

阴天和晴天对黄河三角洲芦苇湿地净生态系统CO₂交换的影响

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摘要 云量以及大气气溶胶含量变化引起的阴天和晴天会对局地的微气候环境产生综合效应, 影响地面接收的太阳辐射强度, 同时引起环境因子的变化, 最终对净生态系统CO₂交换(NEE)产生影响。该文通过涡度相关系统以及微气象梯度观测系统, 对黄河三角洲芦苇(*Phragmites australis*)湿地NEE以及环境要素进行了观测。在自然条件下选择12对相邻阴天和晴天数据, 在生物要素(生物量、叶面积指数)、土壤水分以及养分特征保持不变的前提下, 揭示了阴天和晴天变化对湿地生态系统NEE的光响应和温度响应的影响。结果表明: 12对阴天和晴天生态系统NEE的日平均动态均呈“U”型曲线, 但阴天NEE的变幅较小。晴天条件下湿地生态系统NEE的日均值显著高于阴天($p < 0.01$)。阴天和晴天湿地生态系统NEE与光合有效辐射(PAR)之间均呈直角双曲线关系, 但晴天条件下, 最大光合速率(A_{\max})显著大于阴天($p < 0.01$), 同时白天生态系统呼吸($R_{\text{eco, daytime}}$)也显著大于阴天($p < 0.01$)。不论阴天还是晴天, $R_{\text{eco, daytime}}$ 与气温均呈显著的指数关系。晴天湿地生态系统呼吸的温度敏感系数 Q_{10} (5.5)远大于阴天(1.9)。阴天和晴天昼间PAR差值以及气温差值对NEE差值的协同影响达到63%。

关键词 阴天, 晴天, 净生态系统CO₂交换, 白天生态系统呼吸, 光响应, 温度响应

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Net ecosystem exchange of CO₂ on sunny and cloudy days over a reed wetland in the Yellow River Delta, China

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Abstract

Aims Clouds and aerosols change the radiation level on the land surface and indirectly alter the microclimate. Shifts in sunny and cloudy days, for example, would affect the net ecosystem exchange of CO₂ (NEE) between land surface and the atmosphere. Our objective was to analyze the influence of shifts in sunny and cloudy days on NEE, its responses to light and temperature in a reed (*Phragmites australis*) wetland in the Yellow River Delta, China.

Methods Using the eddy covariance technique, we measured the temporal changes in NEE during the growing season over the reed wetland. We selected 12 paired-days during the measurement period following two criteria: (1) the two paired days are adjacent, with one sunny day and another cloudy day; (2) no rain event during the two days. We assumed that: (1) live biomass and leaf area index (LAI) are the same during any paired-days; (2) soil moisture has no significant difference between the two adjacent days. With these criteria, we expected that radiation condition exerted the major control on NEE.

Important findings Diurnal change of NEE showed a distinct U-shaped pattern on both sunny and cloudy days, but with substantial variation in its amplitude. During the daytime, NEE on sunny days was significantly higher ($p < 0.01$) than that on the cloudy days ($n = 12$). The daytime NEE response to photosynthetically active radiation (PAR) was modeled with the rectangular hyperbolic function (Eq. (1)) for both sunny and cloudy days. There

appeared a significant reduction ($p < 0.01$) in light-saturated NEE (A_{\max}) on cloudy days compared to the sunny days. Similarly, there was a significant decrease ($p < 0.01$) in daytime ecosystem respiration ($R_{\text{eco,daytime}}$) on cloudy days as compared to that of the sunny day although there existed significant exponential relationships between $R_{\text{eco,daytime}}$ and air temperature on both sunny and cloudy days. In addition, the temperature sensitivity of ecosystem respiration (Q_{10}) on cloudy days (1.9) was significantly lower than that of sunny days (5.5). Stepwise multiple regression analyses suggested that PAR and T explained 63% of the changes in NEE between sunny and cloudy days. By taking advantage of the natural shift of sunny and cloudy days without disturbance to the plant-soil system, our results indicated that cloud cover significantly reduced the absorption capacity of CO_2 in the wetland. Thus, it is necessary to take into account the shifts between sunny and cloudy days on NEE when predicting the ecosystem responses to future climate in the wetland.

Key words sunny day, cloudy day, net ecosystem CO_2 exchange (NEE), daytime ecosystem respiration ($R_{\text{eco,daytime}}$), light response, temperature response

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近年来, 大气污染、气溶胶粒子增加等环境问题日益严重, 云层和大气气溶胶含量的变化给地面接收的直接辐射和散射辐射带来很大影响(Niyogi *et al.*, 2004; Bar-Or *et al.*, 2010; 马金玉等, 2011)。我国华北地区大气环境由于受到西北地区沙尘的影响, 大量滞留在大气中的沙尘成为对流层气溶胶的主要成分, 影响地-气系统辐射能收支, 从而影响区域的气候及生态环境(Min, 2005; 贾璇等, 2010)。研究表明: 近50年来, 地面太阳总辐射从减少到增加(齐月等, 2014)。而云作为一种天气现象会对局地的微气候环境产生综合效应, 当天空有云层出现时, 地面接收的太阳辐射强度及散射辐射与直射辐射的比例会发生变化, 引起生态系统光能与热能的变化, 植被的光合与呼吸作用发生变化, 最终生态系统与大气间的净 CO_2 交换也会受到影响(Letts *et al.*, 2005; Urban *et al.*, 2007)。

已有研究表明, 阴天和晴天所引起的辐射差异影响着陆地生态系统的交换过程和碳吸收能力(Roderick *et al.*, 2001; Still *et al.*, 2009)。但由于研究方法、地域环境条件以及不同植被类型的差异, 研究结论存在较大差异(Gu *et al.*, 1999, 2002; Alton *et al.*, 2007; Urban *et al.*, 2007)。例如, 中国渭北刺槐(*Robinia pseudoacacia*)生长初期和旺盛期晴天条件下森林日均固碳量比阴天高8%–16% (郑元等, 2011)。中国西北玉米(*Zea mays*)农田生态系统阴天条件下净生态系统 CO_2 交换(NEE)的增长速率却高于晴天, 且生态系统总初级生产力(GPP)最大值出现于阴天(Zhang *et al.*, 2011)。对中国西北草地(Bai

et al., 2012)和不同温带森林类型(Zhang *et al.*, 2010)的研究也得出类似结论。另外, 也有研究发现加拿大常绿灌木(Letts *et al.*, 2005)和西藏高寒草甸(范玉枝等, 2009)生态系统 CO_2 交换不受阴天和晴天天气条件影响。

黄河口近海与海岸湿地是暖温带增长速度最快和最具代表性的新生近海与海岸湿地, 具有海陆过渡性、原生性和脆弱性的特点(布仁仓等, 1999; 崔树强, 2002)。受水沙量变化、陆地和河流淡水径流、咸水海流多重影响以及人类活动的干扰, 黄河三角洲湿地生态系统 CO_2 交换存在着极大的复杂性和不确定性(Sasaki *et al.*, 2009; Han *et al.*, 2014a, 2014b; 邢庆会等, 2014)。研究表明黄河三角洲芦苇湿地生长季 NEE 占全年的80%以上, 且碳吸收集集中在植物生长旺盛期(7–9月)(杨利琼等, 2013; Han *et al.*, 2014a, 2014b)。而这一时期正值黄河三角洲雨季, 其云雨状况影响太阳辐射, 进而影响湿地生态系统的碳吸收功能。在以往的研究中, 温度、水分、太阳辐射等环境因子, 生物量、叶面积等生物因子以及地下水位、地表水深等水文要素对湿地生态系统 NEE 的影响机制受到研究者的极大关注(牟长城等, 2009; Zhao *et al.*, 2010; Han *et al.*, 2013; 邢庆会等, 2014)。目前, 有关阴天和晴天条件对生态系统碳交换影响的研究主要集中在森林生态系统(Liu *et al.*, 2006; Zhang *et al.*, 2010; 周丽艳等, 2010; Jiang *et al.*, 2011; Zhao *et al.*, 2011; 刘佳等, 2014)和草原生态系统(Gu *et al.*, 2003; 范玉枝等, 2009)。阴天和晴天状况引起的太阳辐射变化对湿地生态系统 NEE 和

碳汇功能究竟产生怎样的影响目前尚不清楚。

本文基于2013年黄河三角洲芦苇湿地生长季节中的12对阴天和晴天数据, 对比分析阴天和晴天条件下湿地生态系统CO₂交换动态及其环境控制机制, 以期阐明以下3个科学问题: (1)阴天和晴天对湿地生态系统NEE日动态变化的影响; (2)阴天和晴天对湿地生态系统NEE光响应和温度响应的影响; (3)阴天和晴天对湿地生态系统碳收支功能的影响。通过分析阴天和晴天太阳辐射变化对湿地生态系统CO₂交换的影响, 揭示黄河三角洲地区芦苇湿地生态系统CO₂源/汇功能及其影响机制, 并为预测未来随云雨天变化或大气组成及气溶胶含量变化对湿地生态系统碳收支的影响提供数据支持和理论依据。

1 材料和方法

1.1 研究地概况

研究地点位于山东省东营市垦利县的中国科学院黄河三角洲滨海湿地生态试验站(37.75° N, 118.98° E)。该区域属于温带半湿润大陆性季风气候, 光照充足, 四季分明, 雨热同期。年平均气温12.9 °C, 最高气温41.9 °C, 最低气温-23.3 °C, 年降水量530–630 mm, 其中70%的降水量集中在5–9月, 年内分配不均, 年蒸发量为1 900–2 400 mm。该地区地势平坦, 植物生长茂盛, 土壤质地以轻壤土和中壤土为主, 土壤类型以潮土和盐碱土为主。试验站植被类型以湿地植被为主, 优势种为芦苇(*Phragmites australis*)、盐地碱蓬(*Suaeda salsa*)、柽柳(*Tamarix chinensis*)和白茅(*Imperata cylindrica*)。植被覆盖度为70%–90%。涡度相关系统设在地势平坦、植物生长茂盛的芦苇湿地中央部, 在降水集中的8–10月, 地面有较多积水。芦苇通常在4月中旬萌动, 在5月中旬处于展叶盛期, 8月中旬开始抽穗, 9月中旬开花, 10月份开始进入枯黄期, 10月底芦苇大多枯萎, 植被高度在1.0–1.8 m。

1.2 涡度和环境要素测定

通量数据运用开路式涡度相关设备与常规气象观测仪器进行长期定位观测。涡度相关系统包括三维超声风速仪(CSAT-3, Campbell Scientific, Logan, USA)和开路红外CO₂/H₂O分析仪(IRGA, LI-7500, LI-COR, Lincoln, USA), 架设于距地表3 m处, 原始数据采样频率为10 Hz。微气象观测系统包括2 m高度的风向和风速(034B, Campbell Scientific, Logan,

USA)、空气温度(HMP45C, Vaisala, Helsinki, Finland)、净辐射(CNR4, Kipp & Zonen, Delft, Netherlands)和降水量(TE525MM, Texas Electronics, Dallas, USA)。土壤因子监测主要包括: 5、10、20、30、50 cm深处的土壤温度(109SS, Campbell Scientific, Logan, USA)和10、20、40、60、80、100 cm深处的土壤含水量(EnviroSMART SDI-12, EnviroScan, Lancaster, USA)。所有数据通过数据采集器(CR1000, Campbell Scientific, Logan, USA)在线采集, 并按30 min计算平均值进行存储。NEE数据为负值表示生态系统吸收CO₂, 即碳汇; NEE数据为正值表示生态系统释放CO₂, 即碳源。

1.3 通量数据处理

在野外通量观测中, 由于仪器响应、下垫面的起伏、天气状况、大气稳定度及供电系统故障等因素, 会产生异常数据及数据的丢失(Falge *et al.*, 2001)。在对原始通量数据进行分析之前, 需先进行数据的预处理: 坐标旋转、野点去除、WPL校正、夜间通量校正等。分析数据时进行以下处理: 1)去除所有降水时段对应的数据; 2)去除生长季|NEE| > 1 μmol CO₂·m⁻²·s⁻¹的数据。

白天缺失的NEE数据(净辐射> 20 W·m⁻²), 采用Michaelis-Menten模型(Ruimy *et al.*, 1995)进行插补。

$$NEE = R_{eco, daytime} - \frac{A_{max} \times \alpha \times PAR}{A_{max} + \alpha \times PAR} \quad (1)$$

式中, $R_{eco, daytime}$ 为白天生态系统呼吸(daytime ecosystem respiration, μmol CO₂·m⁻²·s⁻¹), α 为表观量子产量(apparent quantum yield, μmol CO₂·μmol⁻¹), A_{max} 为最大光合速率(maximum photosynthesis rate, μmol CO₂·m⁻²·s⁻¹)。NEE为直接从涡度相关仪器测定的CO₂通量数据。

夜间(净辐射< 20 W·m⁻²)缺失的数据采用(1)式, 利用夜间土壤温度(T_s)与夜间通量值($R_{eco, nighttime}$, μmol CO₂·m⁻²·s⁻¹)的指数关系插补(Lloyd & Taylor, 1994)。

$$R_{eco, nighttime} = a \exp(bT) \quad (2)$$

式中, $R_{eco, nighttime}$ 为夜晚生态系统呼吸(μmol CO₂·m⁻²·s⁻¹), T 为空气温度或土壤温度(°C), a 为参考温度下湿地生态系统呼吸速率(μmol CO₂·m⁻²·s⁻¹), b 为温度反应系数。

1.4 数据筛选

基于2013年黄河三角洲芦苇湿地生长季的涡度

相关法碳通量和微气象数据, 我们选择相邻的阴天和晴天数据, 选择标准为: (1)以15天为周期, 做出光合有效辐射(*PAR*)与降水量(*PPT*)随时间变化的日变化曲线, 并去除降雨天(*PPT* > 0.1 mm)数据; (2)从剔除后的数据中找出白天*PAR*日变化表现为光滑

且对称单峰曲线的, 确定为晴天; 从确定出的晴天找出相邻*PAR*日变化表现为曲折多峰的, 确定为阴天。基于以上两条标准, 我们共选取了12对阴天和晴天数据(图1)。由于每对数据是相邻的两天, 且没有降水发生, 因此我们可以假定每对阴天和晴天内

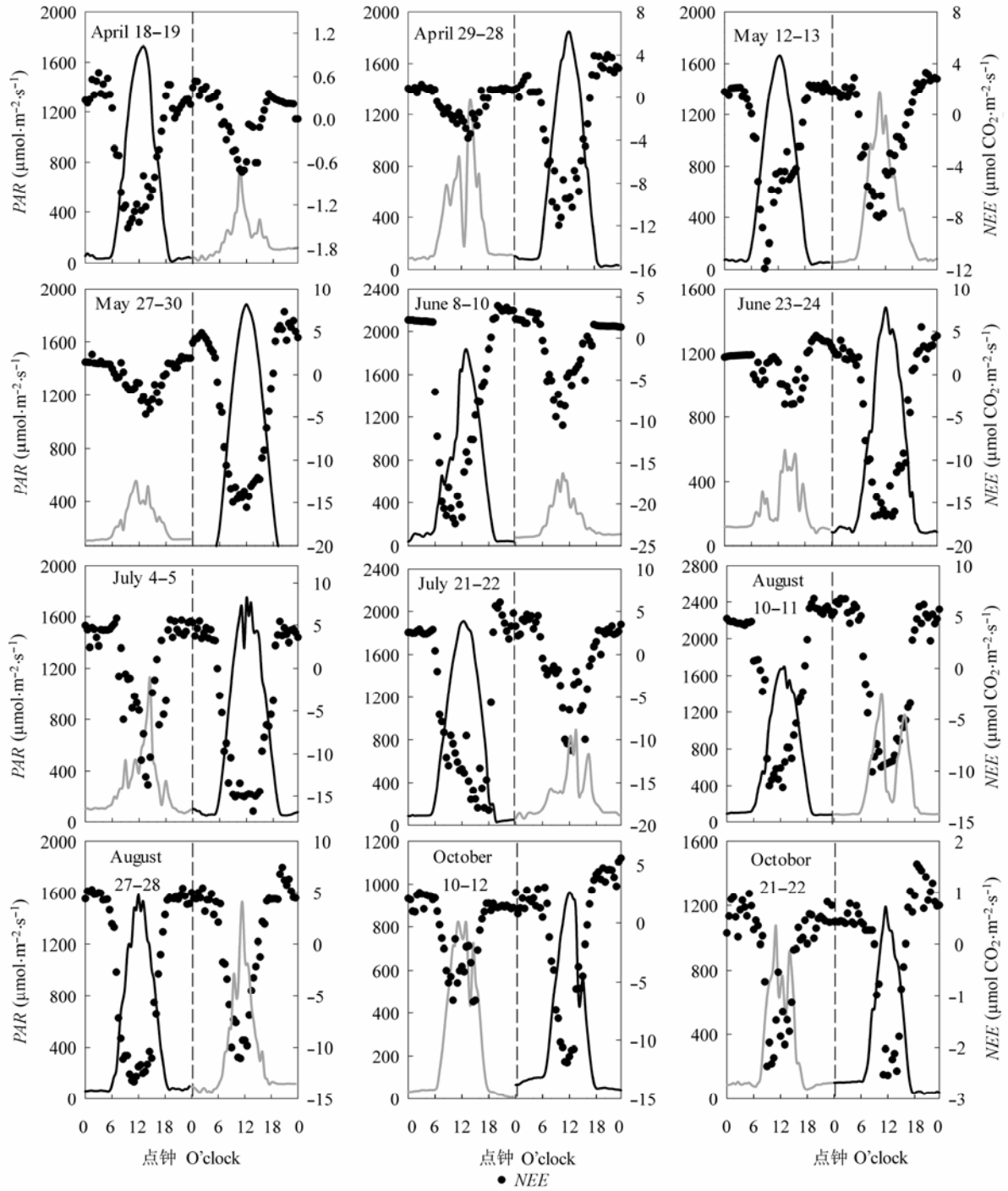


图1 黄河三角洲湿地生态系统2013年生长季12对阴天和晴天的净生态系统CO₂交换(*NEE*)与光合有效辐射(*PAR*)的日动态。黑线代表晴天*PAR*, 灰线代表阴天*PAR*。

Fig. 1 Diurnal changes in net ecosystem exchange of CO₂ (*NEE*) and photosynthetically active radiation (*PAR*) on the 12 paired-days (i.e., a sunny day and an adjacent cloudy day) during the 2013 growing season in the Yellow River Delta wetland. Black and grey solid lines represent *PAR* on sunny and cloudy days, respectively.

生物要素(生物量、叶面积指数、盖度)、土壤湿度以及土壤养分特征在两天内变化不大。在此前提下, 阴天和晴天引起的太阳辐射变化可能是影响湿地生态系统CO₂交换的主导因子。

1.5 数据分析

白天生态系统呼吸的温度响应主要通过以下指数模型进行拟合:

$$R_{\text{eco, daytime}} = a \exp(bT) \quad (3)$$

式中, $R_{\text{eco, daytime}}$ 为白天生态系统呼吸 ($\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$), 由(1)式推出; T 为空气温度 ($^{\circ}\text{C}$), a 为参考温度下湿地生态系统呼吸速率 ($\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$), b 为温度反应系数。

白天生态系统呼吸的温度敏感性系数 Q_{10} 基于以下公式进行计算:

$$Q_{10} = \exp(10b) \quad (4)$$

用单因素方差分析法分析阴天和晴天条件下环境因子 (PAR 、 T) 以及阴天和晴天 NEE 平均值的差异性。运用非线性拟合方法分析阴天和晴天白天 NEE 与光合有效辐射 (PAR) 的直角双曲线关系 (方程(1)); 用指数模型分别拟合 $R_{\text{eco, daytime}}$ 与 T 的关系 (方程(3)) 以及生态系统白天温度敏感性系数 Q_{10} (方程(4)); 对光响应参数 A_{max} 、 α 以及 $R_{\text{eco, daytime}}$ 、温度反应系数 a 与 b 进行方差分析。通过多元回归分析 PAR 与 T 对 NEE 以及 $R_{\text{eco, daytime}}$ 的协同影响作用。所有数据分析均基于统计分析软件 SPSS 16.0 完成, 相关的图形均基于 SigmaPlot 11.0 完成。

2 结果

2.1 阴天和晴天 NEE 日动态变化对比

图1为黄河三角洲湿地生态系统2013年生长季(4–10月) 12对相邻阴天和晴天的 PAR 与 NEE 日动态。晴天, PAR 整体表现为光滑的单峰对称分布, 日出后, PAR 逐渐增强, 在正午前后达到最大 ($1\,500\text{--}2\,000\, \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$), 之后逐渐减弱, 至日落后 PAR 又转为0; 阴天, PAR 变化曲折, 通常有多个峰值, 整体波动性相对晴天较小 (图1, 图2B)。阴天和晴天条件下, NEE 日变化均呈现“U”型曲线, 表现为白天吸收, 晚上释放。但阴天条件下, 白天的 NEE 波动均小于晴天, 说明白天碳吸收能力小于晴天 (图1, 图2A)。

为比较阴天和晴天 NEE 随 PAR 及气温的变化规律, 我们将阴天和晴天 NEE 、 PAR 和 T 按每天从0:00

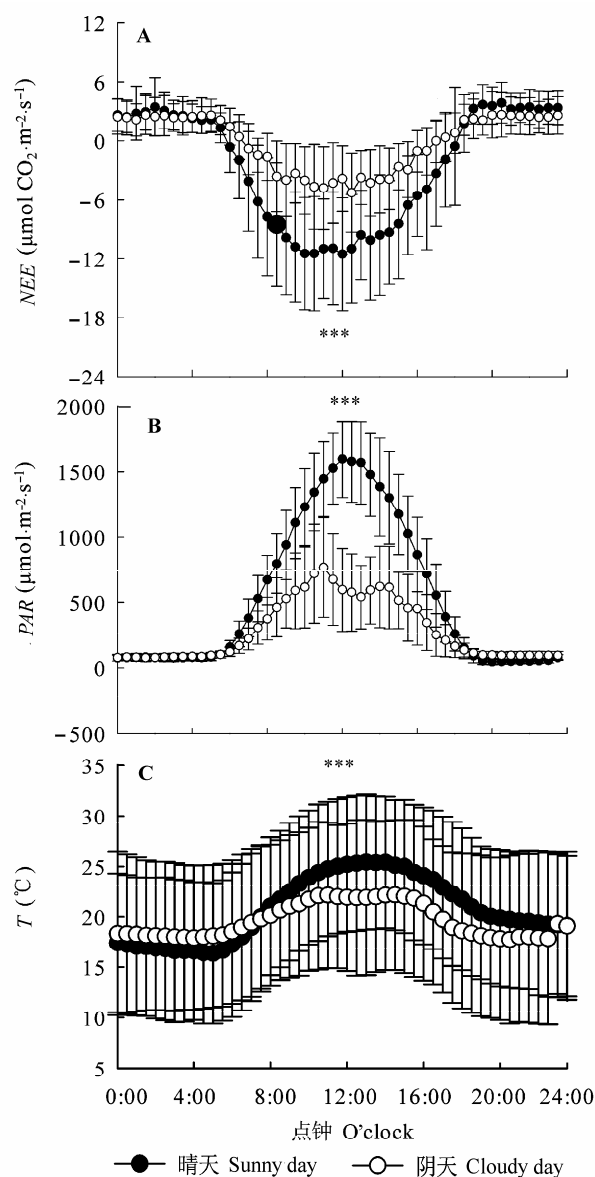


图2 2013年黄河三角洲湿地生长季阴天和晴天净生态系统CO₂交换(NEE)、光合有效辐射(PAR)与气温(T)的平均日动态(平均值±标准误差)。***, $p < 0.001$ 。

Fig. 2 Average diurnal variations of net ecosystem exchange of CO₂ (NEE), photosynthetically active radiation (PAR) and air temperature (T) on sunny days and cloudy days during the 2013 growing season in the Yellow River Delta. Bars represent standard errors of the means of 12 sunny days and 12 adjacent cloudy days (mean \pm SE). ***, $p < 0.001$.

到23:30每0.5 h进行平均, 得到生长季阴天和晴天 NEE 、 PAR 和 T 的日平均变化特征曲线 (图2)。将阴天和晴天昼间 NEE 、 PAR 和 T 在日进程中各实测点的观测值分别取平均发现, 晴天 NEE ($- (7.7 \pm 1.99) \mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) 显著大于阴天 ($- (2.57 \pm 0.57) \mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$), 对环境因子的方差分析发现, 晴天 PAR ($(1001.1 \pm 28.3) \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) 显著大于阴天

表1 2013年湿地生态系统阴天和晴天净生态系统CO₂交换(NEE)和光合有效辐射(PAR)根据Michaelis-Menten模型(方程(3))模拟参数的比较

Table 1 Comparison of the analog parameters from daytime net ecosystem exchange of CO₂ (NEE) and photosynthetically active radiation (PAR) using a Michaelis-Menten model (Eq.(3)) between sunny days and cloudy days in the wetland

晴天 Sunny day						阴天 Cloudy day					
日期 (月-日) Date (month-day)	表观量子产量 Apparent quantum yield (α) ($\mu\text{mol CO}_2\cdot\mu\text{mol}^{-1}$)	最大光合速率 Maximum photosynthe- sis rate (A_{max}) ($\mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	白天生态系统呼吸速率 Ecosystem respiration in daytime ($R_{\text{eco, daytime}}$) ($\mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	n	R^2	日期 (月-日) Date (month-day)	表观量子产量 Apparent quantum yield (α) ($\mu\text{mol CO}_2\cdot\mu\text{mol}^{-1}$)	最大光合速率 Maximum photosyn- thesis rate (A_{max}) ($\mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	白天生态系统呼吸速率 Ecosystem respiration in daytime ($R_{\text{eco, daytime}}$) ($\mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	n	R^2
4-18	0.002	2.80	0.17	22	0.74	4-19	0.006	2.71	0.75	23	0.53
4-29	0.010	28.92	2.08	25	0.74	4-28	0.006	9.45	0.97	21	0.77
5-12	0.024	25.91	4.68	25	0.80	5-13	0.014	18.84	2.71	25	0.79
5-30	0.019	31.46	1.99	27	0.78	5-27	0.034	23.70	8.25	26	0.78
6-8	0.020	32.22	12.29	18	0.57	6-10	0.040	24.39	4.95	24	0.75
6-24	0.070	34.76	12.11	25	0.78	6-23	0.055	24.43	7.07	20	0.72
7-5	0.024	35.95	3.47	28	0.77	7-4	0.062	25.32	10.79	28	0.69
7-21	0.071	37.78	9.29	18	0.77	7-22	0.065	28.07	7.22	22	0.64
8-10	0.130	38.65	24.19	21	0.82	8-11	0.041	25.09	8.87	17	0.68
8-27	0.041	29.18	6.94	23	0.82	8-28	0.050	27.25	9.15	23	0.81
10-12	0.030	28.41	6.62	20	0.62	10-10	0.018	17.36	2.31	17	0.61
10-22	0.007	10.10	2.39	15	0.75	10-21	0.007	8.97	5.92	13	0.53

((472.67 ± 11.62) $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$), 同时晴天气温 T ((23.56 ± 2.62) $^{\circ}\text{C}$)也显著大于阴天((21.26 ± 2.34) $^{\circ}\text{C}$)。

2.2 阴天和晴天条件下白天NEE对PAR的响应

采用Michaelis-Menten方程拟合发现, 晴天拟合参数 A_{max} 、 α 和 R_{eco} 均于8月达到最大值, 分别为38.65 $\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ 、0.13 $\mu\text{mol CO}_2 \cdot \mu\text{mol}^{-1}$ 和24.19 $\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, 阴天 A_{max} 、 α 和 R_{eco} 均在7月达到最大值, 分别为28.07 $\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ 、0.065 $\mu\text{mol CO}_2 \cdot \mu\text{mol}^{-1}$ 和10.79 $\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ 。 t 检验发现, 晴天条件下, A_{max} ((28.01 ± 2.91) $\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)显著大于阴天((19.63 ± 1.33) $\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$), 同时 $R_{\text{eco, daytime}}$ ((7.19 ± 0.67) $\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)也显著大于阴天((5.75 ± 0.39) $\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$), 但 α 间差异不显著($p > 0.05$)。

在整个生长季中, 阴天和晴天条件下NEE与PAR均呈直角双曲线关系, 随PAR的增加NEE呈负向增加趋势(图3)。在PAR强度低于400 $\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ 时, 阴天和晴天NEE对PAR增加的响应程度基本一致, 且NEE增加的幅度基本相等; 随PAR持续增强, 阴天和晴天NEE对PAR的响应差异明显, 当PAR高于400 $\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ 后, 阴天和晴天的响应程度发生明显变化, 晴天的NEE增加幅度明显大于阴天。当晴天PAR大于1 400 $\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, NEE的增加趋势明显变弱, 维持稳定的碳吸收峰值(11 $\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ 左右)。

2.3 阴天和晴天条件下白天生态系统呼吸对温度的响应

采用选取的12对阴天和晴天白天NEE数据通过Michaelis-Menten模型反推得到 $R_{\text{eco, daytime}}$, 结果表明阴天和晴天 $R_{\text{eco, daytime}}$ 与 T 均存在显著的指数关系(图4), 且晴天 $R_{\text{eco, daytime}}$ 显著高于阴天。晴天条件下, 气温可以解释生态系统呼吸变异的64%; 阴天, 气温可以解释其变异的45%。晴天生态系统基础呼吸 a 值(0.09 $\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)小于阴天(1.43 $\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$), 但是其温度反应系数 b (0.17)却大于阴天(0.06)。因此, 晴天生态系统呼吸的温度敏感系数 Q_{10} (5.5)远大于阴天(1.9)。

2.4 阴天和晴天PAR与T对湿地生态系统NEE的协同影响

多元回归分析发现, T 和 PAR 对晴天NEE的协同影响达到40% ($p < 0.01$), 对阴天的协同影响为41%,

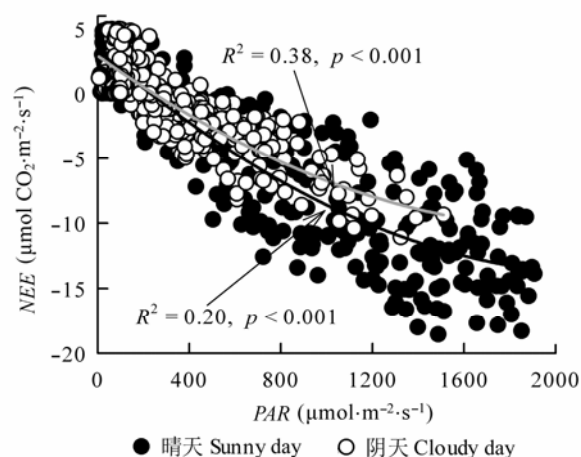


图3 2013年黄河三角洲湿地生长季阴天和晴天昼间生态系统CO₂交换(*NEE*)和光合有效辐射(*PAR*)的关系。黑线代表晴天拟合曲线, 灰线代表阴天拟合曲线。

Fig. 3 Relationships between daytime net ecosystem exchange of CO₂ (*NEE*) and photosynthetically active radiation (*PAR*) between sunny days and cloudy days during the 2013 growing season in the Yellow River Delta wetland. Black solid line represents fitting curve of sunny days, and grey line represents fitting curve of cloudy days.

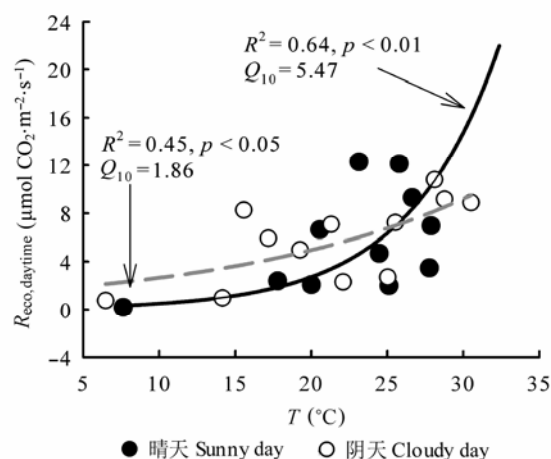


图4 2013年黄河三角洲湿地生长季阴天和晴天昼间生态系统呼吸(*R_{eco, daytime}*)和气温(*T*)的关系。黑线代表晴天拟合曲线, 灰线代表阴天拟合曲线。

Fig. 4 Relationships between daytime ecosystem respiration (*R_{eco, daytime}*) and air temperature (*T*) on sunny days and cloudy days during the 2013 growing season in the Yellow River Delta wetland. Black solid line represents fitting curve of sunny days, and grey line represents fitting curve of cloudy days.

偏相关分析发现 T 是晴天 NEE 变异的主控因子(T : $R^2 = 0.37$, $p < 0.001$; PAR : $R^2 = 0.20$, $p < 0.001$), PAR 是阴天 NEE 变异的主控因子(T : $R^2 = 0.10$, $p < 0.001$; PAR : $R^2 = 0.38$, $p < 0.001$)。多元回归分析表明, ΔPAR 与 ΔT 对 ΔNEE 的协同影响达到63% ($R^2 = 0.63$, $p <$

0.001; 表2), 说明 PAR 与 T 是引起阴天和晴天 NEE 差异的主要环境因子。

3 讨论

3.1 阴天和晴天对湿地生态系统 NEE 光响应的影响

本文研究发现晴天和阴天芦苇湿地 NEE 对 PAR 的响应趋势一致, 均呈直角双曲线关系, 与先前的很多研究结果一致(Falge *et al.*, 2001; Monson *et al.*, 2002; Zhou *et al.*, 2009; 张弥等, 2009; Han *et al.*, 2014a, 2014b; 邢庆会等, 2014)。 PAR 是控制阴天和晴天生态系统生长季昼间 NEE 变化的主要因素(Flanagan & Johnson, 2005; Liu *et al.*, 2006; 薛红喜等, 2012), Michaelis-Menten方程拟合发现, PAR 可以解释晴天单天 NEE 变化的57%–82%, 解释阴天单天 NEE 变化的53%–81%。云层变化会改变地表接收太阳辐射的强度, 影响 PAR 、 T 等环境因子, 进而影响阴天和晴天条件下 NEE 对光的响应特征(Baldocchi, 1997; Freedman *et al.*, 2001)。

在一定光照强度范围内, 光合作用随 PAR 的增强而增加(Glenn *et al.*, 2006; Syed *et al.*, 2006; Hao *et al.*, 2011; 同小娟等, 2011)。光能过剩会对光合作用产生不良影响, 出现光抑制, 致使叶绿体光合效率下降(Jiang *et al.*, 2011; Tholen *et al.*, 2012)。晴天 PAR 显著大于阴天(图2B), 因此, 晴天条件下植被叶片光合作用可能大于阴天, 表现为晴天 A_{max} 显著大于阴天(表1)。Zhou等(2009)研究认为 A_{max} 与植被的环境条件有关, 其中晴天 A_{max} 较阴天条件下提高了30%, 说明在植被生长旺季, 天空有云层覆盖时芦苇的光合能力比晴朗天气无云时有所降低, Law等(2002)总结全球森林、草地、农田以及苔原生态系统碳交换相关研究也得出类似结论。阴天条件下, 伴随天空云量的增多, PAR 显著降低(图2B), 尽管阴天和晴天条件下, NEE 均随 PAR 的增大而增加(图3), 但由于阴天 PAR 较低, 且晴天未出现光抑制现象, 因此其 NEE 显著低于晴天(图2A)。Alton (2008)在分析北美洲和欧洲6种森林类型2–3年的碳通量观测数据后发现, 这些森林阴天的日固碳量比晴天少60%–80%。相反, 在研究太阳辐射对黄河小浪底人工混交林生态系统碳交换的影响中发现, 多云天气下净碳交换会增加(刘佳等, 2014)。造成研究结论不一致的原因是多方面的, 不同的阴天和晴天划分指

表2 多元回归分析黄河三角洲湿地生长季阴天和晴天光合有效辐射(PAR)与气温(T)对净生态系统CO₂交换(NEE), 阴天和晴天PAR差量(ΔPAR)与T差值(ΔT)对NEE差量(ΔNEE)的协同影响

Table 2 Estimated empirical coefficient of multiple liner regression models for changes in net ecosystem exchange (NEE) with photosynthetically active radiation (PAR) and air temperature (T) on sunny and cloudy days during the growing season in the Yellow River Delta

	方程 Equation	R ²	p	n
晴天 Sunny day	NEE = -0.005PAR - 0.28T + 4.06	0.41	<0.001	288
阴天 Cloudy day	NEE = -0.006PAR - 0.107T + 2.67	0.42	<0.001	288
阴天和晴天差量 Difference between sunny and cloudy days	ΔNEE = -0.004ΔPAR - 0.123ΔT - 2.54	0.63	<0.001	288

ΔNEE, 阴天和晴天NEE差量; ΔT, 气温差量。

ΔNEE, NEE difference between sunny and cloudy days; ΔT, air temperature difference between sunny and cloudy days.

标(Graham *et al.*, 2003; Dengel & Grace, 2010)和拟合模型(Zhang *et al.*, 2011)来估计天气对碳通量的影响, 散射光和直射光下的碳交换没有一直处在相同的天气辐射条件下进行对比。此外, 研究地域的差异和不同植被类型的特性也在很大程度上影响了碳交换过程对天气的响应过程。

另外, 太阳辐射变化引起的温度变化也影响NEE对光的响应特征。首先, 温度通过影响酶系列化学反应对光合作用产生影响(Syed *et al.*, 2006), 温度升高有利于光合速率的提高(Pingintha *et al.*, 2010)。相关分析发现, 阴天和晴天A_{max}与T均为显著的线性正相关(晴天: R² = 0.80, p < 0.05; 阴天: R² = 0.63, p < 0.05), 其次, 生态系统呼吸与气温通常显著正相关(Aires *et al.*, 2008; Pingintha *et al.*, 2010)。本研究中虽然晴天条件下R_{eco,daytime}较阴天提高了20%, 但NEE却显著高于阴天的67%, 说明晴天温度对湿地光合固碳能力的提高远超过生态系统呼吸的消耗, 表现为晴天生态系统的碳汇功能更强, 这与已有的研究结果一致(Han *et al.*, 2014a)。

3.2 阴天和晴天对湿地生态系统呼吸温度响应的影响

阴天和晴天生态系统R_{eco,daytime}与T均呈显著的正相关关系, 两者呈指数关系, 与以往很多研究的结果一致(石培礼等, 2006; Zhou *et al.*, 2009; Zhao *et al.*, 2010; Han *et al.*, 2013, 2014a; 邢庆会等, 2014)。T是影响生态系统呼吸的主要因素(Law *et al.*, 2002; Reichstein *et al.*, 2005; Urban *et al.*, 2007), 本文研究发现: 黄河三角洲芦苇湿地晴天气温相对阴天提高了10%, 其阴天和晴天的气温差高于美国阿尔卑斯山脉南部森林的阴天和晴天的气温差(Berry & Smith, 2012), 黄河三角洲芦苇湿地晴天对应的生态系统呼吸相对阴天提高了20% (p < 0.05), 说明阴天条件下, 植被地上部分尤其是叶面温度较晴朗天气

强太阳辐射条件下的低, 叶片以及植被茎干呼吸受到一定的抑制(Urban *et al.*, 2007)。

Q₁₀值被广泛应用于评价生态系统呼吸对温度变化的敏感程度(杨庆朋等, 2011; 杨利琼等, 2013; Han *et al.*, 2014a, 2014b), Q₁₀值越大, 说明生态系统呼吸对温度变化的响应越敏感。黄河三角洲芦苇湿地生态系统阴天和晴天Q₁₀值均在已有的湿地Q₁₀范围(1.0–7.7)内(Chapman & Thurlow, 1996; Silvola *et al.*, 1996; Lafleur *et al.*, 2001; Bonneville *et al.*, 2008; Zhou *et al.*, 2009; 周丽艳等, 2010), 其中晴天白天Q₁₀为5.5, 远高于阴天白天的Q₁₀ (1.9), 说明晴天白天生态系统呼吸对温度变化的敏感性相对较高。分析其原因, 一方面生态系统温度敏感性与气温有关(Kirschbaum, 1995; Xu & Qi, 2001; Janssens & Pilegaard, 2003; Davidson & Janssens, 2006; 张雷明等, 2006; Jassal *et al.*, 2008), 气温对Q₁₀产生影响主要通过影响光合与呼吸作用酶的活性实现(Davidson & Janssens, 2006)。晴天气温T ((23.56 ± 2.62) °C)显著大于阴天((21.26 ± 2.34) °C), 阴天由于酶促反应需要一定的活化酶, 光合与呼吸作用酶的活性一般受到限制; 而晴天随着辐射增强, 气温升高, 越来越多的分子达到或超过了自身的活化能, 反应加快(Xiang & Freeman, 2009; Karhu *et al.*, 2010)。另一方面, 晴天相对阴天较高的PAR使得晴天光合作用更强, 产生输送的有机质增多(Curiel Yuste *et al.*, 2007; Jassal *et al.*, 2008), 自养呼吸增强, 同时地上植被以及土壤异养微生物呼吸对气温的响应能力增强(Edwards *et al.*, 2004; Heinemeyer *et al.*, 2006; Moyano *et al.*, 2008), 而阴天由于底物基质供应不足使得自养、异养呼吸受到抑制(Gershenson *et al.*, 2009)。

3.3 本研究的特色与不足

本研究以黄河三角洲芦苇湿地为研究对象, 在自然条件下选择相邻的阴天和晴天, 在生物要素

(生物量、叶面积指数)、土壤水分以及养分特征保持不变的前提下,分析阴天和晴天引起的辐射变化对生态系统 NEE 的影响机制。目前,有关太阳辐射对生态系统 NEE 的影响机制大都以晴空指数为指标(Gu *et al.*, 2003; Liu *et al.*, 2006; 范玉枝等, 2009; Zhang *et al.*, 2010; 周丽艳等, 2010; 蒋琰等, 2011; Zhao *et al.*, 2011; 刘佳等, 2014)。这种研究方法的最大不足就是研究阶段中,太阳辐射、生物要素(生物量、叶面积指数)、土壤湿度等环境因子都在发生变化,这对阐明太阳辐射这一单因素对 NEE 的控制机制研究带来一定困难。而本研究巧妙地在自然条件下选择相邻的阴天和晴天,在日尺度上实现了对单一变量 PAR 的控制。利用这种研究方法, Han等(2014a)通过对比分析阴天和晴天植物冠层光合作用的差异性,定量分析了光合作用在日尺度上对土壤呼吸的调节作用。此外,我们已有研究发现 PAR 改变所引起的植物光合作用变化对生态系统呼吸会产生一定的影响(Tang *et al.*, 2005; Baldocchi *et al.*, 2006; Moyano *et al.*, 2008; Wingate *et al.*, 2010; Han *et al.*, 2012)。但是,以往的研究多通过夜间生态系统呼吸与气温函数关系外延的方法来估算白天生态系统呼吸(Doughty *et al.*, 2010; Zhang *et al.*, 2011),忽略了 PAR 对白天生态系统呼吸的影响,因而具有一定的局限性。考虑到白天 PAR 的变化,本研究采用 Michaelis-Menten模型对白天生态系统呼吸进行推算,使得生态系统呼吸的温度响应数据更具有说服力。

本研究通过利用自然条件下阴天和晴天的转换,较好地证明了阴天和晴天引起的太阳辐射变化对湿地生态系统碳吸收功能的影响,为云量以及大气气溶胶含量变化对区域CO₂交换的潜在影响提供了有力证据。本研究只涉及生长季节的12对阴天和晴天数据,数据并没有涵盖整个生长季,而且由于9月份连续降雨,我们并没有在9月份找到相邻的阴天和晴天数据对。此外,本次研究我们主要探讨了 PAR 对生态系统生长季 NEE 的影响,而 NEE 是植被光合固定碳(生态系统总生产力, GPP)与生态系统呼吸释放碳(生态系统呼吸, R_{eco})之间相互平衡的结果, PAR 对植被光合作用以及生态系统呼吸强度的影响机制,本次研究没有涉及。因此,在下一步研究中,除了加强对生长季生态系统 NEE 以及环境因子长期的、连续观测外,增加植被光合作用的探讨有

助于深刻理解分析 PAR 变化对黄河三角洲芦苇湿地生态系统碳收支过程产生的影响。

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