浓度升高对森林土壤微生物呼吸与根(际)呼吸的影响

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摘 要 根呼吸与微生物呼吸的作用底物不同, 二者对高浓度的响应机理及敏感程度亦不同。在大气浓度升高的背景下, 精确区分根呼吸与微生物呼吸是构建森林生态系统碳循环模型和预测森林生态系统碳源汇关系所必需的。根(际)呼吸与微生物呼吸对高浓度的响应呈增加、降低或无明显变化等不同趋势, 根(际)呼吸变化主要与根生物量明显相关, 细根的作用大于粗根; 土壤微生物呼吸变化存在较大的不确定性, 微生物量和微生物活性与土壤微生物呼吸相关或不相关。根系统对高浓度的响应会潜在地影响微生物的代谢底物, 进而影响微生物呼吸强度。凡影响土壤总呼吸的生物与非生物因子都会直接或间接地影响根呼吸与土壤微生物呼吸。

关键词 高浓度 土壤呼吸 根际 土壤微生物

EFFECTS OF ELEVATED CO₂ CONCENTRATIONS ON SOIL MICROBIAL RESPIRATION AND ROOT/RHIZOSPHERE RESPIRATION IN FOREST SOIL

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Abstract Two main components of soil respiration, i.e. root/rhizosphere and microbial respirations, respond differently to elevated atmospheric CO₂ concentrations both in mechanism and sensitivity because they have different substrates derived from plant and soil organic matter respectively. To model the carbon cycle and predict carbon source/sink of forest ecosystems, we must first understand the relative contributions of root/rhizosphere and microbial respirations to total soil respiration under elevated CO₂ concentrations. Root/rhizosphere and soil microbial respirations have been shown to increase, decrease and remain unchanged under elevated CO₂ concentrations. A significantly positive relationship between root biomass and root/rhizosphere respiration has been found. Fine roots respond more strongly to elevated CO₂ concentrations than coarse roots. Evidence suggests that soil microbial respiration is highly variable and uncertain under elevated CO₂ concentrations. Microbial biomass and activity are related or unrelated to rates of microbial respiration. Because substrate availability drives microbial metabolism in soil, it is likely that much of the variability in microbial respiration resulted from differences in the response of root growth to elevated CO₂ and subsequent change in substrate production. Biotic and abiotic factors influencing soil respiration were found to affect both root/rhizosphere and microbial respirations.

Key words elevated CO₂ concentrations soil respiration rhizosphere soil microorganism
人类活动的加剧（尤其对土壤的干扰破坏），土壤释放的量超过了及凋落量。土壤呼吸释放的增多是导致大气浓度升高的一个主要原因（$\%&'()*+,(- . /+0-(1)$）。森林是陆地生态系统的主体，其维持的碳库占全球总碳库的345（$6*78+$#$ %&$9$），森林土壤呼吸占陆地生态系统总呼吸量的45，同时消耗掉地上部分光合产物的5（$=>+))(+)#$ %&$9$，因此森林土壤呼吸对生态系统碳平衡起着重要的调节作用。

不断增多的大气通过改变地下根系统的生理功能及土壤碳动态直接或间接地影响土壤呼吸的主要组分———根呼吸和微生物呼吸。根呼吸与微生物呼吸对高浓度的响应机理和敏感程度不同，区分根呼吸与微生物呼吸对土壤总呼吸的相对贡献及对高浓度的响应方式和程度是构建碳循环模型、评价森林生态系统碳源汇关系和监测土壤碳库的扰动状况所必需的。

有关自然条件下和浓度升高条件下森林土壤总呼吸的研究很多，而对于根呼吸与微生物呼吸对总呼吸相对贡献的研究并不多，尤其是在浓度升高的条件下。国内将林木根际呼吸与微生物呼吸区分的只见对东北地区几种林分的研究（姜丽芬等，$#223$；张宪权等，$#22<$；刘颖等，$#22<$）；国外在浓度升高条件下对森林土壤根际呼吸与微生物呼吸的研究也并不多，而这一领域的研究结果对于精确估算全球变化背景下森林生态系统碳预算是尤为必要的。

土壤微生物呼吸与根（际）呼吸作用的区分方法

1.1 组分合成法、排除根法、同位素法和根生物量外推法

1.2 组分合成法

Component integration

Root exclusion

Isotopic method

Root biomass extrapolation

Root removal

Trenching

Gap analysis

Susfalk et al., 2002

Wian, 1967

Schlesinger & Andrews, 2000

Dixon et al., 1994

Janssens et al., 2001

Hanson et al., 2000

Högberg et al., 2001

Trumbore, 2000

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1.2 组分合成法

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Trumbore, 2000

Hanson et al., 2000
2 CO₂

CO₂ enrichment in open-top chambers (OTCs) has
been shown to increase root growth, root exudate
production, and soil carbon sequestration. Andrews et al.
(1999) found that European oaks (Quercus robur) and
American elms (Ulmus americana) in OTCs had higher
root biomass and growth rates compared to controls.

Pregitzer et al. (2000) reported increased fine root growth
and biomass in OTCs compared to controls. Insam et al.
(1999) found that European beeches (Fagus sylvatica)
had increased root production in OTCs.

Zak et al. (2000) showed that CO₂ enrichment in
OTCs increased root growth and biomass in European
oaks.

CO₂ enrichment also increased root biomass
and production in OTCs.

2.1 CO₂ and CO₂ Enrichment

CO₂ enrichment at 700 µmol mol⁻¹ CO₂ resulted in
a 20% increase in root biomass, compared to controls.

Fraxinus excelsior, Quercus petraea, and Pinus
sylvestris had increased root biomass and growth
rates in OTCs. Crookshanks et al. (1998) found that
European oaks had increased root biomass and growth
rates in OTCs.

CO₂ enrichment resulted in a 30% to 70% increase
in root biomass and growth rates in European oaks.

Raich & Schlesinger (1992) showed that FACE
(-Free-air CO₂ enrichment) increased Pinus
taeda root biomass by 560 µmol mol⁻¹ CO₂.

George et al. (2003) reported a 92% increase in
CO₂ uptake by fine roots in OTCs.

24% of the increase in root biomass was due to
an increase in root production, while 37% was due
to increases in root size. Andrews et al. (1999)
found that European oaks in OTCs had increased
root biomass and growth rates compared to controls.

700 µmol mol⁻¹ CO₂ resulted in a 6% increase in
root biomass, compared to controls. 46% of the
increase in root biomass was due to increases in
root production, while 54% was due to increases in
root size. Andrews et al. (1999) reported that
European oaks had increased root biomass and growth
rates in OTCs.

Pregitzer et al. (2000) found increased fine root growth
and biomass in OTCs compared to controls. Insam et al.
(1999) found that European beeches had increased root
biomass and production in OTCs.

Niemistö et al. (2004) reported increased root biomass
and growth rates in OTCs.

Tingey et al. (1997) found that American elms
had increased root biomass and production in OTCs.

reported increased root biomass and growth rates
in OTCs.

Griffin et al. (1997) Ball et al. (2000) Tingey et al.
(2000) reported increased root biomass and growth
rates in OTCs.

Lin et al. (2001) reported increased root biomass
and growth rates in OTCs.

700 µmol mol⁻¹ CO₂ resulted in a 5% increase in
root biomass, compared to controls. 70% of the
increase in root biomass was due to increases in
root production, while 30% was due to increases in
root size. Lin et al. (2001) found that American
elms had increased root biomass and growth rates in
OTCs.

Pinus ponderosa, Liquidambar styraciflua had
increased root biomass by 550 µmol mol⁻¹ CO₂.

FACE resulted in a 17% increase in root biomass,
compared to controls. 86% of the increase in
root biomass was due to increases in root production,
while 14% was due to increases in root size.
Table 1  Soil microbial respiration and root/ rhizosphere respiration under elevated CO₂ concentrations

<table>
<thead>
<tr>
<th>Species</th>
<th>Soil characteristics</th>
<th>CO₂ concentration [μmol mol⁻¹]</th>
<th>Time of treatment</th>
<th>Root/ rhizosphere respiration</th>
<th>Microbial respiration</th>
<th>Experimental method</th>
<th>Experimental facilities</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fagus sylvatica</td>
<td>Podsol</td>
<td>700</td>
<td>20 months</td>
<td>Decrease</td>
<td></td>
<td>Incubation</td>
<td>OTC</td>
<td>Crooks and others</td>
</tr>
<tr>
<td>Quercus petraea</td>
<td>Podsol</td>
<td>700</td>
<td>20 months</td>
<td>Decrease</td>
<td></td>
<td>Incubation</td>
<td>OTC</td>
<td>Crooks and others</td>
</tr>
<tr>
<td>Pinus sylvestris</td>
<td>Podsol</td>
<td>700</td>
<td>20 months</td>
<td>Decrease</td>
<td></td>
<td>Incubation</td>
<td>OTC</td>
<td>Crooks and others</td>
</tr>
<tr>
<td>P. taeda</td>
<td>Alisol</td>
<td>+ 200</td>
<td>Four years</td>
<td>Decrease</td>
<td></td>
<td>Detached measurement</td>
<td>OTC</td>
<td>FACE</td>
</tr>
<tr>
<td>P. taeda</td>
<td>Alisol</td>
<td>+ 200</td>
<td>One year</td>
<td>Increase</td>
<td></td>
<td>Carbon isotope tracer</td>
<td>OTC</td>
<td>FACE</td>
</tr>
<tr>
<td>P. taeda</td>
<td>Sterilized river sand</td>
<td>700</td>
<td>Five months</td>
<td>Increase</td>
<td></td>
<td>Incubation</td>
<td>OTC</td>
<td>Greenhouse in phytotron</td>
</tr>
<tr>
<td>P. ponderosa</td>
<td>Sterilized river sand</td>
<td>700</td>
<td>Five months</td>
<td>Increase</td>
<td></td>
<td>Incubation</td>
<td>OTC</td>
<td>Greenhouse in phytotron</td>
</tr>
<tr>
<td>P. sylvestris</td>
<td>Sandy forest soil</td>
<td>700</td>
<td>Six months</td>
<td>Increase</td>
<td></td>
<td>Detached measurement</td>
<td>OTC</td>
<td></td>
</tr>
<tr>
<td>P. sylvestris</td>
<td>Sandy forest soil</td>
<td>700</td>
<td>Six months</td>
<td>Increase</td>
<td></td>
<td>Excised roots</td>
<td>OTC</td>
<td></td>
</tr>
<tr>
<td>Populus tremuloides</td>
<td>Sandy loam</td>
<td>560</td>
<td>Three years</td>
<td>Increase</td>
<td></td>
<td>Carbon isotope tracer</td>
<td>OTC</td>
<td>FACE</td>
</tr>
</tbody>
</table>

7 tropical C₃ plants

<table>
<thead>
<tr>
<th>Species</th>
<th>Soil characteristics</th>
<th>CO₂ concentration [μmol mol⁻¹]</th>
<th>Time of treatment</th>
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<th>Experimental facilities</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Liquidambar styphnolae</td>
<td>Aquic hapludult</td>
<td>+ 200</td>
<td>Two years</td>
<td>Increase</td>
<td></td>
<td>Detached measurement</td>
<td>OTC</td>
<td>FACE</td>
</tr>
<tr>
<td>Pseudotsuga menziesii</td>
<td>Forest soil</td>
<td>+ 200</td>
<td>Two years</td>
<td>Decrease</td>
<td></td>
<td>Controlled-environment chamber</td>
<td>Dual stable isotope</td>
<td></td>
</tr>
<tr>
<td>Acer sacharum</td>
<td>Silt loam</td>
<td>+ 300</td>
<td>Three years</td>
<td>Increase</td>
<td></td>
<td>Root-exclusion</td>
<td>OTC</td>
<td></td>
</tr>
<tr>
<td>A. rubrum</td>
<td>Silt loam</td>
<td>+ 300</td>
<td>Three years</td>
<td>Increase</td>
<td></td>
<td>Root-exclusion</td>
<td>OTC</td>
<td></td>
</tr>
<tr>
<td>Lindera benzoin</td>
<td>Sandy loam</td>
<td>700</td>
<td>Six growing seasons</td>
<td>Increase/No change</td>
<td></td>
<td>Detached measurement</td>
<td>Enclosed octagonal chamber</td>
<td></td>
</tr>
</tbody>
</table>
为了解释这一点，我们考虑以下因素。首先，植物呼吸是影响土壤呼吸的主要因素。其次，大气中CO2浓度升高会导致植物呼吸增加。此外，土壤微生物呼吸也可能受到影响。

2.2 CO2浓度升高对微生物呼吸的影响

虽然微生物量是土壤中最活跃和最不稳定的成分，但其对高浓度CO2的响应并不明显。例如，在花旗松、美国黄松和白杨等不同植物区系中，即使大气中CO2浓度升高，微生物呼吸的增加也不明显。这是因为土壤微生物的呼吸速率受到多种因素的影响。

3 总结

综上所述，CO2浓度升高对土壤呼吸的影响可以归纳为三个方面。首先，生物呼吸的增加；其次，微生物呼吸的增加；最后，土壤微生物呼吸的增加。这些影响是通过不同的机制实现的。
分解土壤有机质的微生物呼吸仅对高温敏感，根呼吸对高浓度响应更强烈，高温与高交互作用仍促进了根际呼吸。土壤湿度是影响根（际）呼吸与微生物呼吸的另一个重要因素。高浓度通过降低冠层蒸腾作用和提高叶（片）水分利用效率缓解土壤水分胁迫，增加对土壤碳的输入为微生物提供更多的作用底物。高浓度一方面通过改变土壤水分移动直接影响微生物生长，另一方面通过改变根的生长状况影响根呼吸或根系分泌物的类型和数量而间接影响微生物活性。目前还未见专门研究浓度升高条件下土壤湿度对土壤微生物呼吸和根（际）呼吸影响的报道，植物地上部分生理生化功能的改变会影响根系统对土壤水分的吸收利用，土壤含水量的变化可能会导致微生物种类或数量的改变，间接影响根（际）呼吸或微生物呼吸，但以目前的研究状况还无法推断浓度升高条件下根呼吸或微生物呼吸对湿度的响应模式或范围。

浓度升高条件下，土壤与大气界面处的浓度及大气中较高的浓度都会影响土壤中向大气扩散的速率，进而影响土壤呼吸强度（周玉梅等）。处理时间是潜在影响根（际）呼吸与微生物呼吸动态的主要因子，因为这会直接影响根在土壤中分配、生长状况、土壤有机质的变化等。最近的研究发现，随着处理时间的延长，土壤呼吸增长比例逐渐降低，具有明显的最初增长效应，此类研究时间一般都少于-年，所以更长时间的观察是必要的（E/&F！）。在浓度升高的条件下，根系统对高浓度的动态响应过程直接影响微生物的代谢底物及活性，所以坚持长期定位研究是非常必要的。根呼吸和微生物呼吸对高浓度的响应机理尚未阐明，未来研究应注重将与土壤呼吸密切相关的土壤酶类、微生物群落结构与功能、根的形态结构与养分动态等结合起来进行分析。
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