生物群区和林龄对森林土壤呼吸及其组分的影响

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摘要:森林土壤呼吸(R_S)一般分为自养呼吸(R_A)和异养呼吸(R_H)两个组分,各组分对环境变化具有不同的响应,对土壤和生态系统的碳平衡产生重要影响。对全球不同生物群区、林龄的森林 R_S 及其组分 R_H 的研究文献进行检索与分析,结果表明:林地 R_S 沿北方森林-温带针叶林-温带落叶林-热带林次序逐步升高,非相邻区系之间差异显著($\alpha < 0.05$)。土壤异养呼吸组分(R_H)及其贡献率(R_H/R_S),仅北方森林与热带林之间有显著性差异,其余区系之间无显著性差异($\alpha > 0.05$)。异养呼吸组分贡献率(R_H/R_S),随着 R_S 的不断增加,呈现出 R_H/R_S 率降低的总体趋势。对于林地 R_S,幼龄林显著高于中龄林和成熟林。R_H/R_S 率随树龄增加而略微升高,但龄组之间没有显著性差异($\alpha > 0.05$)。各生物群区及林龄的 R_H 与 R_S 之间显著性相关分析,为全球森林碳收支的估测提供有效的方法和数据基础。

关键词:土壤呼吸; 生物群区; 林龄; 森林
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Biome and stand ages impacts on soil CO_2 efflux and partitioning: a global trends

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Abstract: Soil surface CO_2 flux (R_S) is overwhelmingly the product of respiration by roots (autotrophic respiration, R_A) and soil organisms (heterotrophic respiration, R_H). Partitioning soil carbon dioxide efflux with highly variable results has received considerable attention, as differential responses of these components to environmental change have profound implications for soil and ecosystem C balance. The contribution of each group needs to be understood to evaluate implications of environmental change on soil carbon cycling and sequestration. We present results of a strict literature search of soil surface CO_2 flux and partitioning studies and analyze global trends in soil carbon dioxide flux and partitioning between biomes, and age classes. There are statistically different and increasing trends in soil surface CO_2 flux between biomes following the sequence of biome types as boreal < temperate coniferous < temperate deciduous and tropical, whereas, it is somewhat surprising that no difference was found between neighboring biomes. R_H is each strongly ($R^2 = 0.62$) correlated to annual R_S across a wide range of forest ecosystems, biome type, measurement method and stand ages. Published data from all biome types indicate relatively wide range for the 95% confidence intervals, spanning 60% of flux contributions throughout the range of R_S. The results for forest ecosystems in different biomes confirm the general decline of R_H/R_S with

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increasing R_S. Of the groups and R_H included in this comparison, only boreal and tropical forest sites are significantly different from each other. Boreal sites showed significantly higher ($\alpha<0.05$) R_H/R_S ratios than tropical sites, while either temperate or tropical forests did not differ in ratios from any of the other forest types. Significant difference emerged from the comparison of R_S and R_H/R_S for forest stands of different age ($\alpha<0.05$). Increasing stand age corresponded to smaller confidence intervals and generally lower flux sums for R_S, while, there is no significant difference between the three age groups ($\alpha>0.05$). While chronosequence studies report mild increase in the R_H/R_S ratio with age, for the mean of R_H/R_S ratio and variance, of young class is larger than that of intermediate and mature groups, no significant difference could be detected for different age groups in the global data set ($\alpha>0.05$). Site-specific measurements are always more desirable than the application of inferred broad relationships. Measuring R_S is straightforward and commonly done; however, belowground measurements are difficult and expensive. Thus the relationships and R_H/R_S rate for each biome presented here provide a new approach and useful baselines that can help constrain estimates of terrestrial carbon budgets.

Key Words: soil respiration; biome; stand age; forest

森林生态系统是陆地最大碳库,其地下部分含 790 ~930P g C,其微小变化将对大气 CO_2浓度、全球碳循环和碳平衡产生深远的影响。因而,土壤呼吸受到越来越多的关注。森林土壤呼吸的研究重点为时间动态(昼夜、季节或年际)和非生物要素(如温度)的影响效应[1-3],土壤呼吸组分的分离量化及其相互关系的分析[4],森林土壤呼吸对生态系统碳平衡的贡献,是理解森林碳循环及估测区域森林生态系统碳平衡的重要基础,森林土壤呼吸是森林生态系统碳平衡的重要组分,对光合作用输入和呼吸输出敏感。但各组分的测定方法以及总量的估测没有共识。

森林土壤呼吸随森林生态系统演替过程而变化,各林龄土壤呼吸测定具有十分重要的意义。区域或其以上尺度,主要森林植被类型的地带性分布,土壤呼吸水平和呼吸组分贡献差异形成不同的土壤呼吸空间分布格局,导致不同的碳平衡。如周国逸等[5]研究发现热带成熟森林在地上部分净生产力几乎为零的情况下,土壤持续积累有机碳而表现为强大碳汇。森林土壤呼吸的时空变化的研究,生物群区和林龄对森林土壤呼吸组分及其分布格局的影响,这对评估森林生态系统碳源/碳汇功能具有重要意义。本文主要探索森林土壤呼吸随生物群区、林龄的分异性、变化趋势和分布范围,尤其是异养呼吸组分的贡献率的数据分析,为全球森林土壤碳循环和碳平衡研究提供新的方法和数据依据。

1　数据获取与分析方法

1.1　文献与数据获取

文献获取主要基于 OVID 平台(CABI、AGRIS、AGRICOLA)数据库、Science Citation Index Expands 引文数据库及 ScienceDirect、Blackwell 等全文数据库,检索主题为森林土壤呼吸及组分测定,通过回溯 30a 的联合检索,获取全文及或摘要近 300 篇文献,国内有 75 篇文献涉及到森林土壤呼吸。

土壤呼吸总量中来自活根系的部分是土壤碳库的独立部分,但现实测定和研究方法的局限性,难以实现对根系呼吸进行单独的量化。多数文献是直接测定 R_H 和 R_S,选择 R_H、R_H/R_S 的进行呼吸组分贡献率的比较分析,可以更为直接揭示土壤呼吸的环境变化响应。根据检索论文的引文链接及其所引用文献的评述资料,获取土壤呼吸的观测方法、观测时间、生物群区或森林类型以及林龄等相关资料,确定其土壤呼吸通量水平 R_S 和 R_H 或 R_A值。

1.2　数据分组

根据文献所提供的森林林分特征(生物群区、林龄)、土壤呼吸组分分离方法等对文献数据进行归类与分组。

对文献常见的土壤呼吸组分测定方法及过程进行分组,大致分为四大类:根排除法、组分物理分离、同位素方法和间接方法。

(1)排除根法 包括壕沟法(trenching)、环剥法(girdling)和林窗法(gap)。该类方法主要应用于林分水平的土壤自养呼吸和异养呼吸的区分和估测。

(2)组分物理分离 包括组分法(components)、根系剪切(root excising)和活根系呼吸(live root respiration)[6,7]。

(3)同位素方法 包括同位素标记(isotopic labelling)和放射性碳素(radiocarbon),从总土壤呼吸中区分植物呼吸释放 CO_2[8] 以及用同位素标记的组分代替一个或多个土壤组分[9,10]。

(4)间接方法 基于模型(modeling)、质量平衡(mass-balance)、扣除法(subtraction)和根量回归(root mass regression)等模拟、相关性和输入输出平衡等方法估测土壤呼吸通量及其组分分布[11]。

生物群区(Biome) 根据森林林分所属生物群区,分为北方森林、温带(寒温带和暖温带)针叶林、温带落叶林和热带(亚热带)森林。

林龄(组) 不同树种龄阶划分标准和范围不一,基于实际树龄、文献描述或林龄划分,将林分粗略分组为幼龄林(<10a)、中龄林(10~40a)、成熟林(40~80a)和老龄林(>80a),但也将林龄大于80a的也归为成熟林。

2 分析结果

2.1 生物群区与森林土壤呼吸

北方森林、温带针叶林、温带落叶林和热带森林的 R_S 平均水平分别为680、834、937 g C m^{-2} a^{-1}和1084 g C m^{-2} a^{-1}(图1),沿生物群区渐次增加,且生物群区之间的 R_S 水平差异达到显著性水平($\alpha<0.05$)。多重比较分析(LSD)结果,按照北方森林-温带针叶林-温带落叶林-热带林的次序,相邻生物群区森林土壤呼吸没有显著性差异,非相邻生物群区之间差异显著($\alpha<0.05$),各生物群区的 R_S 值域范围及均值方差也随之扩大,反映森林土壤呼吸明显的生物群区分异趋势。森林土壤呼吸通量总体平均水平为855 g C m^{-2} a^{-1},值域为85~2400 g C m^{-2} a^{-1}。

北方森林-温带针叶林-温带落叶林-热带林土壤异养呼吸平均水平(R_H)分别为:366、443、469和493 g C m^{-2} a^{-1}。各区系之间的 R_H 比较,北方森林显著低于热带林,其余区系之间则无显著性差异($\alpha>0.05$)。森林土壤异养呼吸(R_H)总体平均水平为443 g C m^{-2} a^{-1},其值域范围为20~1414 g C m^{-2} a^{-1}。

表1 各生物群区的总土壤呼吸通量 R_s(g C m^{-2} a^{-1})、异养呼吸组分所占比例(R_H/R_S)以及林龄等相关变量

Table 1 Partitioning studies, total annual soil CO_2 efflux (R_S) in g C m^{-2} a^{-1}, heterotrophic flux fraction (R_H/R_S), and its variance

生物群区 Biome1)	测定方法 Method2)	林龄 Age3)	土壤呼吸通量 Total annual soil CO_2 efflux (R_S)	异养呼吸率 heterotrophic flux fraction (R_H/R_S)	参考文献 References
北方森林	^{14}C	M	633	0.49	[12]
Boreal forest	^{14}C	I	500\560	0.09\0.14	[12]
	^{14}C	Y	680	0.03	[12]
	Trench	M	496\415\377	0.42\0.59\0.52	[13]
	Mod	I	1215	0.39	[11]
	Mod	I	660	0.48	[14]
	Trench	M	540\338\375\375	0.73\0.86\0.88\0.94	[15]
	Trench	I	425\337\551\570\484\397	0.67\0.71\0.70\0.62\0.78\0.83	[15]
	Trench	Y	137\85\513	0.98\0.89\0.97	[15]
	Trench	M	640\1170\1520	0.62\0.44\0.36	[16]
	Trench	M	564\319	0.78\0.83	[17]
	r exc	M	470	0.43	[18]
	r exc	M	330\327	0.5\0.7	[19]
	r exc	M	1780\1780\1780	0.67\0.76\0.71	[20]
	^{14}C	M	533	0.65	[21]
	Subtr	M	592	0.76	[22]

续表

生物群区 Biome[1)]	测定方法 Method[2)]	林龄 Age[3)]	土壤呼吸通量 Total annual soil CO_2 efflux (R_S)	异养呼吸率 heterotrophic flux fraction (R_H/R_S)	参考文献 References
	Subtr	M	905	0.4	[23]
	r exc	I	905\338	0.65\0.55	[24]
	M bal	I	858	0.53	[25]
	r exc	M	564	0.66	[24]
	Mod	M	438\967\1124\1050\1003	0.34\0.11\0.27\0.38\0.23	[26]
温带针叶林 Temperate coniferous forest	Trench	M	513\405\	0.17\0.48\	[27]
	Trench	M	564	0.5	[28]
	Trench	I	686\556	0.43\0.43	[28]
	Trench	Y	991	0.41	[28]
	r reg	M	670\648\576	0.16\0.40\0.52	[29]
	r reg	M	644\773\1015	0.26\0.47\0.58	[29]
	Trench	M	596	0.65	[30,31]
	Trench	M	800	0.77	[32]
	Trench	M	727\841	0.77	[32]
	m bal	I	811	0.65	[33]
	m bal	M	518	0.62	[34]
	r exc	M	597	0.46	[35]
	r exc	I	427	0.52	[35]
	r exc	M	780	0.52	[36]
	r exc	I	654	0.49	[36]
	m bal	M	856\849	0.69\0.61	[37]
	Trench	I	710	0.7	[38]
	m bal	I	710	0.75	[38]
	r exc	I	1263	0.48	[39]
	^{14}C	M	1713	0.8	[21]
	r exc	Y	1263	0.48	[39]
	Gap	I	618	0.43	[40]
	^{13}C	I	1183	0.45	[8]
	Subtr	Y	950	0.33	[41]
	Trench	Y	1703	0.45	[42]
	Gap	M	1299\987\1255	0.54\0.49\0.54	[43,44,45]
温带落叶林 Temperate deciduous forest	Trench	I	1184	0.56	[46]
	Isot	I	485	0.7	[47]
	Trench	M	892\812\951\678\451	0.59/0.57/0.67/0.65/0.75	[30]
	r exc	M	660	0.61	[14]
	r exc	M	1627\1824\1801\2176	0.45\0.29\0.46\0.65	[48]
	Trench	M	815\783\785\784	0.23\0.31\0.33\0.38	[27]
	Trench	M	532	0.57	[49]
	Excl	I	1097	0.55	[50]
	Mod		1067	0.55	[51]
	r exc	I	1754	0.3	[52]
	Isot	I	840	0.42	[10]
	m bal	M	387	0.57	[53]
	Mod	M	538\1668	0.57\0.29	[52]
	Gap	M	940	0.49	[54]
	Gap	M	642	0.61	[55]
	Gap	M	487	0.96	[56]
	m bal	M	660	0.77	[57]
	m bal	M	494\1100	0.57\0.48	[58]
	Trench	I	660	0.39	[59]
	Subtr	M	754	0.48	[22]
	Trench	M	1123	0.48	[60]
	r exc	Y	987	0.72	[61]

续表

生物群区 Biome[1)]	测定方法 Method[2)]	林龄 Age[3)]	土壤呼吸通量 Total annual soil CO_2 efflux (R_S)	异养呼吸率 heterotrophic flux fraction (R_H/R_S)	参考文献 References
	Trench	M	371	0.67	[62]
	r exc	M	650	0.77	[63]
	Trench	I	1290	0.37	[64]
	Trench	Y	850	0.49	[64]
热带林	Trench	I	478\430\435	0.54	[65]
Tropical forest		I	1374\944\454	0.48\0.40	[66]
	Trench	I	1105\912	0.34\0.53	[67]
	Trench	M	779\821\899	0.52\0.46\0.46	[67]
	Trench	M	1373	0.524	[68]
	Trench	I	944\455	0.575\0.598	[68]
	Model	M	610.9	0.54	[69]
	Subtr	M	1650	0.59	[22]
	r exc	Y	1610	0.3	[6]
	Isot	Y	2400	0.37	[70]
	Gap	Y	1570	0.42	[71]
	Trench	I	850	0.44	[72]
	Subtr	M	1210	0.45	[73]
	^{13}C	Y	2220	0.27	[74]
	Subtr	M	1650	0.59	[22]
	r reg	I	835	0.5	[75]

1）北方森林 Boreal forest，温带针叶林 Temperate Coniferous forest，温带落叶林 Temperate Deciduous forest，热带森林 Tropical forest；2）^{14}C 放射性碳\^{13}C 标记\ Isot 同位素，剪切 Clip，组分综合 Comp，环剥 Gird，质量平衡 m bal，模型 Mod，扣除 Subtr，根量回归 r reg，根系切除 r exc，壕沟 Trench，林窗 Gap；3）Y、I、M 分别表示幼龄林、中龄林和成熟林

总体上，R_S 和 R_H 沿着北方森林—温带针叶林—温带落叶林—热带森林生物群区渐次增加，但与此相反，R_H/R_S 表现为沿生物群区逐步下降的趋势，其各区系 R_H/R_S 平均值分别为 58%、52%、53% 和 48%（图 1），R_H/R_S 均值方差也随生物群区逐步减小，北方森林是热带森林的 7.4 倍。除北方森林林地的 R_H/R_S 比率显著高于热带林地外，而其余区系之间都没有显著差异（$\alpha>0.05$）。森林土壤异养呼吸贡献率（R_H/R_S）总体平均水平为 52.5%，其分布区间为 3% ~98%。

北方森林土壤呼吸有 51% ~65% 来自异养呼吸，温带针叶林和落叶林，异养呼吸的贡献率范围为 47% ~57% 和 48% ~59%，热带森林的异养呼吸贡献率为 44% ~51%（95% 的置信区间）。

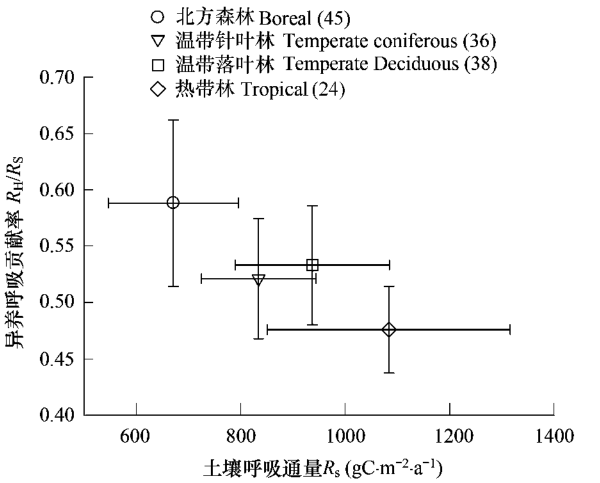

图 1 不同生物群区森林土壤呼吸通量及其异养呼吸贡献率

Fig. 1 Mean heterotrophic flux contributions to total efflux and mean total soil CO_2 efflux (R_S) for each biome type. Error bars are 95% confidence intervals, and numbers of studies per group are indicated in the legend

2.2 R_H 与 R_S 的关系

图 2a 表示 143 个样地数据检验所得的总体相关关系，其拟合模型为 $R_H=0.431\ R_S+68.78$，$R^2=0.619$。图例的双点划线、点线分别表示土壤呼吸异养通量的可信值域与预测值域（95% 置信区间内）。

对不同生物群区的土壤异养呼吸与土壤呼吸通量之间关系（图 2b），北方森林、温带针叶林、温带落叶林和热带林的 R_H 与 R_S 之间的相关系数分别为 0.79、0.83、0.75 和 0.84，都达到极显著相关水平（$\alpha<0.01$）。

幼龄林、中林龄和成熟林的 R_H 与 R_S 之间的相关系数分别为 0.79、0.77 和 0.82，都达到极显著相关水平（$\alpha<0.01$）。

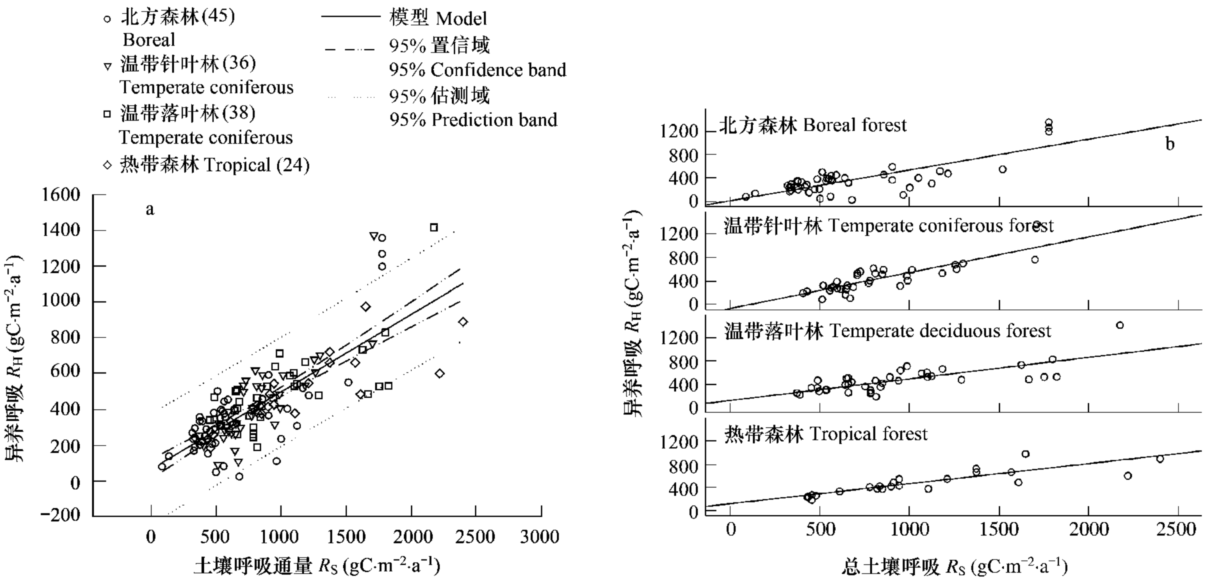

图 2　总体森林土壤呼吸通量(R_S)与异养呼吸(R_H)之间关系(a)各生物群区土壤呼吸通量与异养呼吸关系(b)

Fig. 2　Global relationship between annual soil respiration (R_S) and its heterotrophic (R_H) component (a) Annual soil respiration (R_S) and its heterotrophic (R_H) component by each biome(b)

图 3 是对森林土壤异养呼吸贡献率(R_H/R_S)进行分析,总体上,土壤异养呼吸贡献率分布为倒“S”形,在不同土壤呼吸通量范围内,随着土壤呼吸通量的增加,异养呼吸贡献率呈现下降的趋势。

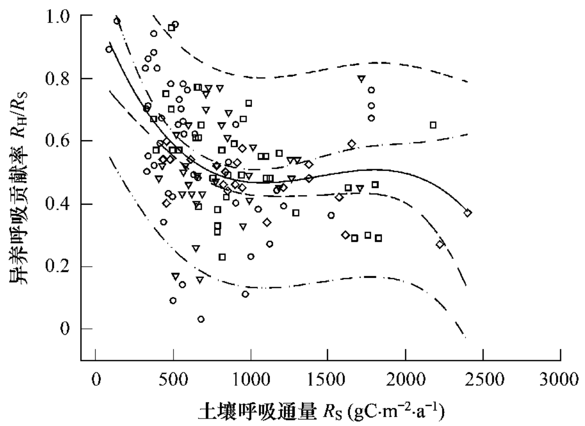

图 3　各区系的森林土壤呼吸通量与异养呼吸贡献率之间的关系

Fig. 3　Heterotrophic flux contribution (R_H/R_S) in relation to total soil carbon dioxide efflux (R_S) in forest systems

2.3　林龄对土壤呼吸的影响

幼龄林、中龄林和成熟林 R_S 均值分别为 1140、768 g C m^{-2} a^{-1}和 852 g C m^{-2} a^{-1},随林龄增加而降低。对林地 R_S、R_H 及 R_H/R_S 进行比较,不同林龄之间的 R_S 均值具有显著性差异,而 R_H 及 R_H/R_S 均值无显著性分异($\alpha>0.05$)。对 R_S 进行多重比较,幼龄林 R_S 显著大于中龄林和成熟林,而中龄林和成熟林之间没有显著性差异。R_S 的值域范围和方差,幼龄林远大于中龄林和成熟林,幼龄林 R_S 均值方差是中龄林和成熟林的 2.6 倍和 4.5 倍。

统计结果证实 R_H/R_S 比率随着林龄增加而升高,幼龄林、中龄林和成熟林的 R_H/R_S 均值分别为 50.8%、51.7% 和 54.8%,均值比较没有显著性差异,但 R_H/R_S 的上、下限差分别为 32% (35% ~67%)、9%(47% ~56%)和 8%(51% ~59%)(图 4)。明显地,幼龄林的 R_H/R_S 分布范围远大于中龄林和成熟林,其平均值方差分别是中龄林和成熟林的 2.5 和 3.4 倍。

在生物群区内不同林龄之间的 R_S、R_H 和 R_H/R_S 进行比较,仅有热带森林的幼龄林与中龄林、成熟林差异显著($\alpha<0.05$),其余生物群区的龄组之间无显著差异。图 5 显示,北方森林和温带落叶林,各林龄的 R_H/R_S 值顺序为中龄林 < 成熟林 < 幼龄林,而温带针叶林和热带林则表现为幼龄林 < 中龄林 < 成熟林。

3　结论与讨论

近些年,关于土壤呼吸 R_S 的组分区分研究快速增加,并能够获取更加详尽和全面的实验信息,也使全球土壤呼吸变化趋势的分析成为可能。本文的土壤异养呼吸贡献率计算结果,与前人对自养呼吸贡献率估计比较,二者是相互印证与吻合[76]。森林土壤呼吸通量是森林生态系统碳循环的重要特征,尤其是森林生态系统

呼吸的组分及其贡献,与凋落物输入结合可以评估森林土壤碳平衡,森林生态系统呼吸量的 2/3 归于土壤呼吸[77],土壤呼吸的微小变化可能导致森林净碳平衡的重要改变[78]。

在区域及全球尺度,森林土壤呼吸特征(R_S、R_H 和 R_H/R_S)具有明显的生物群区分异。林地 R_S 沿北方森林-温带针叶林-温带落叶林-热带林次序逐步升高,异养呼吸组分贡献率(R_H/R_S)下降的总体趋势,北方森林的 R_H/R_S 平均值和值域范围都大于热带森林,反映森林土壤呼吸受气候地带性与生态系统生产力格局共同作用的特征。森林生产力较高,光合同化产物碳分配到自养呼吸比例较高,R_H/R_S 率随年度 R_S 值增加而下降,对于净生态系统交换量的变化,生态系统呼吸可能比光合作用具有更大的决定作用[79]。

森林土壤碳平衡随森林演替发育阶段而变化,林龄差异导致不同的森林生态系统碳平衡,不同林龄(组)可能形成不同的土壤呼吸特征(R_S、R_H 和 R_H/R_S)。如西黄松幼龄林(14a)和老熟林(250a)土壤呼吸的年际和季节格局反差极大[35]。从幼龄林到成熟林,总生态系统呼吸一般随之增加,但从成熟林到过熟林,总生态系统呼吸则是下降趋势[79]。对过熟林与邻近的幼龄林及次生成熟林比较,林龄是决定呼吸的数量和所占比例的重要因素之一。本文关于成熟林组的 R_H/R_S 值变化趋势的结论,间接证实周国逸等长期研究结果[5]。

由于生态系统多样性、技术方法和测定时间的分异,会引入潜在偏差与分异。与其它林龄(组)比较,幼龄林立地数量较少,土壤呼吸表现为较大的不确定性(偏差)和分异性(方差)。这可能与幼龄林林分构建的扰动程度、森林类型及凋落物数量与质量分异有关。另外,多数测定是在生长季节,呼吸组分的时间格局可能不同[14],土壤呼吸具有急剧的季节变化[80]。土壤 CO_2 的来源及其响应机制的理解不足,如对土壤温度[81~84]及大气 CO_2 浓度升高[85,86],森林碳收支对全球变化响应还保持很大不确定性。

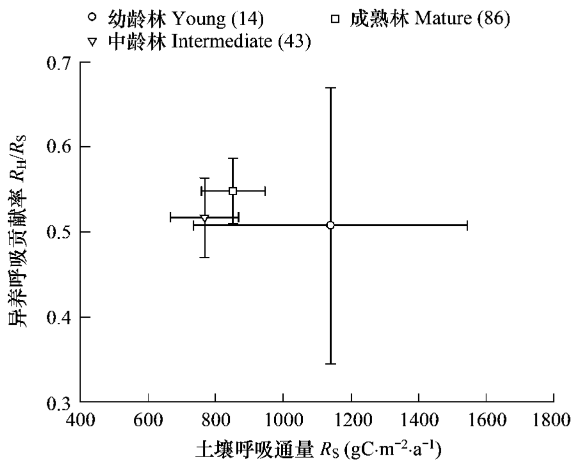

图4 不同林龄的土壤异养呼吸贡献率分布范围

Fig. 4 Effect of stand age on heterotrophic flux contributions (R_H/R_S) in dependence of total soil carbon dioxide efflux (R_S) at forest sites

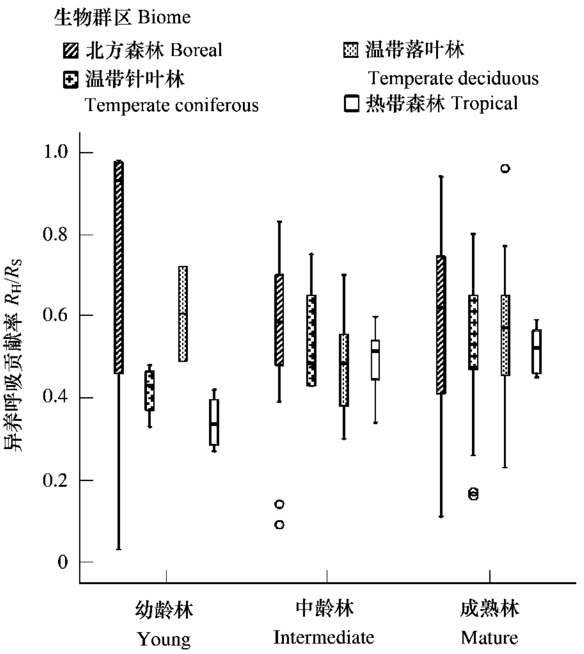

图5 不同林龄及生物群区的森林土壤异养呼吸贡献率

Fig. 5 Soil heterotrophic flux contributions (R_H/R_S) for all biome types and stand age classes

本文对生物群区及林龄对土壤呼吸的影响分析,呼吸组分的区分及其贡献的量化,R_H 与 R_S 之间存在显著线性相关,拟合模型具有广泛适用性,可以有助于对森林生态系统碳预算进行限定,评估森林根系碳分配和净生产力,揭示同化 C 在生物量和自养呼吸的分配对变化环境条件的响应,有助于评估全球气候变化对陆地 C 循环的效应。

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