

武夷山亚高山草甸土壤呼吸组分特征及影响因素

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摘要 武夷山亚高山草甸是亚热带中国东南部地区分布海拔最高的草甸, 分析亚热带亚高山草甸土壤碳通量组分的变化特征, 探究其与环境因子的关系及温度敏感性(Q_{10}), 对准确估计区域土壤碳收支和完善对亚高山草甸碳通量的认识具有重要意义。于2020年5月至2021年4月采用LI-8100 CO₂通量测定仪对武夷山山顶草甸土壤呼吸速率(RS)进行监测, 并利用根去除法区分自养呼吸速率(RA)和异养呼吸速率(RH)。结果显示: (1)亚热带武夷山亚高山草甸土壤呼吸速率及组分动态均呈双峰曲线, 5–10月, RS、RA、RH均高于其他月份。全年RA的变异幅度大于RH, RA在RS中占比约45%。(2)多模型比较分析表明武夷山亚高山草甸土壤温度(T)与土壤呼吸速率及组分呈指数增长关系, 土壤呼吸速率及各组分的 Q_{10} 排序为RA ($Q_{10} = 1.96$) > RS ($Q_{10} = 1.94$) > RH ($Q_{10} = 1.67$)。土壤湿度(W)对RS有一定影响, 但与RA、RH关系不显著。 T 、 W 双因素模型对RS的拟合优于单因素模型, 二者可共同解释48%的RS变异。综上, 武夷山亚高山草甸土壤呼吸以异养呼吸为主, 自养呼吸比异养呼吸对温度更敏感, 土壤温度和湿度是影响武夷山亚高山草甸土壤呼吸的重要环境因子, 低温和湿度大对土壤呼吸有抑制作用。该研究有助于增强对亚高山草甸土壤呼吸及组分季节动态和影响因素的认识, 为区域土壤碳通量和碳循环研究提供数据支持。

关键词 土壤呼吸; 自养呼吸; 异养呼吸; 温度敏感性; 亚高山草甸

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Characteristics of soil respiration components and influencing factors in the subalpine meadows of Wuyi Mountain

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Abstract

Aims The subalpine meadow of Wuyi Mountain is the highest meadows in the subtropical region of southeastern China. Identifying the variation characteristics of soil carbon flux components, and exploring their relationships with environmental factors and temperature sensitivity (Q_{10}) are of great significance for accurately estimating regional soil carbon balance and improving the knowledge about carbon flux dynamics in subalpine meadows.

Methods From May 2020 to April 2021, the LI-8100 CO₂ flux analyzer was utilized to systematically monitor the soil respiration rate (RS) in the meadow located at the summit of Wuyi Mountain. Additionally, the root exclusion method was applied to distinguish between the autotrophic respiration rate (RA) and heterotrophic respiration rate (RH).

Important findings (1) The dynamics of RS, RA and RH followed bimodal patterns, with consistently higher rates record from May to October compared to other months. Notably, the RA exhibited greater variability than RH throughout the year, accounting for 45% of RS. (2) A multi-model comparative analysis suggested that the temperature (T) exhibited an exponential correlation with soil respiration rate and its components in the subalpine meadow soil of Wuyi Mountain. The ranking of Q_{10} values for soil respiration rate and its components was RA ($Q_{10} = 1.96$) > RS ($Q_{10} = 1.94$) > RH ($Q_{10} = 1.67$). Although soil moisture (W) had a certain effect on RS, there

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was no significant relationship between RA and RH. The two-factor models including both T and W provided a better fit for RS than single-factor models, jointly explaining 48% of the variation in RS. In conclusion, soil respiration was primarily driven by heterotrophic respiration, while autotrophic respiration was more sensitive to temperature. Additionally, soil temperature and humidity were crucial environmental factors influencing soil respiration in the subalpine meadow of Wuyi Mountain, with soil respiration inhibited by low temperatures and high humidity. This study contributes to enhancing our understanding of the seasonal dynamics and influencing factors of soil respiration and its components in the subalpine meadow, providing valuable insights for regional soil carbon flux and carbon cycle research.

Key words soil respiration; autotrophic respiration; heterotrophic respiration; temperature sensitivity (Q_{10}); subalpine meadow

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土壤中储存着大量的碳, 其总量超过大气碳库和植物碳库的总和(Bertora et al., 2009; Scharlemann et al., 2014)。土壤呼吸已成为陆地生态系统向大气释放 CO_2 的最大通量(Shi et al., 2016; Liang et al., 2019a), 其微小变化都能对大气碳库产生巨大影响(Koven et al., 2011), 进而影响陆地生态系统的生态过程。土壤呼吸是土壤中的植物根系、土壤动物和微生物的所有新陈代谢过程中消耗有机物, 产生 CO_2 的过程(魏书精等, 2013; Ma et al., 2019)。因受多种生物和非生物因素的影响, 如土壤温度、湿度、养分有效性等非生物因素和植物群落结构、植物根系、土壤微生物等生物因素(Raich & Schlesinger, 1992; Chen et al., 2017a), 准确估算土壤呼吸比较困难。此外, 土壤呼吸主要包括自养呼吸(根和根际微生物释放的 CO_2)和异养呼吸(土壤微生物和土壤动物分解土壤有机质释放的 CO_2)两个组分(杨玉盛等, 2004), 每个组分代表不同的土壤生态学过程, 即土壤呼吸是不同过程共同作用的结果, 其单个过程的显著变化可能会掩盖其他过程对整体影响的可见性(Buyanovsky & Wagner, 1995)。因此, 将土壤呼吸划分成不同组分并研究其影响机制对扩展我们对土壤呼吸相关机理的认识和模型预测意义重大(Hopkins et al., 2013)。

在过去的20年间, 大量的实验数据和长期观测的结果表明, 土壤温度和土壤湿度是控制土壤呼吸速率的两个主要的环境因子(Chen et al., 2014; Liu et al., 2016)。土壤温度控制土壤根系和微生物酶活性, 影响着整个土壤呼吸过程(Luo & Zhou, 2006), 随着土壤温度的上升, 土壤呼吸速率会显著增加(Schindlbacher et al., 2007)。土壤湿度增加利于底物扩散(Pang et al., 2013), 虽然土壤湿度与土壤呼吸

的关系不明确, 但土壤湿度过高或过低都会抑制土壤呼吸速率(陆彬等, 2010)。模拟研究的结果表明, 土壤呼吸速率与土壤温度、土壤湿度的相关系数 $|r|$ 在0.04–0.64之间(Hanson et al., 2000), 说明陆地生态系统土壤呼吸对温度变化的响应还存在着很大的不确定性。通常用温度敏感性指数(Q_{10} , 温度每变化 10°C , 土壤呼吸速率的变化比率)研究土壤呼吸与温度的关系, Q_{10} 是反映气候变化和陆地生态系统碳循环过程的关键参数(郑甲佳等, 2020)。由于植物根系与土壤微生物对温度的响应程度不同, 所以自养呼吸与异养呼吸的 Q_{10} 存在差异(盛浩等, 2007)。国内外学者虽然对土壤呼吸的影响因素、时空异质性方面开展了长期研究, 取得了重要成果, 但对亚热带非气候敏感区的研究相对较少(马志良等, 2018), 同时研究多在森林、草原等地带性植被中进行, 对于草甸这种非地带性植被研究较少。

草甸作为一种非地带性植被, 是一种分布在气候和土壤湿润、无林地区或林间地段中的多年生草本植物群落。草地生态系统因其显著的净初级产量、丰富的植物多样性及土壤碳储量(Liang et al., 2019b), 展现出了巨大的研究潜力和生态价值。目前已有对草甸土壤呼吸的影响因素展开探讨, 大部分结果均表明土壤温度是影响草甸土壤呼吸的主要因素, 土壤呼吸速率随土壤温度的增加呈指数增长或线性增长, 如高寒草甸(Liang et al., 2019b), 但在降水变率较大的草甸, 土壤湿度的影响会超过温度, 如Wang等(2023)在研究内蒙古东部草甸时发现土壤水分是控制土壤呼吸年际变化的主要因素。同时, 不同土壤水分条件影响草甸土壤呼吸组分变化, 如在内蒙古呼伦贝尔草甸极端降雨对土壤呼吸的影响研究中, 与干旱处理相比, 降水处理后的土壤更湿

润, 异养呼吸比例显著增加(Legessee et al., 2022), 在鄱阳湖湿地草甸呼吸研究中发现异养呼吸对生态系统呼吸的贡献大于自养呼吸(Hu et al., 2015)。Wang和Fang (2009)在综述草地生态系统土壤呼吸时, 认为全球草地根系呼吸对总呼吸的贡献平均为36%, 总体从8%–64%不等, 但在全球尺度上, 自养呼吸在总呼吸中的占比小于异养呼吸(Jian et al., 2022)。

武夷山亚高山草甸是亚热带中国东南部海拔最高的草甸, 相比青藏高原高寒草甸和温带草甸年平均气温更高, 降水更充足, 雾日长, 湿度较大, 其中分布有大量多年生草本植物, 夏茂冬枯, 季相明显, 特殊的土壤水热条件深刻影响草甸土壤呼吸。故基于土壤呼吸的影响因素、草甸土壤呼吸组分特征及武夷山自身特点, 提出两点科学假设: 1)在亚高山草甸, 同时考虑土壤温度和湿度比只考虑单一环境因子更能解释土壤呼吸的季节动态。2)自养呼吸在年内土壤呼吸中的比例小于异养呼吸。故本研究选取亚热带武夷山亚高山草甸为研究对象, 力图发现亚热带亚高山草甸规律及与温度、湿度的关系, 深入了解亚热带亚高山草甸土壤呼吸及各组分的温度敏感性变化机理, 以期为区域尺度的土壤碳通量及碳循环研究提供理论基础。

1 材料和方法

1.1 研究区概况

研究区位于江西与福建西北部两省交界处的武夷山国家公园江西片区(27.33°–27.54° N, 117.27°–117.51° E), 亚高山草甸分布在黄岗山峰顶的四周, 东西宽约2 km, 南北长约10 km, 最高峰黄岗山海拔2 160.8 m。气候为中亚热带季风气候, 年平均气温约8.5–10 °C, 年降水量在1 813–3 544 mm之间, 年蒸发量为553–941 mm。7–10月易受台风的影响, 降水集中, 积雪日4到5天, 风力5到6级(徐欢欢, 2007)。年总日照时间约959 h, 全年无霜期平均为231天, 大气相对湿度在85%左右。样地地下10 cm深的土壤温度全年在2.66–17.68 °C间, 土壤湿度在21%–46%间。土壤类型为草甸土(朱鹤健等, 1982)。0–10 cm土层土壤有机碳含量为(73.62 ± 6.21) g·kg⁻¹, 总氮含量为(5.37 ± 0.45) g·kg⁻¹, 微生物生物量碳含量为(1777.85 ± 355.61) mg·kg⁻¹, 微生物生物量氮含量为(206.44 ± 40.86) mg·kg⁻¹, 土壤pH为

(4.83 ± 0.02)。主要植被类型为亚高山草甸, 零散分布着灌木矮林, 草甸的主要物种为: 日本麦氏草(*Molinia japonica*)、野青茅(*Deyeuxia pyramidalis*)和芒(*Miscanthus sinensis*) (安德帅等, 2021)。

1.2 样地设置与土壤呼吸测定

在武夷山主峰黄岗山2 100 m海拔样地中, 随机选择10个1 m × 1 m较均一平缓地设立样方, 每个样方间隔5–10 m。在样方中设置去根(RR)与对照(CT)两个处理, 每个处理5次重复。根处理采用壕沟法, 在呼吸区组内设置0.8 m × 0.8 m的正方形壕沟, 壕沟平均深度0.5 m, 在壕沟里用两层200目尼龙网阻断根系生长, 在每个样方正中间都垂直打入一个PVC土壤呼吸圈(直径20 cm, 高10 cm), 嵌入土壤深度约6 cm(孙俊, 2021)。

土壤呼吸监测: 在根处理稳定后, 从2020年5月至2021年4月, 每月下旬选择两天晴朗天气, 使用LI-8100 CO₂通量测定仪(LI-COR, Lincoln, USA)进行土壤呼吸观测, 以此代表每月的土壤呼吸。同时采用呼吸通量测定仪自带的温度与水分传感器对每个样方内的10 cm深的土壤进行温度和水分的测定并记录, 以此代表每月的土壤温度和水分。野外测量时间为8:00–16:00。

1.3 数据处理

使用Microsoft Excel 2021、SPSS 27和R 4.2.1软件对数据进行分析计算, 用Origin 2022软件作图。对照(CT)即土壤总呼吸速率(RS), 异养呼吸速率(RH)为去根(RR)处理下的土壤呼吸, 自养呼吸速率(RA)由RA = RS – RH得到。文中的误差均表示标准误。

土壤呼吸速率及组分与土壤温度(*T*)的关系分别采用公式(1)中线性模型(Gupta & Singh, 1981)、乘幂模型(Kucera & Kirkham, 1971)、多项式模型和指数模型拟合(Davidson et al., 1998; Luo et al., 2001), 比较4种模型的决定系数(*R*²), 选择*R*²最高的模型与公式(4)计算土壤呼吸速率及组分的*Q*₁₀。土壤呼吸速率及各组分与土壤湿度(*W*)的关系采用公式(2)拟合, 土壤呼吸速率与土壤温度和土壤湿度的关系采用双因素模型公式(3)拟合。使用公式(5)计算出土壤呼吸年通量、自养呼吸年通量和异养呼吸年通量。式中, *a*、*b*、*c*为待定参数, *R*为不同处理下的土壤呼吸速率, *T*为10 cm深度的土壤温度, *W*为10 cm深度土壤湿度。

$$\left. \begin{aligned} R &= aT + b \\ R &= a(T + 10)^b \\ R &= aT^2 + bT + c \\ R &= ae^{bT} \end{aligned} \right\} \quad (1)$$

$$R = aW^2 + bW + c \quad (2)$$

$$R = ae^{bT}W^c \quad (3)$$

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

$$R = \sum_d ae^{bT} 3600 \times 24 \times (12/1000000) \quad (5)$$

2 结果和分析

2.1 RS、RA、RH的动态变化

RS、RA、RH的动态变化在一年内均呈双峰曲线, 但具体峰值存在差异(图1)。RS在5–10月高于其他月份, 最大峰值出现在8月, 此时10 cm土层T达到一年中最高值, 9月有短暂低值时T出现较大降幅, W上升(图1, 图2)。10月为第二大峰值, RS的最小值出现在11月, 年呼吸均值为 $(1.318 \pm 0.088) \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ 。RH与RA的最大峰值也均出现在8月, 第二大峰值均出现在10月, 但最小值均出现在次年2月, 此时W达到全年最高值, T值较低(图1, 图2)。RA与RH的月均值分别在 $(0.286 \pm 0.477) - (1.374 \pm 0.149) \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, $(0.39 \pm 0.255) - (1.158 \pm 0.219) \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ 间波动, 用变异系数(CV, 月平均土壤呼吸速率最大值/最小值) (王莹等, 2014)表示RH与RA的月均值波动情况为: RA (CV = 4.8) > RH (CV = 3.89)。总体计算得出RA:RS = 0.45, 即根呼吸在总呼吸中占比约45%, 呼吸总体以异养呼吸为主。经拟合计算, 土壤呼吸年碳通量约为 $516.177 \text{ g} \cdot \text{m}^{-2} \cdot \text{a}^{-1}$, 异养呼吸年碳通量约为 $299.908 \text{ g} \cdot \text{m}^{-2} \cdot \text{a}^{-1}$, 自养呼吸年碳通量约为 $199.069 \text{ g} \cdot \text{m}^{-2} \cdot \text{a}^{-1}$, RH的年通量均值高于RA。

2.2 土壤呼吸与温度和湿度的关系

多模型比较显示, RS、RH、RA与T符合指数增长关系(表1)。但三者对T的响应不同, RS对T的响应最明显, RH大于RA (图3; 表1)。表明土壤温度是影响土壤呼吸及组分变化的重要因素, 土壤微生物和动物呼吸对温度的响应较根呼吸明显。同时RS、RH、RA的动态变化与T并不完全对应, 但T较高的月份, 土壤呼吸速率也高(图1, 图2)。利用 $Q_{10} = e^{10b}$ 计算RS、RH、RA的 Q_{10} 值, 得出 Q_{10} 值排序为RA ($Q_{10} = 1.96$) > RS ($Q_{10} = 1.94$) > RH ($Q_{10} = 1.67$) (表1)。

选取二次项模型拟合W与RS、RH、RA的关系, 得到全年土壤呼吸速率与土壤湿度的关系为: $RS = 20.70W^2 - 31.28W - 1.78$ (表2)。根据模型计算得出当W在33%时, RS到达峰值, 以33%为界, 低于33%则RS随着W的增加而上升, 高于33%则RS随着W的增加而降低。此外, W与RH和RA的关系不显著(表2)。

土壤温度与土壤湿度并非割裂存在, 而是相互影响, 协同作用于土壤呼吸。通过双因素指数模型拟合T、W与RS的关系, 拟合效果较单因素模型好, 有更高的决定系数(表2)。10 cm土壤温度和土壤湿度共同解释了土壤呼吸速率变化的48%, 相较于单

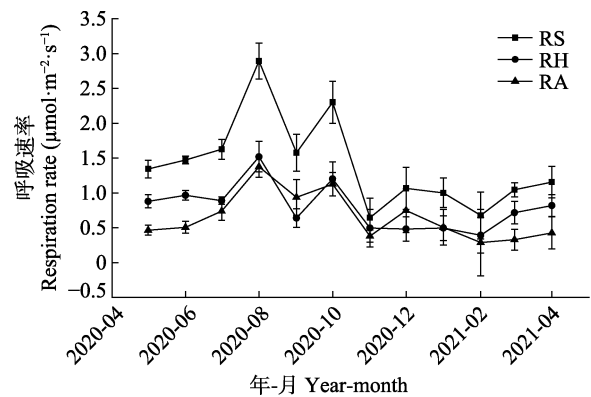


图1 武夷山海拔2100 m处土壤呼吸动态变化(平均值±标准误差, $n = 5$)。RA, 自养呼吸速率; RH, 异养呼吸速率; RS, 土壤呼吸速率。

Fig. 1 Dynamics of soil respiration rates at an altitude of 2100 m in Wuyi Mountain (mean ± SE, $n = 5$). RA, autotrophic respiration rate; RH, heterotrophic respiration rate; RS, soil respiration rate.

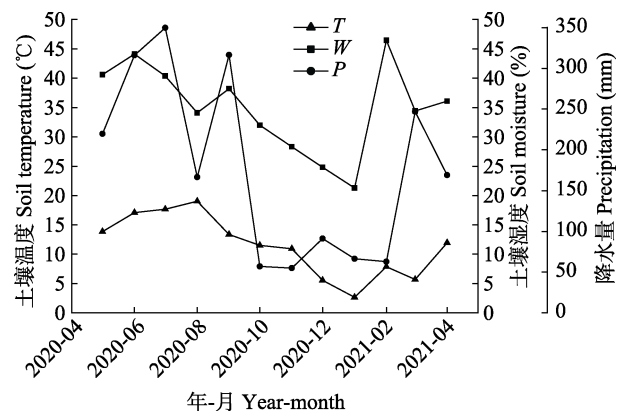


图2 武夷山海拔2100 m处土壤温度、土壤湿度和降水量月动态。P, 降水量; T, 10 cm土壤温度; W, 10 cm土壤湿度。

Fig. 2 Monthly dynamics of soil temperature, soil moisture and precipitation at an altitude of 2100 m in Wuyi Mountain. P, precipitation; T, soil temperature measured at depth of 10 cm in the soil layer; W, soil moisture measured at depth of 10 cm in the soil layer.

表1 土壤呼吸组分与10 cm土壤温度的拟合关系(平均值±标准误, $n = 5$)
Table 1 Fitting relationships between soil respiration components and soil temperature at depth of 10 cm (mean ± SE, $n = 5$)

$R = aT + b$						
T	R	a	b	R^2	p	
	RS	0.07 ± 0.01	0.55 ± 0.17	0.33	<0.001	
	RH	0.05 ± 0.01	0.23 ± 0.13	0.29	<0.001	
	RA	0.03 ± 0.01	0.22 ± 0.10	0.19	<0.001	
$R = a(T + 10)^b$						
T	R	a	b	R^2	p	
	RS	0.02 ± 0.02	1.34 ± 0.25	0.38	<0.001	
	RH	0.01 ± 0.01	1.45 ± 0.33	0.30	<0.001	
	RA	0.01 ± 0.01	1.29 ± 0.37	0.20	<0.001	
$R = aT^2 + bT + c$						
T	R	a	b	c	R^2	p
	RS	-0.07 ± 0.06	0.007 ± 0.003	1.16 ± 0.31	0.38	<0.001
	RH	-0.03 ± 0.05	0.004 ± 0.002	0.59 ± 0.25	0.31	<0.01
	RA	-0.06 ± 0.04	0.004 ± 0.002	0.60 ± 0.18	0.27	<0.001
$R = ae^{bT}$						
T	R	a	b	R^2	p	Q_{10}
	RS	0.62 ± 0.10	0.08 ± 0.01	0.41	<0.001	1.94
	RH	0.34 ± 0.08	0.07 ± 0.02	0.31	<0.001	1.67
	RA	0.25 ± 0.06	0.06 ± 0.02	0.22	<0.001	1.96

RA, 自养呼吸速率; RH, 异养呼吸速率; RS, 土壤呼吸速率。T, 土壤温度。Q₁₀, 温度敏感性系数。
RA, autotrophic respiration rate; RH, heterotrophic respiration rate; RS, soil respiration rate. T, soil temperature. Q₁₀, temperature sensitivity.

表2 土壤总呼吸速率(RS)、自养呼吸速率(RA)、异养呼吸速率(RH)与10 cm土壤湿度(W)、土壤温度(T)和土壤湿度双因素的拟合关系(平均值±标准误, $n = 5$)
Table 2 Fitting relationships of soil respiration rate (RS), autotrophic respiration rate (RA), and heterotrophic respiration rate (RH) with soil moisture (W) and the dual factors of soil temperature and soil moisture at depth of 10 cm (mean ± SE, $n = 5$)

$R = aW^2 + bW + c$						
W	R	a	b	c	R^2	p
	RS	20.70 ± 7.03	-31.28 ± 10.59	-1.78 ± 1.12	0.14	<0.05
	RH	12.06 ± 5.82	-17.90 ± 8.72	-1.07 ± 0.92	0.05	>0.05
	RA	6.83 ± 3.94	-10.74 ± 5.92	-0.42 ± 0.62	0.04	>0.05
$R = ae^{bT}W^c$						
T, W	R	a	b	c	R^2	p
	RS	0.04 ± 0.12	0.07 ± 0.01	-0.36 ± 0.18	0.48	<0.001

因素模型, 土壤温度与土壤湿度的双因素模型解释度更高。

3 讨论

3.1 土壤呼吸及组分特征

土壤呼吸的动态变化受环境因子和生物机制的影响(Vargas & Allen, 2008)。实验表明, 一年内土壤呼吸的最大值一般出现在夏季或者生长季, 而最小值出现在冬季或者非生长季(Han & Jin, 2018), 本研究结果与之相似。因为雨热同期的气候条件为植

物提供了良好的生长条件, 夏季气温上升, 土壤温度随之升高, 草地生物量、根系的数量和活性增加, 这些变化促进了根系呼吸和土壤微生物活性, 使土壤有机质分解速率增高, 导致土壤呼吸及各组分呼吸速率加快(Wang et al., 2023)。在生长季后期, 由于温度和土壤水分降低、植物根系活动减少, 土壤呼吸速率也逐渐下降(Knapp et al., 1998)。多数研究显示土壤呼吸月际变化呈单峰曲线(胡毅等, 2016; 刘顺等, 2019), 但本研究监测到武夷山亚高山草甸土壤呼吸动态呈双峰曲线, 这可能是由于武夷山脉地

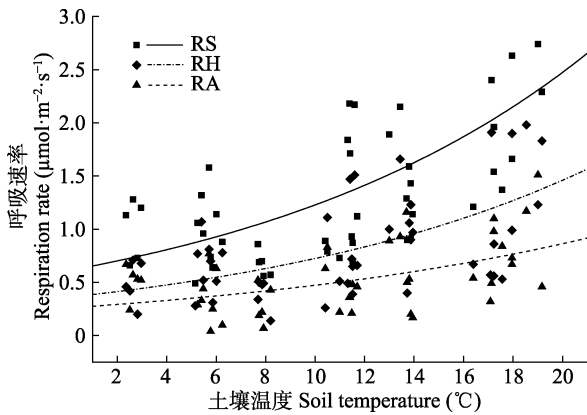


图3 土壤呼吸组分和土壤温度的指数拟合。RA, 自养呼吸速率; RH, 异养呼吸速率; RS, 土壤呼吸速率。

Fig. 3 Exponential fitting of soil respiration components to soil temperature. RA, autotrophic respiration rate; RH, heterotrophic respiration rate; RS, soil respiration rate.

处华南, 为东北—西南走向, 黄岗山海拔较高, 9月受台风天气影响且地形抬升致雨水较多, 土壤湿度较大而抵消温度上升对土壤呼吸的影响(Wu et al., 2013), 同时本研究监测得出9月降水量增加伴随土壤湿度上升和土壤温度下降证实了这一解释。

研究发现土壤根系呼吸增速较微生物呼吸大, 变异幅度较高。有证据表明, 自养呼吸与根系生物量密不可分(Geng et al., 2012), 植物生物量在生长季波动很大, 这种波动很可能对土壤呼吸产生很大影响(Han et al., 2014)。武夷山高山草甸分布大量禾本科植物, 夏茂冬枯, 季节性明显, 根系活性随之变化, 因此自养呼吸变异幅度较大。

3.2 土壤呼吸速率与土壤温度和湿度的关系

土壤温度是影响土壤呼吸速率的重要因素。本研究对比得出, 自养呼吸、异养呼吸、总呼吸速率与土壤温度均符合指数增长关系, 这与多数研究结果一致。但异养呼吸速率对温度的响应要大于自养呼吸速率, 这可能是由于亚高山草甸土壤微生物生物量高, 土壤有机质十分丰富, 土壤活性较强, 微生物底物有效性高(Singh et al., 2010)。本研究中土壤呼吸速率对土壤温度的响应较为显著, 这与大部分研究结果(Zhang et al., 2010; 唐夫凯等, 2016; Tian et al., 2022)基本一致。而且有学者研究发现, 除沙漠生物群系外, 其他群系的土壤呼吸速率都遵循高斯响应, 即以25 °C为界, 当土壤温度低于25 °C时, 土壤呼吸速率随着土壤温度的增加而增加, 超过该阈值则降低(Carey et al., 2016)。本研究得出亚高山草甸全年土壤温度均低于25 °C, 因此, 可以

得出武夷山亚高山草甸土壤呼吸速率受温度控制, 温度是该地区土壤呼吸的限制因素。

土壤湿度是土壤呼吸的又一重要的环境因子。土壤湿度对土壤呼吸的作用主要是通过土壤水分的高低对CO₂和O₂的运输速率和根活性产生影响所致(Kelting et al., 1998)。一般来说, 在较干旱地区控制土壤呼吸的动态方面, 土壤湿度超过土壤温度(Olchev et al., 2013), 而在更潮湿或更寒冷的草原地区, 情况正好相反, 例如本研究区。王妮和郭继勋(2006)、黄湘等(2007)研究发现, 土壤湿度在适中范围内时土壤呼吸速率较高, 过高或过低的土壤湿度都会抑制土壤呼吸速率, 唐夫凯等(2016)发现土壤水分超过36%时, 土壤水分会对呼吸产生抑制效应。本研究得出武夷山亚高山草甸的这个临界值为33%, 且区内全年土壤湿度均高于20%, 有8个月超过33%, 潮湿草甸环境下, 土壤湿度对土壤呼吸速率的贡献降低, 故只能解释土壤总呼吸速率变化的14%, 并与自养呼吸速率和异养呼吸速率无关。因此土壤湿度不是亚高山草甸土壤呼吸的限制因子, 反而因湿度过大抑制土壤呼吸(Wu et al., 2013)。

通过对温度和湿度双因素对土壤呼吸速率的拟合, 其解释度优于单因素模型, 表明该区土壤根系活性和土壤微生物受土壤温度和土壤湿度的交互作用, 这与Saiz等(2006)的研究结果一致。但其48%的解释度相对较低, 这可能还是较高的土壤湿度降低了土壤孔隙氧含量, 限制好氧微生物代谢活性, 从而抑制了土壤呼吸(Han et al., 2018)。同时土壤呼吸还受植被类型、土壤质地、降水频率、碳基质的数量和质量以及养分有效性, 微生物群落等的影响(Chen et al., 2017b; Ma et al., 2019; Morris et al., 2022), 后续仍需继续深入研究。

3.3 武夷山亚高山草甸土壤呼吸的特点对比

武夷山亚高山草甸分布在亚热带地区海拔1900 m以上, 相比于高寒草甸和温带草甸, 亚高山草甸土壤有机质含量和土壤微生物生物量更高。如: 武夷山亚高山草甸土壤有机碳含量平均约为73.62 g·kg⁻¹, 比内蒙古温带草地平均土壤有机碳含量(陈颖洁等, 2023)高约5倍, 比青藏高原东北部季节冻土区(李世珍等, 2024)高约1.3倍, 可见亚高山草甸土壤有机碳含量之丰富。不仅如此, 亚高山草甸土壤微生物生物量碳含量范围在893.6–2163.07 mg·kg⁻¹, 比祁连山高寒草甸(吴建国和艾丽, 2008)

高出约5倍, 相比于青藏高原东北缘疏勒河源多年冻土区高寒草甸 $165.11\text{--}257.52\text{ mg}\cdot\text{kg}^{-1}$ (刘放等, 2020)高出5–8倍。土壤微生物生物量氮含量比祁连山高寒草甸高约5倍, 比青藏高原东北缘疏勒河源多年冻土区高寒草甸高出约16倍。丰富的土壤微生物生物量影响着土壤呼吸速率变化。

研究显示, 青藏高原高寒草甸自养呼吸占总呼吸的52.8%–68.8% (Du et al., 2023), 内蒙古荒漠草原通过线性回归估计得出根呼吸对土壤总呼吸贡献了48% (Bao et al., 2010)。黄土高原温带草地年平均根系呼吸贡献率为52.5% (Wei et al., 2016), 本研究得出武夷山亚高山草甸自养根呼吸占土壤呼吸总量的45%, 相较于温带草地和青藏高原高寒草甸, 武夷山亚高山草甸根呼吸占比较低。这可能是因为寒冷地区根呼吸会在土壤呼吸中占有较高比例(唐燕飞等, 2008), 同时这也与干旱草地环境相反, 在干旱草地中, 土壤水分是限制因子, 土壤含水量增加会通过影响根系和根际活动显著影响土壤呼吸, 故自养呼吸在很大程度上主导了土壤呼吸(Moinet et al., 2019)。

实验得出, 青藏高原高寒草甸土壤呼吸碳通量约为 $200\text{--}300\text{ g}\cdot\text{m}^{-2}\cdot\text{a}^{-1}$ (Wang et al., 2021), 内蒙古半干旱温带草甸在干旱年为 $390\text{ g}\cdot\text{m}^{-2}\cdot\text{a}^{-1}$, 丰水年为 $866\text{ g}\cdot\text{m}^{-2}\cdot\text{a}^{-1}$ (Wang et al., 2004), 本研究经拟合得出, 武夷山亚高山草甸土壤呼吸碳通量约为 $516\text{ g}\cdot\text{m}^{-2}\cdot\text{a}^{-1}$, 既高于高寒草甸又高于干旱年的温带草甸。这种情况是因为在青藏高原随海拔升高, 土壤水分含量和土壤温度降低, 太阳辐射和大气干燥度增加(Yao et al., 2019), 低温和半干旱环境限制了草甸生态系统呼吸(Chen et al., 2019), 温度仍是很强的限制性因素, 而干旱草甸易受降雨影响, 土壤呼吸在丰水年和枯水年变化较大。

青藏高原东北部高山草甸土壤总呼吸、异养呼吸和自养呼吸的 Q_{10} 值范围为1.52–6.42, 平均值为4.63 (Wang et al., 2020), 温带草原为0.52–2.12, 草甸草原为1.35–3.22。本研究得出武夷山亚高山草甸土壤总呼吸速率、自养呼吸速率和异养呼吸速率的温度敏感性 Q_{10} 值分别为1.94、1.96、1.67, 符合草甸草原范围。土壤呼吸的温度敏感性中自养呼吸比异养呼吸更敏感, 这与许多研究结果(Makita et al., 2021; Luo et al., 2023)相同。因为土壤微生物会通过生理自动调节功能适应温度变化(Li et al., 2017), 在

温度较高的条件下, 土壤微生物酶活性增强, 更多地将不稳定底物作为能量来源, 使其消耗的活化能较少, 导致 Q_{10} 较低(Lefèvre et al., 2014)。有些研究与之相反主要是认为自养呼吸对温度变化做出的反应更受水分因子的影响(Poulter et al., 2014; 刘鹏等, 2018)。

4 结论

研究证实了土壤温度是影响武夷山亚高山草甸土壤呼吸及组分的重要因素, 并与土壤湿度协同作用于土壤呼吸的季节动态, 与假设相同, 武夷山亚高山草甸异养呼吸在年内占比大于自养呼吸。年土壤呼吸通量高于高寒草甸和干旱草甸, 低于丰水年温带草甸。相比于青藏高原高寒草甸和温带草甸, 武夷山亚高山草甸土壤有机质含量和土壤微生物生物量更高。本研究主要从非生物因素角度对亚高山草甸土壤呼吸特征进行分析, 同时土壤呼吸结果受野外测量土层深度、年限、测量时间及土壤质地限制, 未来可做改进并进一步探讨生物因素对土壤呼吸影响的深层机理。本研究对亚高山草甸土壤呼吸月际变化特征做了有效补充, 为区域尺度碳通量和碳循环研究提供数据支持。

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