI; Tucker, 1979), photochemical reflectance index (PRI; Gamon et al., 1992), and chlorophyll index (Chlorophyll_{RS}; Datt, 1999; Magney et al., 2019) were calculated using the below equations using canopy reflectance observed by the broadband Flame spectrometer (Ocean Optics Inc.). R_λ represents the reflectance at a wavelength of λ nm, or in the red (620-670 nm) or near-infrared (NIR; 830-860 nm) regions of the electromagnetic spectrum.

$$\text{NDVI} = (R_{\text{NIR}} - R_{\text{Red}})/(R_{\text{NIR}} + R_{\text{Red}}) \quad (\text{S1})$$

$$\text{PRI} = (R_{531} - R_{570})/(R_{531} + R_{570}) \quad (\text{S2})$$

$$\text{Chlorophyll}_{\text{RS}} = (R_{850} - R_{710})/(R_{850} + R_{680}) \quad (\text{S3})$$

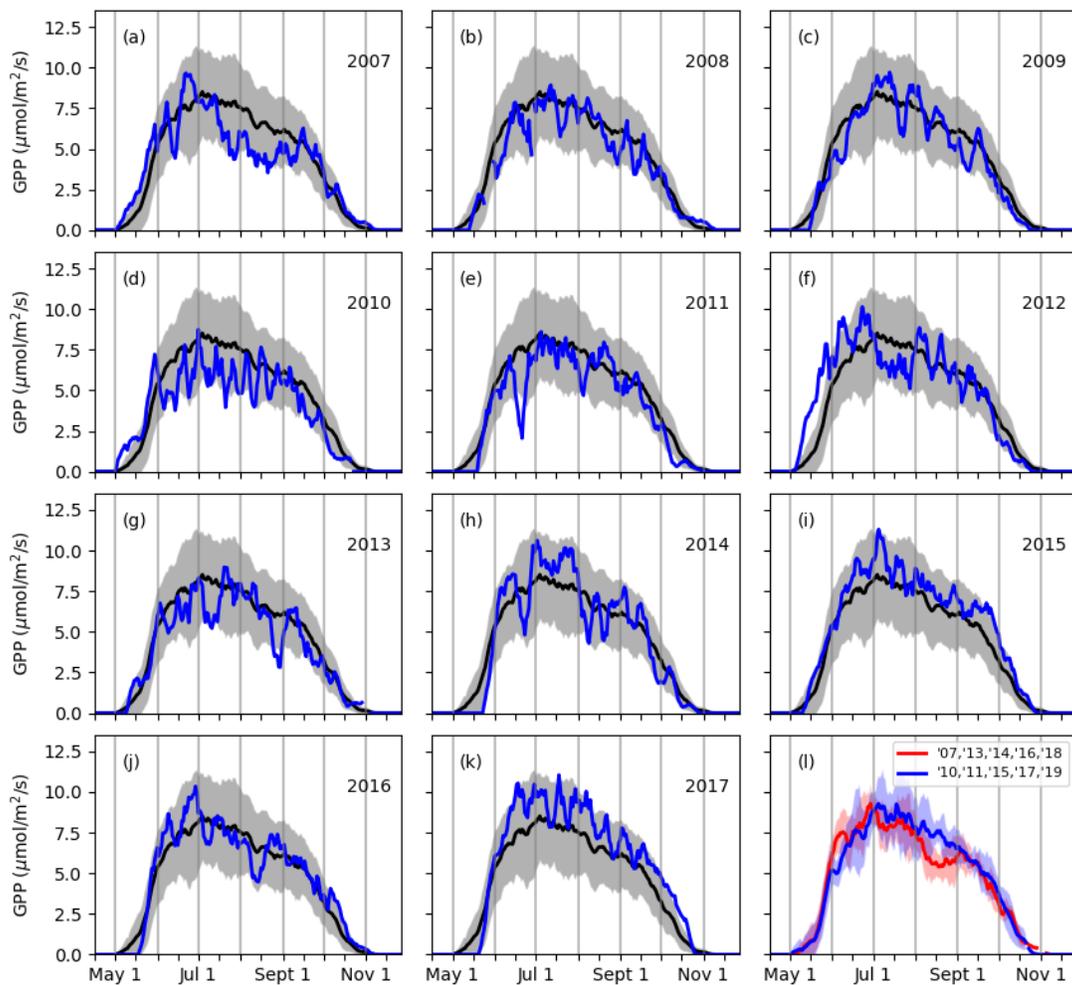


Figure S1. Observations of gross primary productivity (GPP) at US-UMB for 2007-2017 (a-k) and composite means of years with and without late-summer dips in productivity (l). In panel l, the mean of 2007, 2013, 2014, 2016, and 2018 is shown in red as years experiencing summer losses in productivity, while the mean of 2010, 2011, 2015, 2017, and 2019 is shown in blue as years that did not see summer losses (see also Figure 1a). The black line in panels a-k represents the 2007-2019 multi-year mean. Shading in all panels represents ± 1 standard deviation of the respective multi-year means.

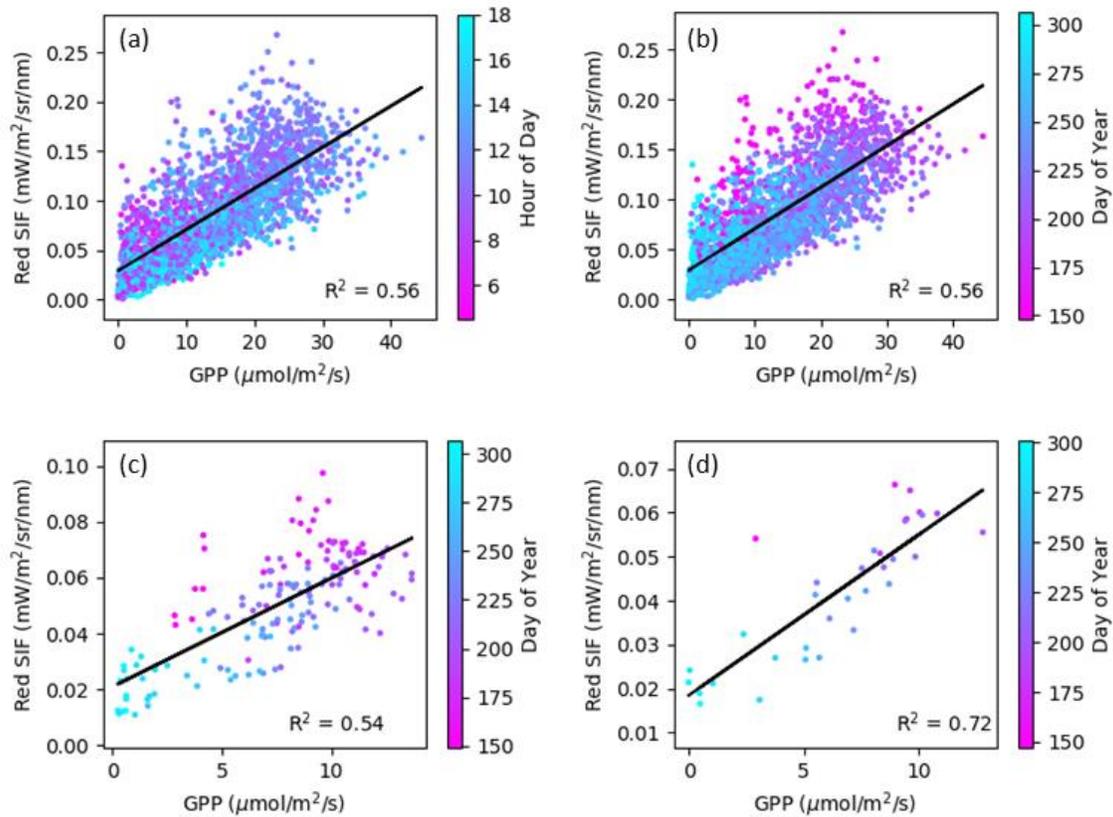


Figure S2. Correlation plots between red solar-induced chlorophyll fluorescence (SIF) and GPP at 90-minute (a, b), daily (c), and weekly (d) temporal resolution observations. Color bars are weighted by day of year (b-d) or by hour of day (a).

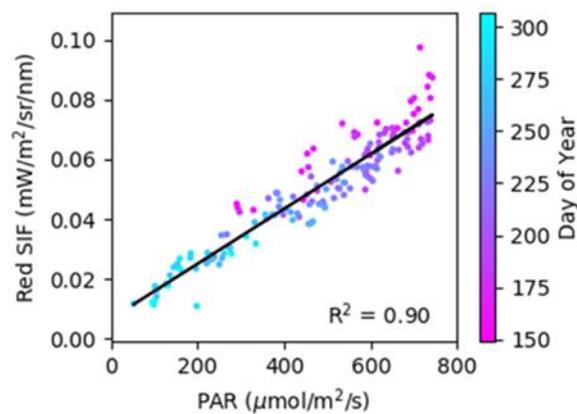


Figure S3. Correlation plot between daily-averaged red SIF and photosynthetically active radiation (PAR). Color bar is weighted by day of year.

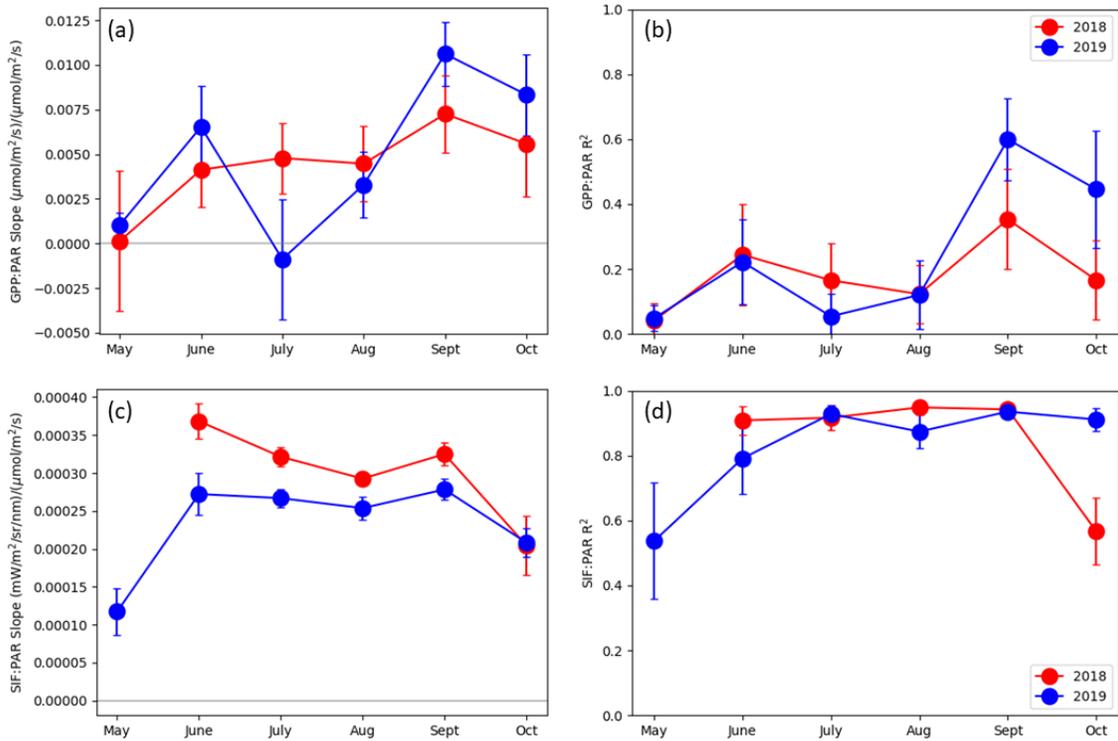


Figure S4. Slopes and correlation coefficients from monthly linear fits of daily-averaged GPP (a, b) and far-red SIF (c, d) with PAR. Data from 2018 are in red, while 2019 data are in blue. Error bars represent the standard deviations of results from a bootstrapping method used to test the robustness of the linear regressions.

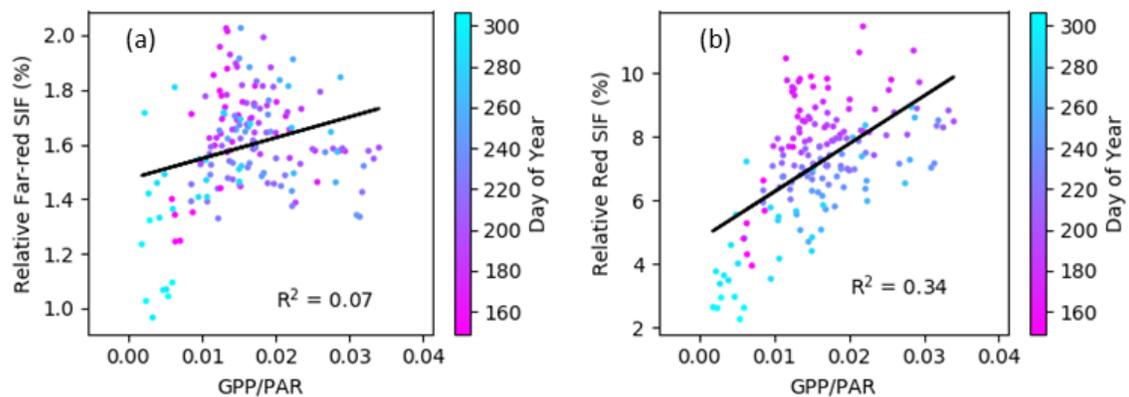


Figure S5. Correlation plot between daily-averaged relative far-red (a) and red (b) SIF and GPP/PAR, an LUE proxy. Color bar is weighted by day of year.

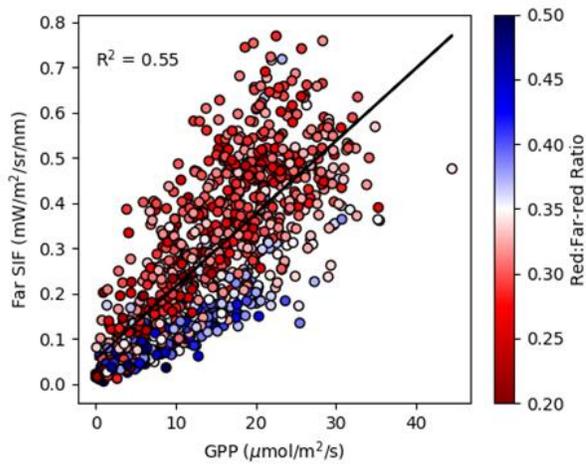


Figure S6. Correlation plot between 90-minute far-red SIF and GPP observations. Color scale is weighted by the red:far-red SIF ratio. (Compare with Figure 7b from Magney et al., 2019.)

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