Satellite-Detected Contrasting Responses of Canopy Structure and Leaf Physiology to Drought

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***Abstract*—Disentangling drought impacts on plant photosynthesis is crucial for projecting future terrestrial carbon dynamics. We examined the separate responses of canopy structure and leaf physiology to an extreme summer drought that occurred in 2011 over Southwest China, where the weather was humid and radiation was the main growth-limiting factor. Canopy structure and leaf physiology were, respectively, represented by near-infrared reflectance of vegetation (NIRv) derived from MODIS data and leaf scale fluorescence yield (Φ_f) derived from both continuous SIF (CSIF) and global OCO-2 SIF (GOSIF). We detected contrasting responses of canopy structure and leaf physiology to drought with a 14.0% increase in NIRv, compared with 12.6 or 19.3% decreases in Φ_f from CSIF and GOSIF, respectively. The increase in structure resulted in a slight carbon change, due to water deficit-induced physiological constraints. The net ecosystem effect was a 7.5% (CSIF), 1.2% (GOSIF), and −2.96% (EC-LUE GPP) change in photosynthesis. Our study improves understanding of complex vegetation responses of plant photosynthesis to drought and may contribute to the reconciliation of contrasting observed directions in plant responses to drought in cloudy regions via remote sensing.**

***Index Terms*—Canopy structure, leaf physiology, plant photosynthesis, solar-induced chlorophyll fluorescence (SIF), summer drought.**

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I. Introduction

EXTREME drought events are expected to increase in frequency and intensity under ongoing global warming [1], [2]; however, effects of drought on vegetation dynamics represent a key source of uncertainty in projection models of climate change impacts on plant photosynthesis and the terrestrial carbon (C) pool [3]. Main impacts of drought on plant photosynthesis are mediated through changes in canopy structure and leaf physiology [4], such as increases in leaf abscission and senescence that reduce the area of transpiration and associated water demand and increase the risks of xylem embolism and plant desiccation [5], and closure of stomata and inhibition of photosynthetic enzyme activity [6], [7], respectively. Thus, changes in photosynthetically active radiation (PAR) and carbon dioxide (CO_2) assimilation rates due to canopy structure and leaf physiology responses to drought conditions co-determine rates of ecosystem photosynthesis [8].

Large-scale monitoring of drought impacts on vegetation is currently achieved through remote sensing techniques [9], where greenness vegetation indices (VIs), such as the normalized difference vegetation index (NDVI), enhanced vegetation index (EVI), and near-infrared reflectance of vegetation (NIRv), are used to diagnose ecosystem-level effects of drought [10], [11]. However, as these VIs principally indicate green biomass [12], they may capture long-term effects of drought on canopy structure, but not immediate physiological responses [13].

Satellite-recorded solar-induced chlorophyll fluorescence (SIF) data provide an alternative approach to monitoring effects of drought [14], [15], [16], because they represent the emission of energy emanating from excited chlorophyll molecules, following light absorption; given photosynthesis and SIF compete for the same type of excited energy, SIF carries information on leaf-scale rates of photosynthesis [17], [18]. Satellite-recorded SIF comprises an integrated signal that may be decomposed as the product of absorbed PAR (APAR), fraction of leaf-scale SIF photons escaping the canopy (canopy escape fraction), and intrinsic leaf-scale fluorescence yield, where the first two terms represent canopy structure and the third term represents leaf physiology [19], [20], [21]; therefore, leaf physiological responses to drought may be decoupled from canopy responses

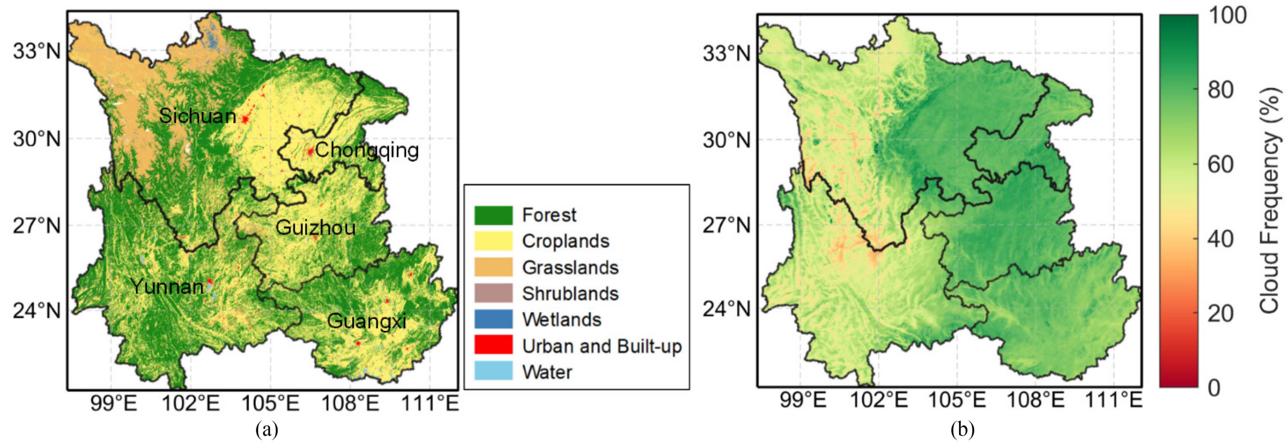

Fig. 1. Land cover (a) and cloud frequency (b) in Southwest China. The climate change initiative land cover product in 2011 was used to represent land cover [22]. Cloud frequency was quantified as the proportion of cloudy days from the MOD35 product [23].

by normalizing SIF, using APAR, to obtain canopy-scale fluorescence yield that is equivalent to the product of leaf-scale fluorescence yield and canopy escape fraction [24], [25], [26]. However, the canopy-scale fluorescence yield is confounded by canopy structure information, due to the involvement of the canopy escape fraction that itself is difficult to estimate precisely, as a result of the complexity of canopy radiative transfer processes [27], [28]. Zeng et al. [21] proposed a practical approach to improve the precision of canopy escape fraction estimates, by combining the NIRv with the fraction of absorbed PAR (fPAR) that allows information on leaf physiology to be disentangled from the integrated SIF signal.

The aim of this article was to decouple and compare responses of leaf physiology and canopy structure to an extreme drought event that occurred in summer 2011 in the region of southwest China. Using satellite greenness VIs, Song et al. [29] detected enhanced plant structural growth in response to the drought, during which there was a 40% decrease in average rainfall, and attributed this counterintuitive finding to increased levels of radiation that occurred during the drought period and radiation is known to be a main limiting factor for plant growth therein [30]. Given drought reduces photosynthesis [31], this unexpected finding reported by Song et al. [29] led us to investigate: whether current satellites can detect contrasting responses of canopy structure and leaf physiology to the summer 2011 drought and (2) the net effect of this episode on ecosystem photosynthesis.

II. Materials and Methods

A. Study Area

Croplands, forests, and grasslands are the dominant land covers of the Southwest China study area [see Fig. 1(a)]; this area accounts for >30% of assimilated CO_2 nationally (mainland) and represents the largest C reservoir in the country [11]. The study area is dominated by a subtropical monsoon climate, with an annual average temperature of 15°C and cumulative precipitation of 1100 mm that results in high levels of humidity. Ecosystems tend to be susceptible to droughts, due to the widespread distribution of karst landform in the region [29], [32], and plant growth is radiation-limited [30], particularly in the east, as a result of high levels of cloud cover [see Fig. 1(b)].

B. Dataset

1) Satellite Data:

a) MCD43A4: Land surface reflectances were derived from the MCD43A4 v006 nadir bidirectional reflectance distribution function adjusted reflectance product, with a daily and 500 m resolution [33]. The retrieved values are produced daily, based on a 16-day retrieval period, with the nominal date occurring on the ninth day. We only selected observations with high quality (quality flag indicating "processed, good quality").

b) Continuous SIF: Continuous SIF (CSIF) is a machine learning derived SIF product with a 4-day and 0.05° resolution. Training of the machine learning algorithm was based on the discrete orbiting carbon observatory-2 (OCO-2) SIF observations, using MODIS reflectances and fPAR as inputs. CSIF is correlated with satellite SIF retrievals and *in situ* flux based gross primary productivity (GPP)estimates [34].

c) Global OCO-2 SIF: To obtain robust results, we also used global "OCO-2" SIF (GOSIF), with an 8-day and 0.05° resolution, to monitor variation in vegetation photosynthesis during drought. Like CSIF, GOSIF was generated using a machine learning method, based on discrete OCO-2 observations, MODIS EVI, MERRA-2 reanalyzed data (including PAR), vapor pressure deficit, and air temperature [35].

d) EC-LUE GPP: EC-LUE GPP is derived from the light use efficiency (LUE) model based on eddy covariance (EC) measurements. The model is driven by NDVI, PAR, air temperature, and the Bowen ratio of sensible to latent heat flux [36].

e) Climate change initiative (CCI) land cover: We used the CCI land cover product, which identifies land cover types at an annual and 300-m resolution [22], for 2011. We merged evergreen, deciduous, and mixed forests into a simplified "forests" class.

2) Climate Data:

a) ERA-5 LAND: The ERA-5 land reanalysis dataset provides continuous climate variables with a 0.1° spatial and hourly temporal resolution. We used monthly mean 2 m air temperature, total precipitation, and surface solar radiation downwards data, calculated from the original hourly dataset by the European Centre for Medium-Range Weather Forecasts [37].

b) Standard precipitation-evapotranspiration index (SPEI): Given the SPEI is based on the balance between precipitation and potential evapotranspiration, it is a good proxy for water availability mediated by surface water supply and atmospheric water demand. SPEI integrates the cumulative effects from the preceding 1 to 48 months and the gridded SPEI dataset is available at a 0.5° and monthly resolution [38]. To maintain consistency with existing studies, we used a 3-month time-scale SPEI and identified a drought event as SPEI <-0.5 [39].

C. Methods

1) Decoupling structural and physiological responses to drought: We used NIRv to characterize canopy structural responses to drought, expressed as the product of NDVI and near-infrared reflectance:

$$\mathrm{NIRv} = \mathrm{NDVI} \times \mathrm{NIR} = \frac{\mathrm{NIR} - \mathrm{Red}}{\mathrm{NIR} + \mathrm{Red}} \times \mathrm{NIR} \tag{1}$$

where NIR and Red are near-infrared and red reflectances, respectively, derived from the MCD43A4. NIRv is directly related to the number of NIR photons reflected by plants, with a lower contribution by soil contamination and represents the vegetation capacity of capturing light. Changes in chlorophyll content (canopy structure) in response to drought stress lead to shifts in reabsorption and canopy scattering patterns that affect vegetation NIR; therefore, NIRv is a reliable proxy for canopy structure [40], [41], [42].

Leaf physiology information was extracted from the decomposition of satellite-recorded SIF [19], [20], [21]

$$\mathrm{SIF} = \mathrm{PAR} \times f\mathrm{PAR} \times \Phi_\mathrm{f} \times f_{esc} \tag{2}$$

where, fPAR is the absorbed fraction of PAR, Φ_f represents leaf-scale fluorescence yield, and f_esc is the canopy escape fraction. As Φ_f and photosynthesis compete for the same excited energy at the leaf-scale [17], [18] and there is a positive relation between Φ_f and light-use efficiency of photosynthesis [43], we used Φ_f as an indicator of leaf physiology, by inversing (2)

$$\Phi_f = \frac{\mathrm{SIF}}{\mathrm{PAR} \times f\mathrm{PAR} \times f_{esc}} \tag{3}$$

where f_{esc} may be approximated [21]

$$f_{esc} = \frac{\mathrm{NIRv}}{f\mathrm{PAR}} \tag{4}$$

so that Φ_f may be simplified from (4) and (3)

$$\Phi_f = \frac{\mathrm{SIF}}{\mathrm{PAR} \times \mathrm{NIRv}}. \tag{5}$$

Surface solar radiation downwards from ERA-5 datasets was used to represent PAR and, to increase the robustness of our results, CSIF and GOSIF datasets were used as SIF proxies.

2) Data Analysis: The extracted datasets varied in spatial and temporal resolutions, so they were resampled to 0.05° and restricted to summer observations (June, July, and August). We used cumulative ERA-5 precipitation data across the summer months, while data for the other indicators were averaged to improve robustness of our analyses, because temporal aggregation of data alleviates uncertainty associated with cumulative and lagged effects of drought on canopy structure [44].

We compared data for multiple vegetation and climate variables from the drought summer of 2011 relative to normal summers (in 2007 and 2008) for the study area, as done elsewhere [29], when no drought episodes were detected, based on SPEI <-0.5. To improve the robustness of the comparison, we calculated relative changes between the drought and normal years (ΔI)

$$\Delta I = \frac{Id - Ir}{Ir} \tag{6}$$

where Id is the summer (June, July, and August) mean value of NIRv and Φ_f indicators in the drought year 2011 and Ir is the reference value, computed as the 2-year summer average of the indicators over 2007–2008. Using a long time scale (3 months) can partially minimize influence of the "memory" effect on our results. In addition, we explored the responses of ΔNIRv and $\Delta\Phi_f$ to SPEI through the Pearson's correlation in the drought pixels, respectively.

III. Results

In summer 2011, Southwest China experienced widespread drought (SPEI < -0.5), with 43.8% of the area, particularly in Guizhou province and its environs, exposed to severe and extreme levels of drought (SPEI < -1.5) [see Fig. 2(a)]. There were high levels of precipitation deficit in the areas under drought conditions, where 21.8% of the study area experienced a $>$ 40% decrease in precipitation [see Fig. 2(b)], and spatial increases in solar radiation and air temperature [see Fig. 2(c) and (d)] tended to reflect the precipitation anomaly.

There was a general positive response in canopy structure to drought, as indicated by relative changes in NIRv (ΔNIRv) (see Fig. 3) and there was a significantly negative spatial correlation between ΔNIRv and SPEI ($r = -0.23$ and $P < 0.001$). The spatial distribution of the pixels with positive ΔNIRv agrees with that of drought [low SPEI and decreased precipitation in Fig. 2(a) and (b), respectively].

In contrast to the positive response of vegetation structure to drought, analysis of leaf physiology based on CSIF and GOSIF showed spatially similar negative responses, albeit with contrasting magnitudes [see Fig. 4(a) and (b)] and a positive spatial correlation with SPEI [see Fig. 2(a)] (r = 0.21 and 0.25, respectively, both with a $P < 0.001$). GOSIF generally detected lower levels of leaf physiology responses than CSIF (mean relative change in leaf-scale fluorescence yield: -19.3 and -12.6%, respectively).

NIRv increased and Φ_f decreased for all the vegetation types during drought period. Specifically, NIRv increased by 16.78%,

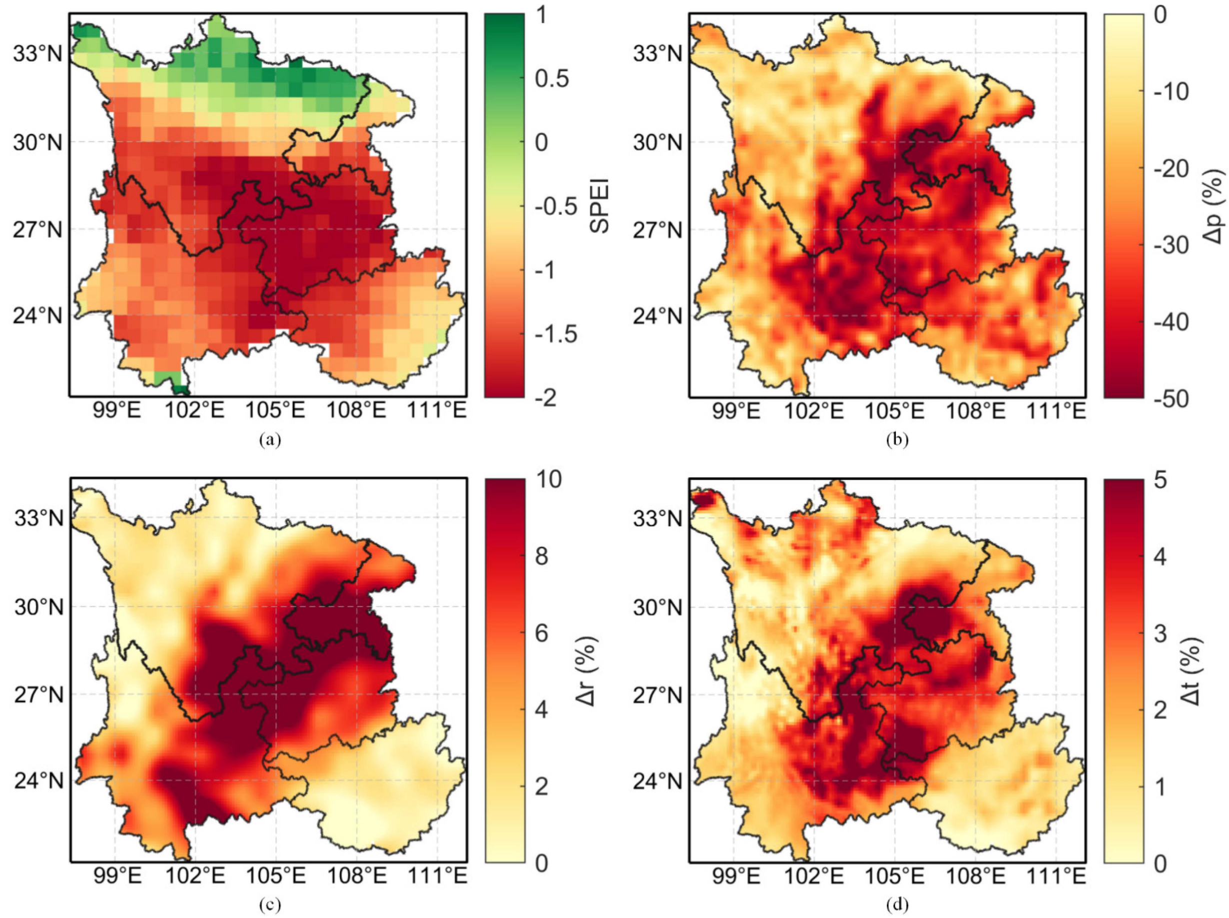

Fig. 2. Spatial distributions of (a) SPEI and relative changes in (b) Precipitation (Δp), (c) solar downward radiation (Δr), and (d) temperature (Δt) between summer 2011 and 2007–2008 across Southwest China.

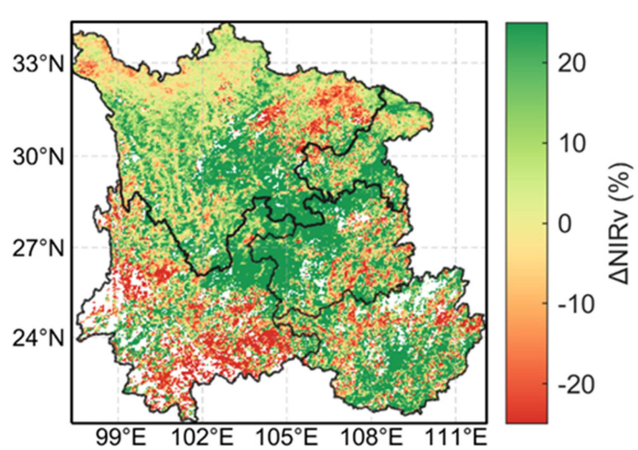

Fig. 3. Canopy structure responses to the 2011 summer drought over Southwest China, based on relative change in NIRv for summer 2011 compared with 2007–2008.

17.26%, and 10.89% for croplands, forests and grasslands, respectively, during drought period, compared to the base year (see Fig. 5).

ΔNIRv increased with intensifying drought (decreasing SPEI), while CSIF and GOSIF derived Φ_f both decreased with intensifying drought. The similar results were observed for all the vegetation types. The correlation between ΔNIRv / $\Delta\Phi_f$ and SPEI of grasslands was the strongest (absolute correlation coefficient, R, larger than 0.7) among the selected vegetation types, may be due to its shallow root (see Fig. 6).

Analysis of net effects of the 2011 drought event on ecosystem photosynthesis, based on ΔSIF observations from CSIF and GOSIF, shows the 14.0% (see Fig. 3) increase in structural growth resulted in 7.5% (CSIF) and 1.2% (GOSIF) increases in photosynthesis (see Fig. 7), after accounting for effects on leaf physiology (see Fig. 4), and reveals a lack of coincidence with the spatial distribution of SPEI and precipitation [see Fig. 2(a) and (b)].

In order to confirm the net effects of drought on plants more accurately, we also used EC-LUE GPP to investigate change of GPP during summer 2011. The result showed that EC-LUE GPP decreased by -2.96% during drought (see Fig. 8). Like CSIF and GOSIF (see Fig. 7), the direct GPP product also changed slightly.

Partial correlation separated the respective contributions of climatic variables to the variations in canopy structure and leaf

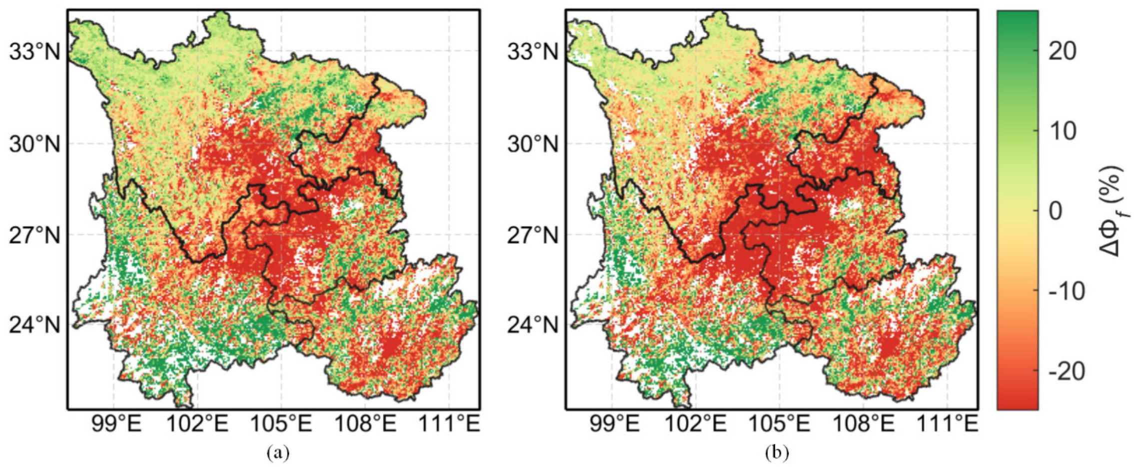

Fig. 4. Responses in leaf physiology to summer drought in 2011, based on analysis of relative changes in leaf-scale fluorescence yield (5) in the (a) CSIF and (b) GOSIF products between 2011 and 2007–2008.

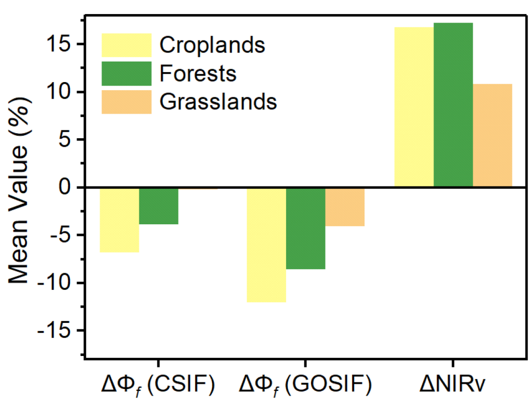

Fig. 5. Relative change of NIRv, and CSIF and GOSIF derived leaf-scale fluorescence yield in summer 2011 compared with 2007–2008.

physiology. Radiation contributed the most to the variation of both canopy structure (NIRv) and leaf physiology [Φ_f (CSIF) and Φ_f (GOSIF)], but with opposite directions (see Fig. 9). The increase of radiation stimulated the growth of canopy structure ($R = 0.16$) and inhibited leaf physiology ($R = -0.13$ and -0.18 for CSIF and GOSIF, respectively). Compared with radiation, temperature and precipitation had slighter effect. Decreased precipitation was often accompanied by increased radiation, so the signs of partial correlation coefficient for precipitation and radiation were opposite. And the same results were found for different vegetation types, such as grassland, croplands and forests, suggesting that the result was independent of vegetation type and was universal across the region.

IV. Discussion

We have demonstrated it is possible to separate canopy structural components of plant photosynthesis from leaf physiological components using NIRv and Φ_f as respective proxies. Using this approach, we detected contrasting responses in canopy structure and leaf physiology to the 2011 summer drought in Southwest China, where increases in structural growth and reductions in leaf physiological function reflect the complexity of drought impacts on plant photosynthesis.

A. Decoupling Vegetation Structure From Physiology

The photosynthetic capacity of plants depends on the integration of APAR with LUE, where APAR is the product of incident PAR and fraction of PAR that is absorbed by green vegetation and is determined by canopy structure [45], while LUE is determined by leaf physiology [46]. Therefore, the net effects of drought on plant photosynthetic activity depend on combined canopy structure and leaf physiology responses.

We used NIRv, which is insensitive to background influences [40], [41], [42], to represent canopy structure and we extracted leaf physiology information from decomposing the satellite-recorded SIF signal (5) to decouple leaf-scale (Φ_f) from canopy-scale fluorescence yield ($\Phi_f \times f_{\mathrm{esc}}$) that has been used in previous studies [24], [25], [26]. Although $\Phi_f \times f_{\mathrm{esc}}$ is highly sensitive to leaf physiology, it remains confounded by canopy structure through reabsorption and multiple scattering, due to the inclusion of f_{esc}, so the greatest challenge in decoupling Φ_f from SIF observations is the estimation of f_{esc}. The complex radiative transfer process of leaf emitted fluorescence renders the precise estimation of f_{esc} near-impossible [27], [28], while variation in canopy structure has been shown affect f_{esc} [47], [48]. Here, we used the approximated estimation method for f_{esc} [21] (4) and successfully extracted Φ_f. A novel method to extract Φ_f involves the normalization of SIF using NIR radiance of vegetation rather than PAR $\times$ NIRv (5) [49] and, as it does not require input PAR at a coarse resolution, it definitively eliminates the impact of canopy structure and sun-sensor geometry. Dechant et al. [47] had compared two normalization methods, NIR radiance of vegetation and PAR $\times$ NIRv, and observed a high consistency between them. Therefore, the normalization used in this article may not cause too much uncertainty to our results. We will implement a deep comparison between the two methods with a latest drought event.

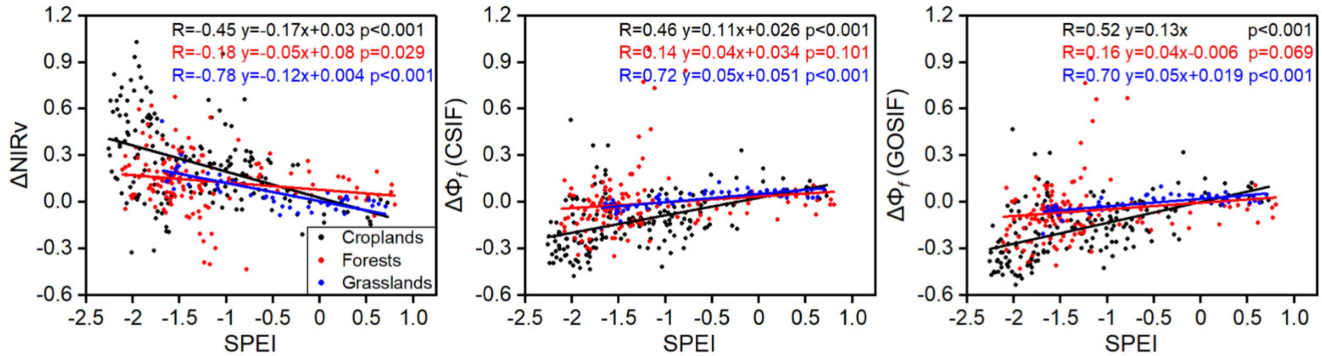

Fig. 6. Scatter plots of SPEI versus ΔNIRv. (a) CSIF derived- and (b) GOSIF derived-$\Delta\Phi_f$ (c). ΔNIRv and $\Delta\Phi_f$ are relative change of NIRv and leaf-scale fluorescence yield in summer 2011 compared with 2007–2008. The regressed results for three land cover types, i.e., croplands, forests and grasslands, were also shown in the figures.

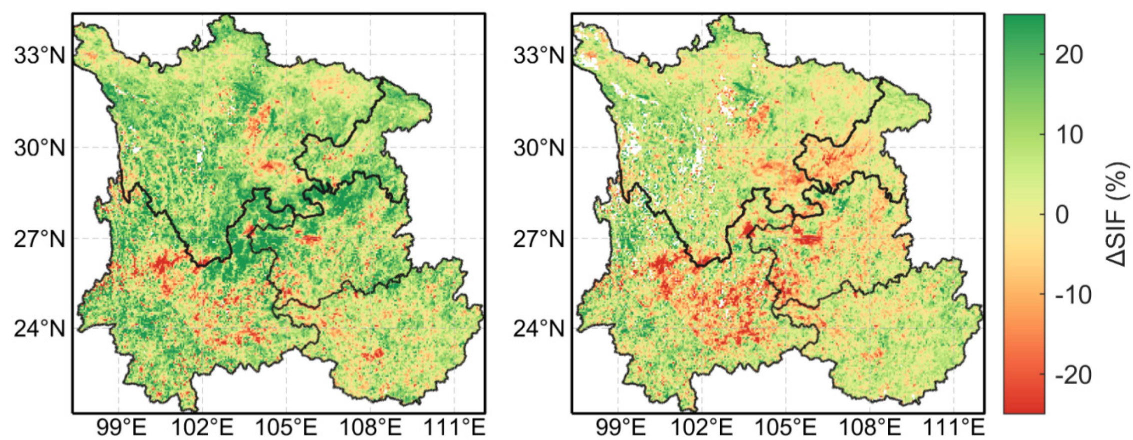

Fig. 7. Ecosystem photosynthesis responses to summer drought in 2011, based on analysis of relative changes in SIF in the (a) CSIF and (b) GOSIF products between 2011 and 2007–2008.

SIF is mechanistically linked to photosynthetic activity so, satellite-recorded SIF has been widely used to represent GPP at large-scales [14]; however, it remains unclear whether satellite-recorded SIF carries leaf physiology information. Although variations in SIF are expected to be driven predominantly by APAR and f_{esc}, rather than Φ_f [21], [50], impacts of environmental stress have yet to be tested, and it is likely to reveal a wider dynamic range of Φ_f. Nevertheless, SIF has been shown to detect drought earlier and stronger than greenness VIs [10], [20], [25], [26], [51], indicating that SIF may indeed reflect leaf physiology under water stress conditions. Under stress conditions, when energy dissipated as heat for photoprotection is saturated, the relationship between fluorescence yield and photochemical yield remains uncertain [43], [52]. In addition, due to the different inputs of reconstructed CSIF and GOSIF, the two datasets yielded an opposite pattern in the central region of our study area where solar radiation was enhanced (see Fig. 7). Therefore, dedicated field measurements are urgently needed to test the reliability of fluorescence yield as an indicator of LUE as well as to collect actual SIF to revise the response of vegetation to drought.

B. Implications

The detection of enhanced structural growth in response to the 2011 summer drought over Southwest China, despite intense levels of water deficit [29] is supported by our study. We suggest this response was driven by increased levels of radiation, which is a limiting factor for plant growth in that region [30], as indicated by the similar spatial patterns of relative changes in radiation and NIRv [see Figs. 2(c) and 3]. In contrast to lag responses of canopy structure to drought conditions, those of leaf physiology, including closure of stomata to avoid cavitation and inhibition of Rubisco enzyme activity [4], are more rapid and reduce leaf photosynthetic rates. We found NIRv increased and Φ_f decreased for all vegetation types during summer drought period at large scale (see Fig. 5). The suppression of leaf physiology (represented by decreased Φ_f) by drought was

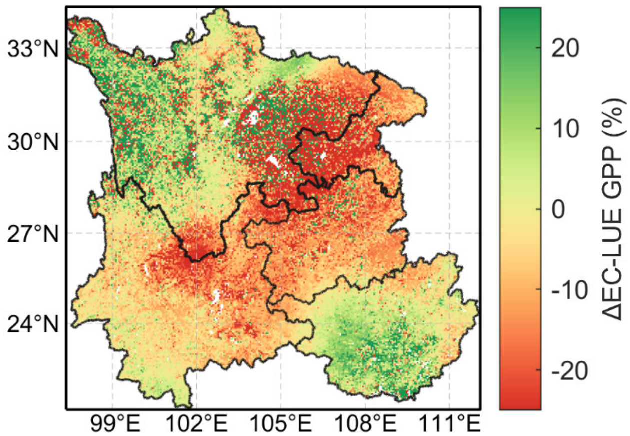

Fig. 8. Ecosystem photosynthesis responses to summer drought in 2011, represented by relative changes in EC-LUE GPP between 2011 and 2007–2008.

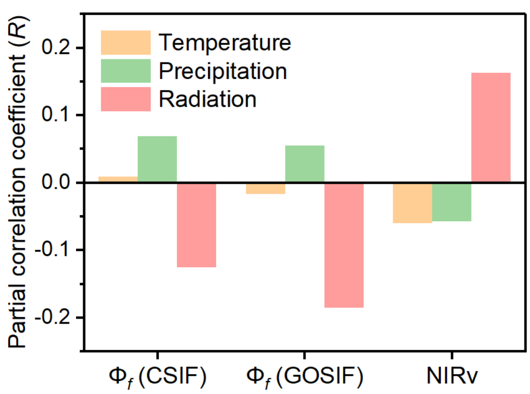

Fig. 9. Partial correlation coefficient between different climatic variables (temperature, precipitation, and radiation) and vegetation parameters (CSIF derived and GOSIF derived Φ_f, and NIRv).

consistently reported by field measurement studies [53], [54]. However, there were still differences in field measurements of the response of canopy structure to drought among different vegetation types, and both the slight impact of drought on canopy structure and the significant enhancement in it were reported [53]. Our study supported the enhancement of canopy during drought event. The inconsistence between the field and satellite observations may be partially explained by the scale effect. Given the lack of availability of synchronous *in situ* plant trait measurement data, we recommend dedicated manipulative experiments to improve understanding of the mechanisms that drive these contrasting responses.

Enhanced structural growth in response to increased radiation under drought conditions in humid regions, such as the Amazon forests, has been reported, based on various structure proxies, such as leaf area index [55], EVI [56], [57], and NDVI [58]. These counter-intuitive impacts of drought on plant photosynthesis contrast with field observations and have previously led to the suggestion that these differences may be explained by remote sensing artifacts, such as atmospheric contamination [59] and angular effects [60]. Thus, our study provides novel insights to drought impacts on plant photosynthesis in cloudy and mesic regions, where radiation-induced structural growth is not fully converted into capacity for C uptake, due to drought-induced constraints on leaf physiology, so that net ecosystem impacts of drought depend on the balance between vegetation structure and leaf physiology responses. We suggest that future research should test for these contrasting responses in Amazon forests, to improve understanding of ecosystem impacts of climate change.

V. Conclusion

This article investigated the impact of the 2011 summer drought in Southwest China on canopy structure and leaf physiology, represented by NIRv and leaf-scale fluorescence yield (Φ_f), respectively. We used a physically based and simple approach to fully decouple Φ_f from satellite-recorded SIF. Results indicate that satellites detected contrasting responses of canopy structure and leaf physiology to the drought: structural growth increased by 13.8%, due to the mitigation of radiation constraints (decreased precipitation resulted in lower cloud cover and increased radiation), whereas leaf physiology decreased by 12.6% (CSIF) or 19.3% (GOSIF), and the compromise between structural enhancement and physiological inhibition resulted in a slightly change in ecosystem photosynthesis (CSIF: 7.5%; GOSIF: 1.2%; EC-LUE GPP: −2.96%). Our study provides a novel insight to the complex responses of plant photosynthesis to drought and may contribute to the reconciliation of contrasting observed directions in plant responses to drought in cloudy and mesic regions.

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