



# 叶绿素荧光主动与被动联合观测应用前景

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**摘 要** 叶绿素荧光是研究植物光合生理机制、量化植被光合作用时空格局以及准确理解气候变化背景下陆地生态系统生产力的关键。然而, 目前对于叶绿素荧光主动与被动联合观测的研究还较少。该文对比了叶绿素荧光主动观测与被动观测的优缺点, 展示了叶片尺度和冠层尺度主动与被动联合观测的仪器设备组成, 探讨了主动与被动联合观测在探索叶绿体尺度-叶片尺度-冠层尺度能量在光合、荧光以及热耗散中的分配, 阐明叶绿素荧光与总初级生产力的关联机制, 验证星基日光诱导叶绿素荧光, 解译叶绿素荧光光谱形状4个方面的应用前景。综上, 叶绿素荧光的主动与被动联合观测对于揭示各尺度上荧光与光合作用之间的关联机制, 改善全球尺度植被生产力模型至关重要。

**关键词** 总初级生产力; 星基日光诱导叶绿素荧光; 非光化学淬灭; 陆地生物圈模型; 能量分配; 荧光光谱形状

丁键浠, 周蕾, 王永琳, 庄杰, 陈集景, 周稳, 赵宁, 宋珺, 迟永刚 (2021). 叶绿素荧光主动与被动联合观测应用前景. 植物生态学报, 45, 105-118. DOI: 10.17521/cjpe.2020.0323

## Application prospects for combining active and passive observations of chlorophyll fluorescence

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### Abstract

Chlorophyll fluorescence (ChlF) is the key to studying the physiological mechanisms of plant photosynthesis, quantifying the spatiotemporal pattern of vegetation photosynthesis, and accurately understanding the productivity of terrestrial ecosystems under the background of climate change. However, few studies have been conducted on combined observations of actively and passively induced ChlF. Here, we compared the advantages and disadvantages of active and passive observations of ChlF and showed the instrument composition of the combined observations of actively and passively induced ChlF at leaf and canopy scales. The application prospects of joint observations of actively and passively induced ChlF focus on exploring energy distribution among photosynthesis, fluorescence and heat dissipation at the chloroplast-leaf-canopy scale, clarifying the mechanism underlying the relationship between ChlF and gross primary productivity, verifying satellite-based sun-induced chlorophyll fluorescence and interpreting the shape of the ChlF spectrum. Our work suggests that the combined observation of actively and passively induced ChlF is essential to reveal the mechanisms underlying the relationships between fluorescence and photosynthesis at various scales and to improve vegetation productivity models at the global scale.

**Key words** gross primary productivity; satellite-based sun-induced chlorophyll fluorescence; non-photochemical quenching; terrestrial biosphere model; energy distribution; fluorescence spectrum shape

Ding JX, Zhou L, Wang YL, Zhuang J, Chen JJ, Zhou W, Zhao N, Song J, Chi YG (2021). Application prospects for combining active and passive observations of chlorophyll fluorescence. *Chinese Journal of Plant Ecology*, 45, 105-118. DOI: 10.17521/cjpe.2020.0323

叶绿素荧光的研究是量化区域以及全球尺度植被生产力的关键(Ryu *et al.*, 2019)。叶绿素荧光是植物叶绿素吸收光能后向外发射的长波信号(650–800 nm), 具有红光(685 nm左右)和近红外(740 nm左右)

收稿日期Received: 2020-09-25 接受日期Accepted: 2020-12-10

基金项目: 国家重点研发计划(2017YFB0504000)和国家自然科学基金(41871084和31400393)。Supported by the National Key R&D Program of China (2017YFB0504000), and the National Natural Science Foundation of China (41871084 and 31400393).

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两个波峰(Damm *et al.*, 2015; Verrelst *et al.*, 2016; Mohammed *et al.*, 2019)。植物光合色素吸收的能量绝大部分被叶绿素所利用进行光合作用, 然而未被利用的部分则以长波的形式向外发射荧光或以热耗散的形式释放出去(Porcar-Castell *et al.*, 2014; Mohammed *et al.*, 2019)。这三种能量之间存在着一定的平衡(Baker *et al.*, 2008; Hmimina *et al.*, 2014), 任何一种能量发生变化都会导致其他两种能量的变化。因此, 叶绿素荧光可以无伤、快速、灵敏地监测植被真实的生理生态过程和受环境胁迫的状况(Cendrero-Mateo *et al.*, 2016; Chen *et al.*, 2016)。

根据激发光源和探测方式的不同, 叶绿素荧光的观测可以分为主动和被动两种观测技术(Porcar-Castell *et al.*, 2014)。虽然单独探讨主动观测(Maxwell & Johnson, 2000; Consalvey *et al.*, 2005; 陈建明等, 2006; 张永江等, 2009; 尤鑫和龚吉蕊, 2012; 李钦夫等, 2013)或者被动观测(Meroni *et al.*, 2009; 王冉等, 2012; 梁寅等, 2013; Porcar-Castell *et al.*, 2014; Wang *et al.*, 2017; Aasen *et al.*, 2019; 纪梦豪等, 2019; Mohammed *et al.*, 2019; 章钊颖等, 2019)的研究较多, 但是目前缺乏叶绿素荧光主动与被动联合观测应用前景的分析。叶绿素荧光主动与被动联合观测有望在考虑热耗散的情况下建立更稳健的荧光与光合的关联, 对于改善全球植被生产力模型以及揭示各尺度上荧光与光合之间的关联机制至关重要。

## 1 叶绿素荧光主动与被动观测对比

### 1.1 主动观测

荧光动力学曲线, 是当植物绿色组织经过黑暗处理后受到可见光或人为激光照射时, 叶绿素分子所产生的荧光信号强度随着时间发生规律性的变化, 在荧光图谱上表现为一条先增后减再趋向平稳的曲线, 也称Kautsky效应(Stirbet & Govindjee, 2011)。目前主动观测大都基于脉冲辐射调制的(PAM)荧光系统。该系统由一个弱的调制测量光源和一个较强的非调制光化光源组成, 弱的测量光源用于测定植物暗适应下绿色组织的最小荧光值( $F_0$ ), 而强的光化光源可以作为饱和脉冲光用来监测经过暗处理后植物绿色组织的最大荧光值( $F_m$ )。通过分析荧光动力学曲线, PAM技术可以获取非光化学淬灭(NPQ)、表观光合电子传递速率(ETR)、植物光化学效率( $\Phi_{PSII}$ )

等参数, 其中NPQ对于植物热保护机制具有重要意义(Kromdijk *et al.*, 2016; Farooq *et al.*, 2018), ETR与光合碳固定存在线性关系(Barranguet & Kromkamp, 2000)。

主动观测的优势表现在以下两点。第一, 借助PAM荧光技术获取的参数可以直观地解释植物光合作用、探讨热耗散对于荧光产量和光化学产量平衡的影响。第二, 由于PAM荧光技术是在相对较宽的光谱范围内获取的, 因此受环境影响较小(Porcar-Castell *et al.*, 2014)。鉴于主动观测的优势, 其已被广泛应用于植物胁迫(McMurtrey *et al.*, 2002; Araus *et al.*, 2010; Agati *et al.*, 2013; Konanz *et al.*, 2014), 追踪植物光合作用变化(Maxwell & Johnson, 2000; Baker *et al.*, 2008; Murchie & Lawson, 2013; Frankenbach *et al.*, 2020)等方面的研究。然而, 主动观测存在劣势, 由于需要人工饱和光脉冲以及精确的脉冲同步和调制荧光技术, PAM荧光技术不适用于大尺度的卫星遥感监测(Kolber *et al.*, 2005; Amoros-Lopez *et al.*, 2008)。

### 1.2 被动观测

以自然光为诱导光源检测植物叶绿素荧光信号的方式称为被动荧光观测技术, 其探测到的信号也称日光诱导叶绿素荧光(SIF)。与主动观测不同, 被动观测不需要精确的饱和脉冲调制光, 其信号反演大都基于夫琅和费线提取算法(FLD)(Plascyk & Gabriel, 1975)。由于大气的吸收作用, 太阳光谱到达地表后有许多波段宽度为0.1–10 nm的暗线, 即夫琅和费吸收暗线。在这些吸收暗线波段, 植被的反射光微弱, 荧光凸显, 可以较好地反演出叶绿素荧光(王冉等, 2012; 章钊颖等, 2019)。被动观测的优势主要体现在无源遥感平台上, 可以进行大面积地表植被生理监测(章钊颖等, 2019)。叶绿素荧光被动观测为陆地碳循环的精确估算提供了新的技术和方向。

目前, SIF卫星数据主要来自GOSAT、GOME-2及OCO-2这3个卫星传感器。GOSAT生产的SIF数据开始于2009年并持续至今, 其地面足迹直径为10 km (Sun *et al.*, 2018; 章钊颖等, 2019), 但由于是基于离散点的观测所以在空间上极不连续(Sun *et al.*, 2018); GOME-2生产的SIF数据开始于2007年并持续至今, 时间尺度较长因此适合研究长时间序列上SIF值的变化, 但是空间分辨率比较低(40 km × 80 km,

2013年以后为40 km × 40 km); OCO-2生产的SIF产品开始于2014年并持续至今, 由于其基于条带状的观测所以在空间上也不连续(Sun *et al.*, 2018), 但空间分辨率有很大的提高(1.3 km × 2.25 km)。自从Joiner等(2011)利用GOSAT卫星获取了首幅全球SIF信号分布图以来, 目前可供SIF探测的在轨卫星还有METOP、TANSAT、Sentinel-5P等, 计划发射卫星包括TEMPO、GeoCARB、FLEX (表1)。

近地面SIF观测建立了站点通量监测与卫星数据产品之间的桥梁。站点涡流协方差(EC)通量监测是估算陆地生态系统总初级生产力(GPP)的关键技术, 但其与卫星SIF监测存在时空不匹配问题(Zhang *et al.*, 2020)。自2010年近地面SIF自动观测系统(Daumard *et al.*, 2010)提出以来, 近地面SIF观测已经被证明可以弥补卫星数据与EC通量塔数据之间的差距(Porcar-Castell *et al.*, 2015)。其观测数据与TROPOMI、OCO-2等卫星SIF产品具有良好的相关性(Magney *et al.*, 2019a; Zhang *et al.*, 2020), 这有助于验证卫星SIF产品的准确性, 推动全球生态系统碳循环的研究。主要的近地面SIF连续观测系统如表2所示, 其中大部分的近地面SIF观测系统都携带了例如HR2000+或者QEpro等高分辨率光谱仪, 有的甚至搭载了两个以上的光谱仪。这些光谱仪最高光学分辨率可达0.035 nm (半峰宽), 最宽的监测波长范围在185–1 100 nm之间, 远大于SIF的发射波长范围(650–800 nm), 可根据实际需求更换光栅满足不同波段SIF的监测任务, 也可以在获取SIF信号的同时获取丰富的植被反射光谱以估算SIF信号在冠层

上的逃逸系数(Zeng *et al.*, 2019)。近地面SIF的连续观测已经在解决卫星SIF监测获取到的植被冠层信息不连续问题(Hu *et al.*, 2018), 因叶片运动以及冠层结构等导致的SIF观测方向差异(Miao *et al.*, 2018; Yang *et al.*, 2018)等方面取得进展。近年来, 欧洲与中国分别建立了地面光谱观测网EUROSPEC和ChinaSpec (Zhang *et al.*, 2020), 其中FluoSpec2、SIFSpec、SIFPrism是ChinaSpec中使用最广泛的系统(Zhang *et al.*, 2020)。

2 叶绿素荧光主动与被动联合观测

2.1 联合观测的必要性

为了更好地理解塔基、机载、星载所测SIF值的时空变化, 迫切需要开展叶绿素荧光主动与被动联合观测。由于星基SIF反演算法波段的单一性, 无法获取到大区域尺度上全波段完整的荧光图谱, 也无法同时获得与热耗散、光合作用等相关的荧光参数, 这使得利用被动荧光探究植被能量分配方式以及直接与GPP建立关联存在挑战性。主动与被动联合观测能够获得一整套叶片尺度光合、荧光、热耗散的参数(图1), 可以为卫星SIF观测值提供可靠的机理解释。

另外, 通过叶片尺度上叶绿素荧光主动与被动联合观测, 以及耦合气体交换测定系统, 可以在获得更为准确的荧光光合关系基础上, 通过模型模拟的方式, 如通用陆面模式(community land model, CLM)和耦合能量平衡的辐射传输模型(soil canopy observation, photochemistry, and energy fluxes,

表1 可用于星基日光诱导叶绿素荧光监测的卫星传感器  
Table 1 Satellite-based sensors used for the retrieval of satellite-based sun-induced chlorophyll fluorescence

传感器 Sensor	卫星 Satellite	发射时间 Launch time	波段 Band (nm)	状态 State	相关文献 Related literature
SCIAMACHY	ENVISAT	2002-03	650–790	失联 Lost contact	Joiner <i>et al.</i> , 2011; Wolanin <i>et al.</i> , 2015
GOME-2	METOP	2006-07	650–790	在轨 On orbit	Joiner <i>et al.</i> , 2013; Guanter <i>et al.</i> , 2014
TANSO-FTS-1	GOSAT	2009-01	757–775	在轨 On orbit	Frankenberg <i>et al.</i> , 2011; Joiner <i>et al.</i> , 2011
OCO-2	OCO-2	2014-07	757–775	在轨 On orbit	Frankenberg <i>et al.</i> , 2014; Sun <i>et al.</i> , 2017
ACGS	TANSAT	2016-12	758–778	在轨 On orbit	Du <i>et al.</i> , 2018; Li <i>et al.</i> , 2018
TROPOMI	Sentinel-5P	2017-10	675–775	在轨 On orbit	Guanter <i>et al.</i> , 2015; Zhang <i>et al.</i> , 2019
TANSO-FTS-2	GOSAT-2	2018-10	757–775	在轨 On orbit	Nakajima <i>et al.</i> , 2017
OCO-3	OCO-3	2019-05	757–775	在轨 On orbit	Eldering <i>et al.</i> , 2019
–	TEMPO	预计2020 Estimate 2020	650–740	计划发射 Planned launch	Zoogman <i>et al.</i> , 2017; Mohammed <i>et al.</i> , 2019
–	GeoCARB	预计2021 Estimate 2021	757–772	计划发射 Planned launch	O’Brien <i>et al.</i> , 2016; Mohammed <i>et al.</i> , 2019
FLORIS	FLEX	预计2023 Estimate 2023	650–780	计划发射 Planned launch	Drusch <i>et al.</i> , 2016; Mohammed <i>et al.</i> , 2019

表2 近地面日光诱导叶绿素荧光连续观测仪器设备

Table 2 Instruments used for the ground-based continuous observation of sun-induced chlorophyll fluorescence

仪器设备 Equipment	光谱仪 Spectrometer	波段 Band (nm)	光学分辨率 Optical resolution (nm)	相关文献 Related literature
TriFLEX	HR2000+	630–815	0.50	Daumard <i>et al.</i> , 2010
	HR2000+	630–815	0.50	
	HR2000+	300–900	2.00	
SpectroFLEX	HR2000+	630–820	0.20	Fournier <i>et al.</i> , 2012
AutoSIF	QE65pro	645–805	0.30	Hu <i>et al.</i> , 2018
S-FluorBox	HR4000	700–800	0.10	Cogliati <i>et al.</i> , 2015
	HR4000	400–1 000	1.00	
SIF-SYS	STS-VIS	337–823	3.00	Burkart <i>et al.</i> , 2015
FluoSpec	HR2000+	680–775	0.13	Yang <i>et al.</i> , 2015
FluoSpec2	QEpro	730–780	0.15	Miao <i>et al.</i> , 2018
	HR2000+	350–1 100	1.10	
PhotoSpec	QEpro1	670–732	0.30	Grossmann <i>et al.</i> , 2018
	QEpro2	729–784	0.30	
	Flame	177–874	1.20	
FLOX	QEpro	650–800	0.30	Wohlfahrt <i>et al.</i> , 2018
	VIS-NIR	400–950	1.50	
SIFSpec	QE65pro	649–805	0.34	Du <i>et al.</i> , 2019
SIFPrism	QEpro	650–800	0.30	Zhang <i>et al.</i> , 2019
FAME	QEpro	730–786	0.15	Gu <i>et al.</i> , 2018

以上光谱仪的波段及光学分辨率根据使用者对仪器配置的不同会有所差异。  
Band and optical resolution of the above spectrometers will vary depending on the user.

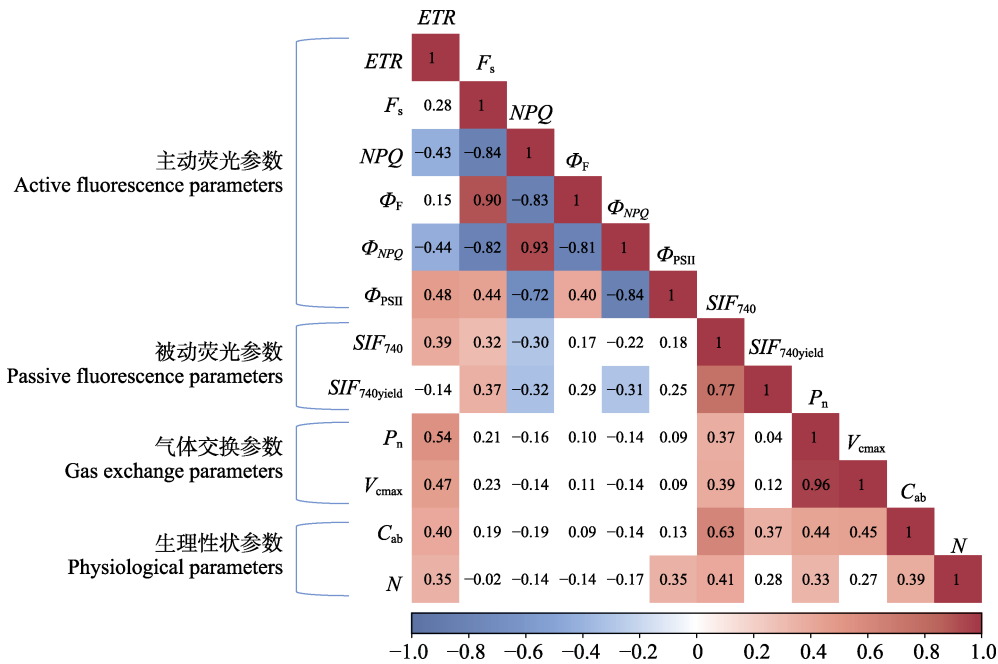


图1 水稻叶绿素荧光主动与被动联合观测耦合气体交换测定参数线性相关性矩阵。该图为野外实际观测数据。色块表示 $p < 0.05$ , 空白表示 $p > 0.05$ 。Cab, 叶片叶绿素浓度; ETR, 表观光合电子传递速率;  $F_s$ , 稳态荧光值; N, 叶片氮含量; NPQ, 非光化学淬灭;  $P_n$ , 净光合速率;  $SIF_{740}$ , 740 nm的日光诱导叶绿素荧光值;  $SIF_{740yield}$ , 740 nm的日光诱导叶绿素荧光量子产率;  $V_{cmax}$ , 最大羧化速率;  $\Phi_F$ , 荧光效率;  $\Phi_{NPQ}$ , NPQ效率;  $\Phi_{PSII}$ , 光化学效率。

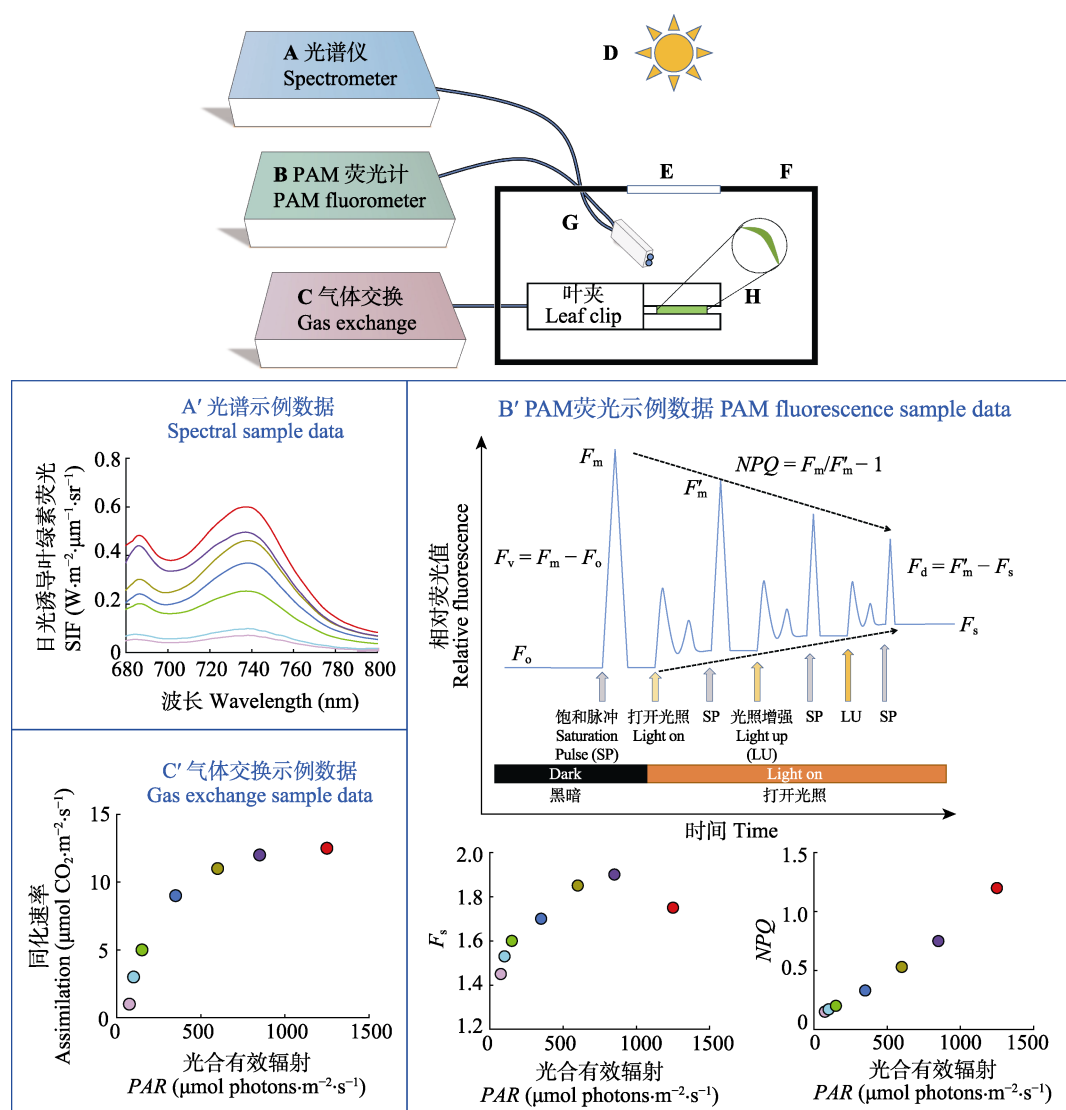
Fig. 1 Linear correlation matrix for combined observation of actively and passively induced chlorophyll fluorescence coupled gas exchange measurement parameter in rice. The figure showed actual observation data in the field. Color black means  $p < 0.05$ , blank means  $p > 0.05$ . Cab, leaf chlorophyll concentration; ETR, apparent combined electron transfer rate;  $F_s$ , steady-state fluorescence value; N, leaf nitrogen content; NPQ, non-photochemical quenching;  $P_n$ , net photosynthetic rate;  $SIF_{740}$ , value of sun-induced chlorophyll fluorescence at 740 nm;  $SIF_{740yield}$ , quantum yield of sun-induced chlorophyll fluorescence at 740 nm;  $V_{cmax}$ , maximum carboxylation rate;  $\Phi_F$ , fluorescence efficiency;  $\Phi_{NPQ}$ , NPQ efficiency;  $\Phi_{PSII}$ , photochemical efficiency.

SCOPE)等模型将 $NPQ$ 及 $\Phi_{PSII}$ 等的参数信息纳入冠层尺度上的SIF-GPP模型, 并通过近地面SIF联网观测所建立的数据库拓展到区域或者全球尺度, 建立更可靠的全球生产力模型(Raczka *et al.*, 2019; Maguire *et al.*, 2020; Marrs *et al.*, 2020; Zhang *et al.*, 2020)。

## 2.2 叶片尺度联合观测的仪器设备组成

主动与被动荧光联合观测的研究目前主要集中在叶片尺度上(Atherton *et al.*, 2016; Magney *et al.*, 2017; Rahimzadeh-Bajgiran *et al.*, 2017; Vilfan *et al.*,

2019; Marrs *et al.*, 2020), 仪器设备主要包括光谱仪(图2A)、PAM荧光计(图2B)。被测叶片(图2H)固定在封闭的叶室(图2F)中以模拟暗适应的环境, PAM荧光计和光谱仪的光纤(图2G)同时以一定倾角插入封闭的叶室中, 在尽可能检测同一视场内叶绿素荧光变化的同时又不能遮蔽入射光线(图2D), 还要尽可能靠近叶片以确保脉冲完全光饱和(Magney *et al.*, 2017)。叶室的进光口(图2E)装载有短通滤波片(<650 nm), 只有小于650 nm波长范围的光才被允



**图2** 叶绿素荧光主动与被动联合观测耦合气体交换测定系统及其示例数据。测定系统主要包括: 光谱仪(A); PAM荧光计(B); 气体交换(C); 入射光线(D); 进光口(E); 封闭的叶室(F); 光纤(G); 被测叶片(H)。  $F_d$ , 光适应下可变荧光值;  $F_m$ , 最大荧光值;  $F'_m$ , 光适应下最大荧光值;  $F_o$ , 最小荧光值;  $F_s$ , 稳态荧光值;  $F_v$ , 最大可变荧光值;  $NPQ$ , 非光化学淬灭。

**Fig. 2** Combined observation of actively and passively induced chlorophyll fluorescence coupled gas exchange measurement system and its sample data. The measurement system mainly includes: spectrometer (A); PAM fluorometer (B); gas exchange (C); incident light (D); light inlet (E); enclosed leaf chamber (F); optical fiber (G); leaves (H).  $F_d$ , variable fluorescence value under light adaptation;  $F_m$ , maximum fluorescence value under light adaptation;  $F'_m$ , maximum fluorescence value under light adaptation;  $F_o$ , minimum fluorescence value;  $F_s$ , steady-state fluorescence value;  $F_v$ , maximum variable fluorescence value;  $NPQ$ , non-photochemical quenching; PAR, photosynthetically active radiation; SIF, sun-induced chlorophyll fluorescence.

许进入叶室。关闭进光口生成黑暗的环境,由PAM荧光计发射饱和脉冲获取植物最大以及最小的荧光值。打开进光口,经过过滤的入射光照射在叶片上诱导产生SIF,并通过光谱仪记录大于650 nm的SIF光谱曲线图(图2A'),同时也可由PAM记录叶片丰富的荧光参数信息及 $F_s$ 、 $NPQ$ 等与光合有效辐射强度的响应关系(图2B')。在入射光源的选择上,可以直接采用自然光源(Cendrero-Mateo *et al.*, 2016; Rahimzadeh-Bajgiran *et al.*, 2017)或者人造光化光源(Magney *et al.*, 2017, 2019b; Vilfan *et al.*, 2019),例如90%红色和10%蓝色的LED组合光源。另外,在叶绿素荧光主动与被动联合观测系统的基础上还可以耦合气体交换装置(图2C),气体交换仪通过气体交换通道与封闭的叶室连接起来,并根据叶室内水汽浓度变化反映叶片光合信息(图2C'),如光合速率、羧化速率、蒸腾速率等,达到同步观测光合、主动荧光参数、SIF信号(Magney *et al.*, 2017, 2019b; Vilfan *et al.*, 2019),并在环境条件(光、温度、湿度)变化背景下建立光合作用与荧光、热耗散之间关系的目的。

### 2.3 冠层尺度联合观测的仪器设备组成

相对于叶片尺度的主动与被动荧光联合观测,冠层尺度的联合观测进展缓慢。Acebron等(2020)最新的研究利用激光诱导荧光瞬变仪(laser induced fluorescence transient, LIFT)与近地面连续观测系统Flox,对拟南芥(*Arabidopsis thaliana*)冠层进行了叶绿素荧光主动与被动联合观测,其中LIFT的传感器距离目标60 cm, Flox的光纤距离目标10 cm,展示了拟南芥SIF值、光合效率、 $NPQ$ 以及叶片反射率之间的定量关系。其搭建的观测平台如图3所示,其中LIFT技术是激光诱导产生荧光的技术,可以将主动荧光观测尺度扩大到几十米的范围(Kolber *et al.*, 2005; Rahimzadeh-Bajgiran *et al.*, 2017; Acebron *et al.*, 2020)。Kolber等(2005)通过LIFT技术对50 m外的目标植物进行了观测,结果发现与近距离PAM技术所测荧光参数几乎没差异。

## 3 叶绿素荧光主动与被动联合观测应用前景

### 3.1 探索光合、荧光以及热耗散的能量分配

在叶绿体尺度,光系统II(PSII)吸收的能量分别用于光合作用、发射荧光以及 $NPQ$ ,三者的效率总和为1(Hmimina *et al.*, 2014; Lee *et al.*, 2015; Cendrero-Mateo *et al.*, 2016)。光系统(PSI和PSII)以

串联的方式进行电子传输,并且都可以产生叶绿素荧光。但是两个光系统对于叶绿素荧光光谱的贡献却不相同:通常PSI的荧光效率较低,常被认为是定值(Franck *et al.*, 2002; Hasegawa *et al.*, 2010; Porcar-Castell *et al.*, 2014),而PSII的荧光效率受到光化学淬灭( $PQ$ )(Magney *et al.*, 2019b)和 $NPQ$ (Franck *et al.*, 2005; Lambrev *et al.*, 2010)的影响。由于 $NPQ$ 的效率取决植物生理状态以及所处的环境,所以荧光效率和光化学效率之间的关系受到 $NPQ$ 效率的调控(Flexas & Medrano, 2002; Baker, 2008; Faraloni *et al.*, 2011; Lee *et al.*, 2013; Porcar-Castell *et al.*, 2014; Farooq *et al.*, 2018)。

在叶片尺度,主动观测可以获取 $\Phi_F$ 、 $\Phi_{PSII}$ 、 $\Phi_{NPQ}$ (Hendrickson *et al.*, 2004; Kramer *et al.*, 2004; Chen *et al.*, 2018),被动观测可以获取SIF的量子效率 $SIF_{yield} = SIF/APAR$ (Acebron *et al.*, 2020; Maguire *et al.*, 2020),气体交换测定系统可以获取光合速率( $P_n$ )。我们通过对水稻进行叶绿素荧光主动与被动联合观测,发现荧光效率和光化学效率的关系受到 $NPQ$ 效率的调控(图4A), $NPQ$ 的变化也影响了760 nm的SIF值与 $P_n$ 间的关系(图4B)。根据同一视场范围内叶绿素荧光主动与被动联合观测的 $\Phi_F$ 、 $\Phi_{PSII}$ 、 $\Phi_{NPQ}$ 、 $NPQ$ 、 $SIF_{yield}$ 、 $P_n$ 等参数,可以分析 $NPQ$ 如何影响 $SIF_{yield}$ 与光合间的关系,探索叶片尺度能量在光合与荧光之间的分配。

在冠层尺度,量化光合、荧光以及热耗散的能量分配仍然存在挑战(Porcar-Castell *et al.*, 2014; van der Tol *et al.*, 2014)。Atherton等(2016)通过对叶片尺度叶绿素荧光主动与被动的联合观测,分析了SIF值、 $\Phi_F$ 、 $\Phi_{PSII}$ 以及 $NPQ$ 之间的动态关系,并利用PHOTOII模型将叶片尺度所确定的参数关系与冠层尺度联系起来。Acebron等(2020)通过LIFT技术以及Flox系统对拟南芥冠层进行了主被动联合观测,探讨了 $\Phi_{PSII}$ 、 $SIF_{yield}$ 、 $NPQ$ 之间的关系。这些研究有助于将能量分配研究扩展到区域甚至全球尺度,为建立更稳健的荧光光合模型以及估算全球植被生产力提供理论基础。通过叶绿素荧光主动与被动联合观测,有助于理解区域以及全球尺度SIF信号与光合、热耗散之间的关系,同时为多尺度SIF信号模拟的辐射传输模型SCOPE、基于生理过程的PHOTOII模型(van der Tol *et al.*, 2014, 2018; Atherton *et al.*, 2016)的优化提供数据支持。



### 3.2 阐明SIF信号与GPP的关联机制

植被SIF值和GPP之间具有很强的线性关系, 这种关系为基于SIF估算GPP的模型提供了坚实的基础(Frankenberget al., 2011; Guanter et al., 2012, 2014; Porcar-Castell et al., 2014; Verma et al., 2017)。然而, 目前这种经验关系缺乏机理解释(Magney et al., 2019a), 并且SIF观测值和GPP之间的关系会随着时空尺度的变化而变化(Cheng et al., 2013; Zarco-Tejada et al., 2016; Goulas et al., 2017; Liu et al., 2017)。在叶片尺度, SIF值与GPP的关系由于红光波段荧光重吸收作用以及远红外波段荧光散射作用的减弱而会比冠层上观察到的SIF-GPP关系更强(Liu et al., 2020); 在冠层尺度, SIF值与GPP之间的关系会因为叶片生理特性以及植被冠层结构的改变而改变(Porcar-Castell et al., 2014; Damm et al., 2015;

Yang et al., 2018); 在区域尺度, 由于卫星每天最多只能获得一个SIF观测值, 并且有效的SIF观测值主要发生在晴天的特定时间段, 复杂的大气传输环境以及时间尺度上的不匹配必定会增加SIF值与GPP关系的不确定性(Hu et al., 2018; Yang et al., 2018)。

叶片尺度的叶绿素荧光主动与被动联合观测, 可以在测定丰富荧光参数的同时获取叶片实际的SIF信号, 还原SIF信号与GPP真实的关系(Liu et al., 2020)。研究表明, 光合效率、荧光效率、电子传递效率、叶龄、叶绿素含量、C<sub>3</sub>/C<sub>4</sub>光合途径、植物生长期等生物因素(Cui et al., 2016; Miao et al., 2018), 以及光照、温度、水分等非生物因素(Porcar-Castell et al., 2014; Wyber et al., 2017; Miao et al., 2018; Campbell et al., 2019; Magney et al., 2019a)会调节SIF值与GPP的关系。例如, Miao等(2018)基于美国

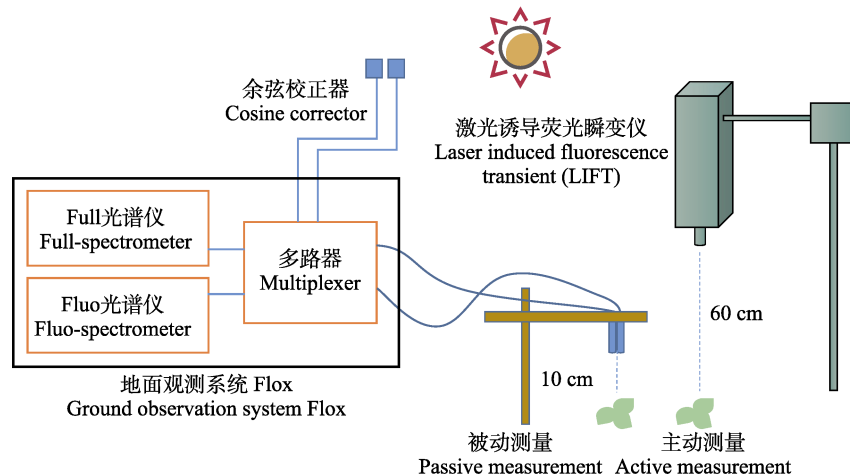
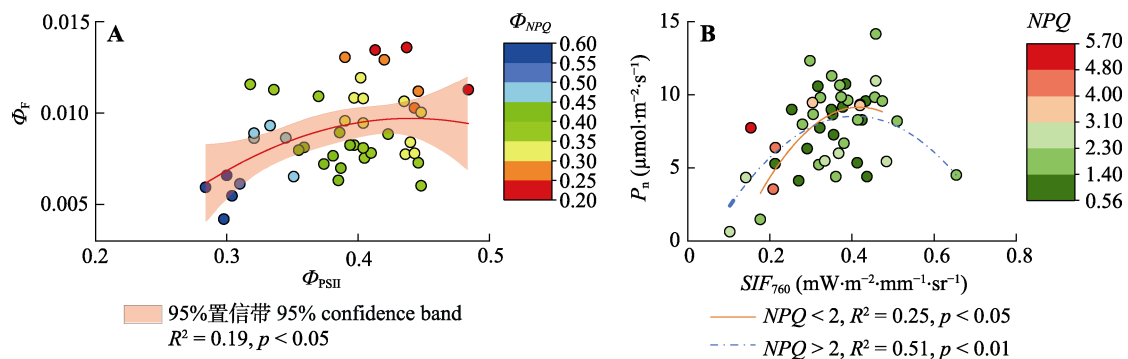


图3 利用LIFT技术及地面观测系统Flox搭建的主被动荧光联合观测系统(修改自Acebrón (2020)的Fig. S2)。

**Fig. 3** Combined observation system of actively and passively induced chlorophyll fluorescence built by the LIFT technology and ground observation system Flox (modified from Fig. S2 of Acebrón (2020)).



**图4** 水稻 $\Phi_F$ 和 $\Phi_{PSII}$ 在 $\Phi_{NPQ}$ 影响下的关系变化(A),  $P_n$ 与 $SIF_{760}$ 在 $NPQ$ 影响下的关系变化(B)。该图野外实际观测数据。 $NPQ$ , 非光化学淬灭;  $P_n$ , 净光合速率;  $SIF_{760}$ , 760 nm的日光诱导叶绿素荧光值;  $\Phi_F$ , 荧光效率;  $\Phi_{NPQ}$ ,  $NPQ$ 效率;  $\Phi_{PSII}$ , 光化学效率。  
**Fig. 4** Relationship between  $\Phi_F$  and  $\Phi_{PSII}$  under the influence of  $\Phi_{NPQ}$  (A), relationship change between  $P_n$  and  $SIF_{760}$  under the influence of  $NPQ$  (B) in rice. The figure showed actual observation data in the field.  $NPQ$ , non-photochemical quenching;  $P_n$ , net photosynthetic rate;  $SIF_{760}$ , value of sun-induced chlorophyll fluorescence at 760 nm;  $\Phi_F$ , fluorescence efficiency;  $\Phi_{NPQ}$ ,  $NPQ$  efficiency;  $\Phi_{PSII}$ , photochemical efficiency.

大豆(*Glycine max*)田的研究发现, 光合效率和  $SIF_{yield}$  差异性的变化会导致SIF-GPP线性关系的改变。Cui等(2016)利用SCOPE模型模拟了GPP以及SIF信号, 结果表明SIF值与GPP的关系会受到不同生态系统叶绿素浓度及叶面积指数差异的影响, 并提出在建立SIF-GPP关系之前, 需要使用模型等方法来修正影响SIF-GPP关系的各种因素。

叶片尺度的叶绿素荧光主动与被动联合观测, 提供了生理参数之间的确定性联系, 是更复杂冠层模型的基石。Vilfan等(2019)将辐射传输模型FLUSPECT耦合到光合作用模型中, 尝试利用叶绿素荧光和反射率来估算植物的光合能力, 并利用叶片尺度主动与被动联合观测所获得的大量样本数据对模型进行测试验证, 结果表明该模型可以运用到冠层尺度对植被实际的光合能力进行估算。Raczka等(2019)通过主动与被动联合观测与CLM模型的结合, 在考虑持续性NPQ作用下, 改进了模型并模拟了科罗拉多州亚高山森林SIF信号的季节变化, 发现更符合塔基、星基SIF观测到的季节模式, 并指出为了更好地了解NPQ在多大程度上影响SIF值和GPP之间的关系, 必须进行更多的叶片尺度叶绿素荧光主动与被动联合观测。主动技术与被动观测系统的结合也有助于阐明SIF-GPP间的关联机制, 如Magney等(2019a)通过冠层SIF值测量仪器PhotoSpec与LI-6800F的PAM荧光方法, 将PAM技术中丰富的荧光参数与冠层SIF信号相结合, 对常绿系统的GPP与SIF信号进行了关联研究, 结果再次证实了GPP与SIF值之间稳定的相关性。

### 3.3 验证卫星SIF产品

卫星SIF产品的真实有效性迫切需要支持验证。叶绿素荧光所占的比例非常小, 属于微弱的电磁波信号, 大约只占地表反射信号的1%–2% (Meroni *et al.*, 2009)。在自然光条件下, SIF信号对于植被冠层辐射的贡献只有不到3% (Zarco-Tejada *et al.*, 2013)。由自然光激发产生的SIF在经过冠层重吸收、散射后又经过复杂的大气结构到达卫星传感器, 这中间的过程使得SIF信号的不确定性不断累积, 也使得荧光信号的检索变得复杂困难。而SIF信号的检索算法大都利用少量的窄波段进行, 如O<sub>2</sub>-B、O<sub>2</sub>-A波段或夫琅和费吸收暗线(Fournier *et al.*, 2012; Burkart *et al.*, 2015; Yang *et al.*, 2015), 这种检索波段的单一性也使得SIF信号的解释存在不确定性。另外, 由于卫

星每天最多只能获得一个SIF观测值, 有效的SIF观测值主要发生在晴天特定时间段(Hu *et al.*, 2018; Yang *et al.*, 2018)。因此, 光照条件、植被结构、背景反射和大气效应等都会影响荧光反演的结果(Guanter *et al.*, 2010; Zarco-Tejada *et al.*, 2013)。为了有效降低卫星SIF观测不确定性所带来的影响, 地面荧光观测网络的建立、拓展以及荧光模型的构建是必不可少的(Zarco-Tejada *et al.*, 2013; Atherton *et al.*, 2016; Drusch *et al.*, 2016; Grossmann *et al.*, 2018; Raczka *et al.*, 2019; Zhang *et al.*, 2020)。

叶绿素荧光主动与被动联合观测获取到的叶片尺度确定性参数关系可通过PHOTOII、CLM、SCOPE等模型扩展到冠层尺度, 在考虑NPQ等参数作用下与卫星SIF产品进行比较验证(van der Tol *et al.*, 2014; Lee *et al.*, 2015; Atherton *et al.*, 2016; Raczka *et al.*, 2019)。例如, Raczka等(2019)通过耦合持续性NPQ作用的CLM模型对科罗拉多州亚高山森林SIF信号进行模拟, 结果与GOME-2卫星SIF数据具备相同的季节模式。Zhang等(2020)通过SCOPE和BEPS-SIF模型对不同生态站点的SIF信号进行模拟, 结果与地面SIF观测结果显著相关。Lee等(2013)通过确定的参数关系, 利用改良的SCOPE对亚马孙地区的SIF信号进行了模拟并与GOSAT的SIF信号产品进行对比, 结果发现显著相关( $R^2 = 0.79$ )。以上结果表明, 基于叶绿素荧光主动与被动联合观测的荧光模型可作为地面SIF观测网的补充, 将不同站点所测数据联系起来并与卫星SIF产品进行比较验证。

### 3.4 解译荧光光谱形状

卫星SIF信号大都集中于近红外区域特定的窄波段, 无法再现完整的荧光光谱曲线(Liu *et al.*, 2020)。然而, 叶绿素荧光光谱形状相关的参数, 如红光与远红外波段荧光的比率等, 对植物胁迫状态及光合信息有指示作用(Cheng *et al.*, 2013; Middleton *et al.*, 2017)。研究表明, 冠层SIF值会受到植被胁迫状态、冠层结构、辐照条件、叶绿素浓度等的影响, 这些影响均会使得冠层SIF光谱曲线呈现不同的变化(Huang *et al.*, 2007; Pinto *et al.*, 2016; Vilfan *et al.*, 2016; Yang *et al.*, 2018; Atherton *et al.*, 2019)。为了将SIF信号与植被生产力关联起来, 有必要对荧光光谱进行重建, 建立全波段的SIF光谱曲线(Zhao *et al.*, 2014; Cogliati *et al.*, 2015; Drusch *et al.*, 2016)。

叶绿素荧光主动与被动联合观测, 在获取丰富



荧光参数的同时又可以获取叶片全波段SIF光谱曲线。叶片尺度的红光波段荧光由于不存在冠层重吸收等的影响, 已被证明同GPP的关系优于远红外波段荧光同GPP的关系(Liu *et al.*, 2020)。Magney等(2017)在同一视场同时测量了PAM荧光和SIF, 结果表明SIF和PAM荧光关系与荧光波长有关, 其斜率遵循荧光光谱曲线的平均形状。Magney等(2019b)在其另一篇文章中也通过叶绿素荧光主动与被动联合观测, 采用奇异值分解(SVD)方法分解了SIF光谱形状的影响成分, 揭示了荧光光谱形状对生理和环境条件变化的响应机制, 指出叶绿素荧光中约85%的光谱变化可以通过平均光谱形状的大小变化来解释。我们对水稻叶片进行了叶绿素荧光主动与被动联合观测, 发现氮会改变水稻叶片的SIF曲线(图5), 表明SIF值受到叶片氮含量、NPQ以及比叶质量(SLM)的共同调控( $R^2 = 0.43$ )。

#### 4 总结和展望

叶绿素荧光主动与被动联合观测是量化全球植被生产力的关键。主动与被动联合观测可以在同一视场范围内获取植物 $\Phi_F$ 、 $SIF_{\text{yield}}$ 、 $\Phi_{\text{PSII}}$ 、 $\Phi_{\text{NPQ}}$ 、NPQ、ETR等信息, 有助于探索光合、荧光以及热耗散的能量分配, 阐明SIF值与GPP的关联机制。将叶片尺度上荧光和光合所建立的确定性关系纳入PHOTOII、CLM、SCOPE等荧光模型中, 有助于更好地理解塔基、机载、星载SIF值的时空变化。叶绿素荧光主动与被动联合观测, 在获取丰富荧光参数的同时又可

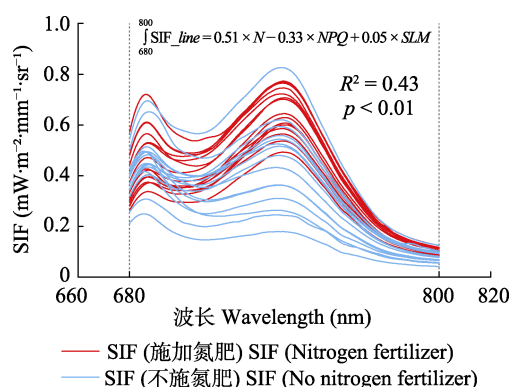


图5 水稻不同处理下叶片日光诱导叶绿素荧光光谱曲线。该图为野外实际观测数据。N, 叶片氮含量; NPQ, 非光化学淬灭; SIF\_line, SIF光谱曲线; SLM, 比叶质量。

**Fig. 5** Leaves spectral curve of sun-induced chlorophyll fluorescence (SIF) under different treatments of rice. The figure showed actual observation data in the field. N, leaf nitrogen content; NPQ, non-photochemical quenching; SIF\_line, SIF spectral curve; SLM, specific leaf mass.

以获取叶片全波段SIF光谱曲线, 探索NPQ等荧光参数与SIF值的光谱依赖性。我们的研究表明, 叶绿素荧光的主动与被动联合观测有望在考虑NPQ等参数信息的情况下建立更稳健的荧光与光合的关联, 对于改善全球植被生产力模型至关重要。

#### 参考文献

- Aasen H, van Wittenberghe S, Medina NS, Damm A, Goulas Y, Wieneke S, Hueni A, Malenovsky Z, Alonso L, Pacheco-Labrador J, Cendrero-Mateo MP, Tomelleri E, Burkart A, Cogliati S, Rascher U, Arthur AM (2019). Sun-induced chlorophyll fluorescence II: review of passive measurement setups, protocols, and their application at the leaf to canopy level. *Remote Sensing*, 11, 927. DOI: 10.3390/rs11080927.
- Acebron K, Matsubara S, Jedmowski C, Emin D, Muller O, Rascher U (2020). Diurnal dynamics of nonphotochemical quenching in *Arabidopsis npq* mutants assessed by solar-induced fluorescence and reflectance measurements in the field. *New Phytologist*, 229, 4, 2104-2119.
- Agati G, Foschi L, Grossi N, Guglielminetti L, Cerovic ZG, Volterrani M (2013). Fluorescence-based versus reflectance proximal sensing of nitrogen content in *Paspalum vaginatum* and *Zoysia matrella* turfgrasses. *European Journal of Agronomy*, 45, 39-51.
- Amoros-Lopez J, Gomez-Chova L, Vila-Frances J, Alonso L, Calpe J, Moreno J, del Valle-Tascon S (2008). Evaluation of remote sensing of vegetation fluorescence by the analysis of diurnal cycles. *International Journal of Remote Sensing*, 29, 5423-5436.
- Araus JL, Sánchez C, Cabrera-Bosquet L (2010). Is heterosis in maize mediated through better water use? *New Phytologist*, 187, 392-406.
- Atherton J, Liu W, Porcar-Castell A (2019). Nocturnal Light Emitting Diode Induced Fluorescence (LEDIF): a new technique to measure the chlorophyll a fluorescence emission spectral distribution of plant canopies *in situ*. *Remote Sensing of Environment*, 231, 111137. DOI: 10.1016/j.rse.2019.03.030.
- Atherton J, Nichol CJ, Porcar-Castell A (2016). Using spectral chlorophyll fluorescence and the photochemical reflectance index to predict physiological dynamics. *Remote Sensing of Environment*, 176, 17-30.
- Baker NR (2008). Chlorophyll fluorescence: a probe of photosynthesis *in vivo*. *Annual Review of Plant Biology*, 59, 89-113.
- Barranguet C, Kromkamp J (2000). Estimating primary production rates from photosynthetic electron transport in estuarine microphytobenthos. *Marine Ecology Progress Series*, 204, 39-52.
- Burkart A, Schickling A, Mateo MPC, Wrobel TJ, Rossini M, Cogliati S, Juliata T, Rascher U (2015). A method for

- uncertainty assessment of passive sun-induced chlorophyll fluorescence retrieval using an infrared reference light. *IEEE Sensors Journal*, 15, 4603-4611.
- Campbell P, Huemmrich K, Middleton E, Ward L, Julitta T, Daughtry C, Burkart A, Russ A, Kustas W (2019). Diurnal and seasonal variations in chlorophyll fluorescence associated with photosynthesis at leaf and canopy scales. *Remote Sensing*, 11, 488. DOI: 10.3390/rs11050488.
- Cendrero-Mateo MP, Moran MS, Papuga SA, Thorp KR, Alonso L, Moreno J, Ponce-Campos G, Rascher U, Wang G (2016). Plant chlorophyll fluorescence: active and passive measurements at canopy and leaf scales with different nitrogen treatments. *Journal of Experimental Botany*, 67, 275-286.
- Chen JM, Yu XP, Cheng JA (2006). The application of chlorophyll fluorescence kinetics in the study of physiological responses of plants to environmental stresses. *Acta Agriculturae Zhejiangensis*, 18, 51-55. [陈建明, 俞晓平, 程家安 (2006). 叶绿素荧光动力学及其在植物抗逆生理研究中的应用. *浙江农业学报*, 18, 51-55.]
- Chen SG, Yang J, Zhang MS, Strasser RJ, Qiang S (2016). Classification and characteristics of heat tolerance in *Agrotis adenophora* populations using fast chlorophyll a fluorescence rise O-J-I-P. *Environmental and Experimental Botany*, 122, 126-140.
- Chen XJ, Mo XG, Hu S, Liu SX (2018). Relationship between fluorescence yield and photochemical yield under water stress and intermediate light conditions. *Journal of Experimental Botany*, 70, 301-313.
- Cheng YB, Middleton E, Zhang QY, Huemmrich K, Campbell P, Corp L, Cook B, Kustas W, Daughtry C (2013). Integrating solar induced fluorescence and the photochemical reflectance index for estimating gross primary production in a cornfield. *Remote Sensing*, 5, 6857-6879.
- Cogliati S, Verhoef W, Kraft S, Sabater N, Alonso L, Vicent J, Moreno J, Drusch M, Colombo R (2015). Retrieval of sun-induced fluorescence using advanced spectral fitting methods. *Remote Sensing of Environment*, 169, 344-357.
- Consalvey M, Perkins RG, Paterson DM, Underwood GJC (2005). Pam fluorescence: a beginners guide for benthic diatomists. *Diatom Research*, 20, 1-22.
- Cui TX, Sun R, Qiao C (2016). Assessing the factors determining the relationship between solar-induced chlorophyll fluorescence and GPP//IEEE. *IEEE International Geoscience and Remote Sensing Symposium*. IEEE, Beijing. DOI: 10.1109/IGARSS.2016.7729910.
- Damm A, Guanter L, Paul-Limoges E, van der Tol C, Hueni A, Buchmann N, Eugster W, Ammann C, Schaepman ME (2015). Far-red sun-induced chlorophyll fluorescence shows ecosystem-specific relationships to gross primary production: an assessment based on observational and modeling approaches. *Remote Sensing of Environment*, 166, 91-105.
- Daumard F, Champagne S, Fournier A, Goulas Y, Ounis A, Hanocq JF, Moya I (2010). A field platform for continuous measurement of canopy fluorescence. *IEEE Transactions on Geoscience and Remote Sensing*, 48, 3358-3368.
- Drusch M, Moreno J, del Bello U, Franco R, Goulas Y, Huth A, Kraft S, Middleton EM, Miglietta F, Mohammed G, Nedbal L, Rascher U, Schuttemeyer D, Verhoef W (2016). The FLuorescence EXplorer mission concept—ESA's earth explorer 8. *IEEE Transactions on Geoscience and Remote Sensing*, 55, 1273-1284.
- Du SS, Liu LY, Liu XJ, Guo J, Hu JC, Wang SQ, Zhang YG (2019). SIFSpec: measuring solar-induced chlorophyll fluorescence observations for remote sensing of photosynthesis. *Sensors*, 19, 3009. DOI: 10.3390/s19133009.
- Du SS, Liu LY, Liu XJ, Zhang X, Zhang XY, Bi YM, Zhang LC (2018). Retrieval of global terrestrial solar-induced chlorophyll fluorescence from TanSat satellite. *Science Bulletin*, 63, 1502-1512.
- Eldering A, Taylor TE, O'dell CW, Pavlick R (2019). The OCO-3 mission: measurement objectives and expected performance based on 1 year of simulated data. *Atmospheric Measurement Techniques*, 12, 2341-2370.
- Faraloni C, Cutino I, Petrucci R, Leva AR, Lazzeri S, Torzillo G (2011). Chlorophyll fluorescence technique as a rapid tool for *in vitro* screening of olive cultivars (*Olea europaea* L.) tolerant to drought stress. *Environmental and Experimental Botany*, 73, 49-56.
- Farooq S, Chmeliov J, Wientjes E, Koehorst R, Bader A, Valkunas L, Trinkunas G, van Amerongen H (2018). Dynamic feedback of the photosystem II reaction centre on photoprotection in plants. *Nature Plants*, 4, 225-231.
- Flexas J, Medrano H (2002). Energy dissipation in C<sub>3</sub> plants under drought. *Functional Plant Biology*, 29, 1209-1215.
- Fournier A, Daumard F, Champagne S, Ounis A, Goulas Y, Moya I (2012). Effect of canopy structure on sun-induced chlorophyll fluorescence. *ISPRS Journal of Photogrammetry and Remote Sensing*, 68, 112-120.
- Franck F, Dewez D, Popovic R (2005). Changes in the room-temperature emission spectrum of chlorophyll during fast and slow phases of the Kautsky effect in intact leaves. *Photochemistry and Photobiology*, 81, 431-436.
- Franck F, Juneau P, Popovic R (2002). Resolution of the photosystem I and photosystem II contributions to chlorophyll fluorescence of intact leaves at room temperature. *Biochimica et Biophysica Acta (BBA): Bioenergetics*, 1556, 239-246.
- Frankenbach S, Ezequiel J, Plecha S, Goessling JW, Vaz L, Kühl M, Dias JM, Vaz N, Serôdio J (2020). Synoptic spatio-temporal variability of the photosynthetic productivity of microphytobenthos and phytoplankton in a tidal estuary. *Frontiers in Marine Science*, 7, 170. DOI: 10.3389/fmars.2020.00170.
- Frankenberg C, Fisher JB, Worden J, Badgley G, Saatchi SS, Lee JE, Toon GC, Butz A, Jung M, Kuze A, Yokota T (2011). New global observations of the terrestrial carbon

- cycle from GOSAT: patterns of plant fluorescence with gross primary productivity. *Geophysical Research Letters*, 38, L17706. DOI: 10.1029/2011GL048738.
- Frankenberg C, O'dell C, Berry J, Guanter L, Joiner J, Köhler P, Pollock R, Taylor TE (2014). Prospects for chlorophyll fluorescence remote sensing from the Orbiting Carbon Observatory-2. *Remote Sensing of Environment*, 147, 1-12.
- Goulas Y, Fournier A, Daumard F, Champagne S, Ounis A, Marloie O, Moya I (2017). Gross primary production of a wheat canopy relates stronger to far red than to red solar-induced chlorophyll fluorescence. *Remote Sensing*, 9, 97. DOI: 10.3390/rs9010097.
- Grossmann K, Frankenberg C, Magney TS, Hurlock SC, Seibt U, Stutz J (2018). PhotoSpec: a new instrument to measure spatially distributed red and far-red solar-induced chlorophyll fluorescence. *Remote Sensing of Environment*, 216, 311-327.
- Gu L, Wood JD, Chang CYY, Sun Y, Riggs JS (2018). Advancing terrestrial ecosystem science with a novel automated measurement system for sun-induced chlorophyll fluorescence for integration with eddy covariance flux networks. *Journal of Geophysical Research: Biogeosciences*, 124, 127-146.
- Guanter L, Aben I, Tol P, Krijger JM, Hollstein A, Köhler P, Damm A, Joiner J, Frankenberg C, Landgraf J (2015). Potential of the TROPospheric Monitoring Instrument (TROPOMI) onboard the Sentinel-5 Precursor for the monitoring of terrestrial chlorophyll fluorescence. *Atmospheric Measurement Techniques*, 8, 1337-1352.
- Guanter L, Alonso L, Gómez-Chova L, Meroni M, Preusker R, Fischer J, Moreno J (2010). Developments for vegetation fluorescence retrieval from spaceborne high-resolution spectrometry in the O<sub>2</sub>-A and O<sub>2</sub>-B absorption bands. *Journal of Geophysical Research: Atmospheres*, 115, D19303. DOI: 10.1029/2009JD013716.
- Guanter L, Frankenberg C, Dudhia A, Lewis PE, Gómez-Dans J, Kuze A, Suto H, Grainger RG (2012). Retrieval and global assessment of terrestrial chlorophyll fluorescence from GOSAT space measurements. *Remote Sensing of Environment*, 121, 236-251.
- Guanter L, Zhang Y, Jung M, Joiner J, Voigt M, Berry JA, Frankenberg C, Huete AR, Zarco-Tejada P, Lee JE, Moran MS, Ponce-Campos G, Beer C, Camps-Valls G, Buchmann N, Gianelle D, Klumpp K, Cescatti A, Baker JM, Griffis TJ (2014). Global and time-resolved monitoring of crop photosynthesis with chlorophyll fluorescence. *Proceedings of the National Academy of Sciences of the United States of America*, 111, 1327-1333.
- Hasegawa M, Shiina T, Terazima M, Kumazaki S (2010). Selective excitation of photosystems in chloroplasts inside plant leaves observed by near-infrared laser-based fluorescence spectral microscopy. *Plant and Cell Physiology*, 51, 225-238.
- Hendrickson L, Furbank RT, Chow WS (2004). A simple alternative approach to assessing the fate of absorbed light energy using chlorophyll fluorescence. *Photosynthesis Research*, 82, 73-81.
- Hmimina G, Dufrêne E, Soudani K (2014). Relationship between photochemical reflectance index and leaf ecophysiological and biochemical parameters under two different water statuses: towards a rapid and efficient correction method using real-time measurements. *Plant, Cell & Environment*, 37, 473-487.
- Hu JC, Liu LY, Guo J, Du SS, Liu XJ (2018). Upscaling solar-induced chlorophyll fluorescence from an instantaneous to daily scale gives an improved estimation of the gross primary productivity. *Remote Sensing*, 10, 1663. DOI: 10.3390/rs10101663.
- Huang D, Knyazikhin Y, Dickinson RE, Rautiainen M, Stenberg P, Disney M, Lewis P, Cescatti A, Tian YH, Verhoef W, Martonchik JV, Myneni RB (2007). Canopy spectral invariants for remote sensing and model applications. *Remote Sensing of Environment*, 106, 106-122.
- Ji MH, Tang BH, Li ZL (2019). Review of solar-induced chlorophyll fluorescence retrieval methods from satellite data. *Remote Sensing Technology and Application*, 34, 455-466. [纪梦豪, 唐伯惠, 李召良 (2019). 太阳诱导叶绿素荧光的卫星遥感反演方法研究进展. 遥感技术与应用, 34, 455-466.]
- Joiner J, Guanter L, Lindstrot R, Voigt M, Vasilkov AP, Middleton EM, Huemmrich KF, Yoshida Y, Frankenberg C (2013). Global monitoring of terrestrial chlorophyll fluorescence from moderate-spectral-resolution near-infrared satellite measurements: methodology, simulations, and application to GOME-2. *Atmospheric Measurement Techniques*, 6, 2803-2823.
- Joiner J, Yoshida Y, Vasilkov AP, Yoshida Y, Corp LA, Middleton EM (2011). First observations of global and seasonal terrestrial chlorophyll fluorescence from space. *Biogeosciences*, 8, 637-651.
- Kolber Z, Klimov D, Ananyev G, Rascher U, Berry J, Osmond B (2005). Measuring photosynthetic parameters at a distance: laser induced fluorescence transient (LIFT) method for remote measurements of photosynthesis in terrestrial vegetation. *Photosynthesis Research*, 84, 121-129.
- Konanz S, Kocsányi L, Buschmann C (2014). Advanced multi-color fluorescence imaging system for detection of biotic and abiotic stresses in leaves. *Agriculture*, 4, 79-95.
- Kramer DM, Johnson G, Kiirats O, Edwards GE (2004). New fluorescence parameters for the determination of QAredox state and excitation energy fluxes. *Photosynthesis Research*, 79, 209-218.
- Kromdijk J, Glowacka K, Leonelli L, Gabilly ST, Iwai M, Niyogi KK, Long SP (2016). Improving photosynthesis and crop productivity by accelerating recovery from photoprotection. *Science*, 354, 857-861.

- Lambrev PH, Nilkens M, Miloslavina Y, Jahns P, Holzwarth AR (2010). Kinetic and spectral resolution of multiple nonphotochemical quenching components in *Arabidopsis* leaves. *Plant Physiology*, 152, 1611-1624.
- Lee JE, Berry JA, van der Tol C, Yang X, Guanter L, Damm A, Baker I, Frankenberg C (2015). Simulations of chlorophyll fluorescence incorporated into the Community Land Model version 4. *Global Change Biology*, 21, 3469-3477.
- Lee JE, Frankenberg C, van der Tol C, Berry JA, Guanter L, Boyce CK, Fisher JB, Morrow E, Worden JR, Asefi S, Badgley G, Saatchi S (2013). Forest productivity and water stress in Amazonia: observations from GOSAT chlorophyll fluorescence. *Proceedings of The Royal Society B: Biological Sciences*, 280, 20130171. DOI: 10.1098/rspb.2013.0171.
- Li QF, Li ZM, Ji JW, Zou QY, Yu H (2013). Applications of chlorophyll fluorescence kinetics in the physiological resistance studies of plant. *Hubei Agricultural Sciences*, 52, 5399-5402. [李钦夫, 李征明, 纪建伟, 邹秋滢, 于辉 (2013). 叶绿素荧光动力学及在植物抗逆生理研究中的应用. 湖北农业科学, 52, 5399-5402.]
- Li SL, Gao MF, Li ZL, Li FJ, Gao Y, Liao QY (2018). Retrieval of chlorophyll fluorescence from Tansat in North-east China. *China Agricultural Informatics*, (6), 53-62. [李石磊, 高懋芳, 李召良, 李方杰, 高雅, 廖前瑜 (2018). 基于碳卫星的中国东北地区叶绿素荧光反演. 中国农业信息, (6), 53-62.]
- Liang Y, Li JY, Zhang YW (2013). Research advances of the remote sensing of solar-induced chlorophyll fluorescence. *Chinese Agricultural Science Bulletin*, 29, 107-112. [梁寅, 李军营, 张云伟 (2013). 日光诱导叶绿素荧光遥感探测的研究进展. 中国农学通报, 29, 107-112.]
- Liu LY, Guan LL, Liu XJ (2017). Directly estimating diurnal changes in GPP for  $C_3$  and  $C_4$  crops using far-red sun-induced chlorophyll fluorescence. *Agricultural and Forest Meteorology*, 232, 1-9.
- Liu XJ, Liu LY, Hu JC, Guo J, Du SS (2020). Improving the potential of red SIF for estimating GPP by downscaling from the canopy level to the photosystem level. *Agricultural and Forest Meteorology*, 281, 107846. DOI: 10.1016/j.agrformet.2019.107846.
- Magney TS, Bowling DR, Logan BA, Grossmann K, Stutz J, Blanken PD, Burns SP, Cheng R, Garcia MA, Köhler P, Lopez S, Parazoo NC, Raczka B, Schimel D, Frankenberg C (2019a). Mechanistic evidence for tracking the seasonality of photosynthesis with solar-induced fluorescence. *Proceedings of the National Academy of Sciences of the United States of American*, 116, 11640-11645.
- Magney TS, Frankenberg C, Fisher JB, Sun Y, North GB, Davis TS, Kornfeld A, Siebke K (2017). Connecting active to passive fluorescence with photosynthesis: a method for evaluating remote sensing measurements of Chl fluorescence. *New Phytologist*, 215, 1594-1608.
- Magney TS, Frankenberg C, Köhler P, North G, Davis TS, Dold C, Dutta D, Fisher JB, Grossmann K, Harrington A, Hatfield J, Stutz J, Sun Y, Porcar-Castell A (2019b). Disentangling changes in the spectral shape of chlorophyll fluorescence: implications for remote sensing of photosynthesis. *Journal of Geophysical Research: Biogeosciences*, 124, 1491-1507.
- Maguire AJ, Eitel JUH, Griffin KL, Magney TS, Long RA, Vierling LA, Schmiede SC, Jennewein JS, Weygint WA, Boelman NT, Bruner SG (2020). On the functional relationship between fluorescence and photochemical yields in complex evergreen needleleaf canopies. *Geophysical Research Letters*, 47, e2020GL087858. DOI: 10.1029/2020GL087858.
- Marrs JK, Reblin JS, Logan BA, Allen DW, Reinmann AB, Bombard DM, Tabachnik D, Hutrya LR (2020). Solar-induced fluorescence does not track photosynthetic carbon assimilation following induced stomatal closure. *Geophysical Research Letters*, 47, e2020GL087956. DOI: 10.1111/nph.16984.
- Maxwell K, Johnson GN (2000). Chlorophyll fluorescence—A practical guide. *Journal of Experimental Botany*, 51, 659-668.
- McMurtrey JE, Middleton EM, Corp LA, Entcheva Campbell PK, Butcher LM, Chappelle EW, Cook WB (2002). Fluorescence responses from nitrogen plant stress in 4 Fraunhofer band regions. *IEEE International Geoscience and Remote Sensing Symposium*, 3, 1538-1540.
- Meroni M, Rossini M, Guanter L, Alonso L, Rascher U, Colombo R, Moreno J (2009). Remote sensing of solar-induced chlorophyll fluorescence: review of methods and applications. *Remote Sensing of Environment*, 113, 2037-2051.
- Miao GF, Guan KY, Yang X, Bernacchi CJ, Berry JA, DeLucia EH, Wu J, Moore CE, Meacham K, Cai YP, Peng B, Kimm H, Masters MD (2018). Sun-induced chlorophyll fluorescence, photosynthesis, and light use efficiency of a soybean field from seasonally continuous measurements. *Journal of Geophysical Research: Biogeosciences*, 123, 610-623.
- Middleton E, Rascher U, Corp L, Huemmrich K, Cook B, Noormets A, Schickling A, Pinto F, Alonso L, Damm A, Guanter L, Colombo R, Campbell P, Landis D, Zhang QY, Rossini M, Schuettemeyer D, Bianchi RM (2017). The 2013 FLEX—US airborne campaign at the parker tract loblolly pine plantation in North Carolina, USA. *Remote Sensing*, 9, 612. DOI: 10.3390/rs9060612.
- Mohammed GH, Colombo R, Middleton EM, Rascher U, van der Tol C, Nedbal L, Goulas Y, Pérez-Priego O, Damm A, Meroni M, Joiner J, Cogliati S, Verhoef W, Malenovsky Z, Gastellu-Etchegorry JP, et al. (2019). Remote sensing of solar-induced chlorophyll fluorescence (SIF) in vegetation: 50 years of progress. *Remote Sensing of Environment*, 231,

111177. DOI: 10.1016/j.rse.2019.04.030.
- Murchie EH, Lawson T (2013). Chlorophyll fluorescence analysis: a guide to good practice and understanding some new applications. *Journal of Experimental Botany*, 64, 3983-3998.
- Nakajima M, Suto H, Yotsumoto K, Shiomi K, Hirabayashi T (2017). Fourier transform spectrometer on GOSAT and GOSAT-2//Sodniks, CugnyB, KarafolasN. *Proc SPIE 10563, International Conference on Space Optics—ICSO 2014*. SPIE, Canary Islands, Spain. DOI: 10.1117/12.2304062.
- O'Brien DM, Polonsky IN, Utembe SR, Rayner PJ (2016). Potential of a geostationary GeoCARB mission to estimate surface emissions of CO<sub>2</sub>, CH<sub>4</sub> and CO in a polluted urban environment: case study Shanghai. *Atmospheric Measurement Techniques*, 9, 4633-4654.
- Pinto F, Damm A, Schickling A, Panigada C, Cogliati S, Müller-Linow M, Balvora A, Rascher U (2016). Sun-induced chlorophyll fluorescence from high-resolution imaging spectroscopy data to quantify spatio-temporal patterns of photosynthetic function in crop canopies. *Plant, Cell & Environment*, 39, 1500-1512.
- Plascyk JA, Gabriel FC (1975). The Fraunhofer line discriminator MKII—An airborne instrument for precise and standardized ecological luminescence measurement. *IEEE Transactions on Instrumentation and Measurement*, 24, 306-313.
- Porcar-Castell A, Mac Arthur A, Rossini M, Eklundh L, Pacheco-Labrador J, Anderson K, Balzarolo M, Martín MP, Jin H, Tomelleri E, Cerasoli S, Sakowska K, Hueni A, Julitta T, Nichol CJ, Vescovo L (2015). EUROSPEC: at the interface between remote sensing and ecosystem CO<sub>2</sub> flux measurements in Europe. *Biogeosciences Discussions*, 12, 13069-13121.
- Porcar-Castell A, Tyystjärvi E, Atherton J, van der Tol C, Flexas J, Pfündel EE, Moreno J, Frankenberg C, Berry JA (2014). Linking chlorophyll a fluorescence to photosynthesis for remote sensing applications: mechanisms and challenges. *Journal of Experimental Botany*, 65, 4065-4095.
- Raczka B, Porcar-Castell A, Magney T, Lee JE, Köhler P, Frankenberg C, Grossmann K, Logan BA, Stutz J, Blanken PD, Burns SP, Duarte H, Yang X, Lin JC, Bowling DR (2019). Sustained nonphotochemical quenching shapes the seasonal pattern of solar-induced fluorescence at a high-elevation evergreen forest. *Journal of Geophysical Research: Biogeosciences*, 124, 2005-2020.
- Rahimzadeh-Bajgiran P, Tubuxin B, Omasa K (2017). Estimating chlorophyll fluorescence parameters using the joint Fraunhofer line depth and laser-induced saturation pulse (FLD-LISP) method in different plant species. *Remote Sensing*, 9, 599. DOI: 10.3390/rs9060599.
- Ryu Y, Berry JA, Baldocchi DD (2019). What is global photosynthesis? History, uncertainties and opportunities. *Remote Sensing of Environment*, 223, 95-114.
- Stirbet A, Govindjee (2011). On the relation between the Kautsky effect (chlorophyll a fluorescence induction) and photosystem II: basics and applications of the OJIP fluorescence transient. *Journal of Photochemistry and Photobiology B: Biology*, 104, 236-257.
- Sun Y, Frankenberg C, Jung M, Joiner J, Guanter L, Köhler P, Magney T (2018). Overview of solar-induced chlorophyll fluorescence (SIF) from the Orbiting Carbon Observatory-2: retrieval, cross-mission comparison, and global monitoring for GPP. *Remote Sensing of Environment*, 209, 808-823.
- Sun Y, Frankenberg C, Wood JD, Schimel DS, Jung M, Guanter L, Drewry DT, Verma M, Porcar-Castell A, Griffiths TJ, Gu L, Magney TS, Köhler P, Evans B, Yuen K (2017). OCO-2 advances photosynthesis observation from space via solar-induced chlorophyll fluorescence. *Science*, 358, eaam5747. DOI: 10.1126/science.aam5747.
- van der Tol C, Berry JA, Campbell PKE, Rascher U (2014). Models of fluorescence and photosynthesis for interpreting measurements of solar-induced chlorophyll fluorescence. *Journal of Geophysical Research: Biogeosciences*, 119, 2312-2327.
- van der Tol C, Vilfan N, Yang PQ, Bayat B, Verhoef W (2018). Modeling reflectance, fluorescence and photosynthesis: development of the SCOPE model//IEEE. *IEEE International Geoscience and Remote Sensing Symposium*. IEEE, Beijing. DOI: 10.1109/IGARSS.2018.8517517.
- Verma M, Schimel D, Evans B, Frankenberg C, Beringer J, Drewry DT, Magney T, Marang I, Hutley L, Moore C, Eldering A (2017). Effect of environmental conditions on the relationship between solar-induced fluorescence and gross primary productivity at an O<sub>2</sub>Flux grassland site. *Journal of Geophysical Research: Biogeosciences*, 122, 716-733.
- Verrelst J, van der Tol C, Magnani F, Sabater N, Rivera JP, Mohammed G, Moreno J (2016). Evaluating the predictive power of sun-induced chlorophyll fluorescence to estimate net photosynthesis of vegetation canopies: a SCOPE modeling study. *Remote Sensing of Environment*, 176, 139-151.
- Vilfan N, van der Tol C, Muller O, Rascher U, Verhoef W (2016). Fluspect-B: a model for leaf fluorescence, reflectance and transmittance spectra. *Remote Sensing of Environment*, 186, 596-615.
- Vilfan N, van der Tol C, Verhoef W (2019). Estimating photosynthetic capacity from leaf reflectance and Chl fluorescence by coupling radiative transfer to a model for photosynthesis. *New Phytologist*, 223, 487-500.
- Wang R, Liu ZG, Yang PQ (2012). Principle and progress in remote sensing of vegetation solar-induced chlorophyll fluorescence. *Advances in Earth Science*, 27, 1221-1228.
- [王冉, 刘志刚, 杨沛琦 (2012). 植物日光诱导叶绿素

- 荧光的遥感原理及研究进展. 地球科学进展, 27, 1221-1228.]
- Wang SH, Zhang LF, Huang CP, Qiao N (2017). Ground-based long-term remote sensing of solar-induced chlorophyll fluorescence: methods, challenges and opportunities. *IEEE International Geoscience and Remote Sensing Symposium*. DOI: 10.1109/IGARSS.2017.8127845.
- Wohlfahrt G, Gerdel K, Migliavacca M, Rotenberg E, Tatarinov F, Müller J, Hammerle A, Julitta T, Spielmann FM, Yakir D (2018). Sun-induced fluorescence and gross primary productivity during a heat wave. *Scientific Reports*, 8, 14169. DOI: 10.1038/s41598-018-32602-z.
- Wolanin A, Rozanov VV, Dinter T, Noël S, Vountas M, Burrows JP, Bracher A (2015). Global retrieval of marine and terrestrial chlorophyll fluorescence at its red peak using hyperspectral top of atmosphere radiance measurements: feasibility study and first results. *Remote Sensing of Environment*, 166, 243-261.
- Wyber R, Malenovsky Z, Ashcroft M, Osmond B, Robinson S (2017). Do daily and seasonal trends in leaf solar induced fluorescence reflect changes in photosynthesis, growth or light exposure? *Remote Sensing*, 9, 604. DOI: 10.3390/rs9060604.
- Yang KG, Ryu Y, Dechant B, Berry JA, Hwang Y, Jiang CY, Kang M, Kim J, Kimm H, Kornfeld A, Yang X (2018). Sun-induced chlorophyll fluorescence is more strongly related to absorbed light than to photosynthesis at half-hourly resolution in a rice paddy. *Remote Sensing of Environment*, 216, 658-673.
- Yang X, Tang JW, Mustard JF, Lee JE, Rossini M, Joiner J, Munger JW, Kornfeld A, Richardson AD (2015). Solar-induced chlorophyll fluorescence that correlates with canopy photosynthesis on diurnal and seasonal scales in a temperate deciduous forest. *Geophysical Research Letters*, 42, 2977-2987.
- You X, Gong JR (2012). Significance and application of chlorophyll fluorescence dynamics process parameters. *Journal of West China Forestry Science*, 41, 90-94. [尤鑫, 龚吉蕊 (2012). 叶绿素荧光动力学参数的意义及实例辨析. 西部林业科学, 41, 90-94.]
- Zarco-Tejada PJ, González-Dugo MV, Fereres E (2016). Seasonal stability of chlorophyll fluorescence quantified from airborne hyperspectral imagery as an indicator of net photosynthesis in the context of precision agriculture. *Remote Sensing of Environment*, 179, 89-103.
- Zarco-Tejada PJ, Morales A, Testi L, Villalobos FJ (2013). Spatio-temporal patterns of chlorophyll fluorescence and physiological and structural indices acquired from hyperspectral imagery as compared with carbon fluxes measured with eddy covariance. *Remote Sensing of Environment*, 133, 102-115.
- Zeng YL, Badgley G, Dechant B, Ryu Y, Chen M, Berry JA (2019). A practical approach for estimating the escape ratio of near-infrared solar-induced chlorophyll fluorescence. *Remote Sensing of Environment*, 232, 111209. DOI: 10.1016/j.rse.2019.05.028.
- Zhang YG, Zhang Q, Liu LY, Wang SQ, Ju WM, Tang JW, Huang Y, Zhu XD, Wang F, Zhang JS, Zhou GS, Zhou L, Tang XG, Zhang ZY, Qiu B, Zhang XK, Wang SH (2020). ChinaSpec: a network for long-term *in situ* measurements of solar-induced fluorescence and reflectance in China. *Earth and Space Science Open Archive*, 30. DOI: 10.1002/essoar.10501911.1.
- Zhang YJ, Liu LY, Hou MY, Liu LT, Li CD (2009). Progress in remote sensing of vegetation chlorophyll fluorescence. *Journal of Remote Sensing*, 13, 963-978. [张永江, 刘良云, 侯名语, 刘连涛, 李存东 (2009). 植物叶绿素荧光遥感研究进展. 遥感学报, 13, 963-978.]
- Zhang ZY, Chen JM, Guanter L, He LM, Zhang YG (2019). From canopy-leaving to total canopy far-red fluorescence emission for remote sensing of photosynthesis: first results from TROPOMI. *Geophysical Research Letters*, 46, 12030-12040.
- Zhang ZY, Wang SH, Qiu B, Song L, Zhang YG (2019). Retrieval of sun-induced chlorophyll fluorescence and advancements in carbon cycle application. *Journal of Remote Sensing*, 23, 37-52. [章钊颖, 王松寒, 邱博, 宋练, 张永光 (2019). 日光诱导叶绿素荧光遥感反演及碳循环应用进展. 遥感学报, 23, 37-52.]
- Zhao F, Guo YQ, Verhoef W, Gu XF, Liu LY, Yang GJ (2014). A method to reconstruct the solar-induced canopy fluorescence spectrum from hyperspectral measurements. *Remote Sensing*, 6, 10171-10192.
- Zoogman P, Liu X, Suleiman RM, Pennington WF, Flittner DE, Al-Saadi JA, Hilton BB, Nicks DK, Newchurch MJ, Carr JL, Janz SJ, Andraschko MR, Arola A, Baker BD, Canova BP, et al. (2017). Tropospheric emissions: monitoring of pollution (TEMPO). *Journal of Quantitative Spectroscopy and Radiative Transfer*, 186, 17-39.

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