

# 生物环境因子对树干呼吸时空变异的影响\*

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**摘要** 树干呼吸是解释森林生态系统生产力变化的关键过程之一。测定树干呼吸速率,理解其生物环境调控机制,有助于构建森林碳循环模型,提供森林碳收支的估测精度。本文比较分析了树干呼吸3种测定方法,指出活体测定法与质量平衡方法的结合使用,可以更深入地进行树干呼吸机理研究。针对树干呼吸速率时空变异,着重探讨温度、树干液流的重要影响机制,并比较分析了不同森林生态系统的维持呼吸年通量,维持呼吸年通量与林龄、纬度、年均温和降水量呈显著线性相关。表4 参84

**关键词** 树干呼吸; 时空变异; 树干温度; 液流; 维持呼吸

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## Effect of Biophysical Factors on Spatio-temporal Variation in Stem Respiration\*

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**Abstract** As one of the key processes, stem respiration play an important role in explaining the variation in forest ecosystem productivity. Measuring stem respiration and understanding its biophysical controlling mechanisms are necessary to develop forest carbon cycling models and improve estimation of forest carbon budgets. The measuring methods, spatio-temporal variation in stem respiration rates were reviewed. The combination between *in vivo* method and mass balance approach would be helpful for exploring the stem respiration mechanism. Special discussion was made on the effects of stem temperature and sap flow on stem respiration. The maintenance respiration annual fluxes of various forest ecosystems were also compared. With the statistical analysis, there were significant linear relationships between annual stem respiration and forest age, latitude, and mean annual temperature and precipitation. Tab 4, Ref 84

**Keywords** stem respiration; temporal and spatial variation; stem temperature; sap flow; maintenance respiration

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森林是陆地生态系统的主体,在生长过程中吸收CO<sub>2</sub>并具有长期的储存能力。全球陆地生态系统约有40%的碳贮存于森林中<sup>[1-2]</sup>,森林在维持全球碳平衡及调节全球气候变化等方面的作用不可替代。近年来对森林碳平衡的研究日益增多,许多研究表明呼吸作用是解释生态系统生产力变化的关键过程<sup>[3]</sup>。自养呼吸作为森林生态系统年碳平衡的重要组成部分,其消耗光合固定碳总量的比例约为40%~60%,在热带森林甚至达90%<sup>[4]</sup>。自养呼吸包括地下和地上两部分,后者由叶片和木质组织组成。树干呼吸,也称木质组织呼吸或者树干CO<sub>2</sub>通量(Stem respiration, woody tissue respiration, stem CO<sub>2</sub> flux),大部分由新生韧皮部和与形成层相连的木质部产生,活射线和轴向薄壁组织细胞也会产生一小部分。树干呼吸作用占地上自养呼吸比例变化范围很大,北方针叶林为25%<sup>[5]</sup>,在某些温带森林高达50%<sup>[6]</sup>。对于树木和林分碳平衡而言,树干呼吸作用起着重要作用。因为成熟林分大部分生物量

是木质组织,而这部分组织的活细胞即使在非生长季(Non-growth season)也持续进行维持呼吸。另外,树干呼吸也是一个良好的生长物候学指示指标,可用于计算生长速率。与叶片光合或者呼吸作用相比,对树干呼吸机制的研究要匮乏得多<sup>[7]</sup>。因此,测定木质组织呼吸,理解其调控机制,不仅有助于提高估算森林碳收支模型的精确性,也是理解全球碳平衡和构建森林与大气间CO<sub>2</sub>交换模型的基本步骤<sup>[8]</sup>。

## 1 树干呼吸测定方法

树干呼吸的研究可以追溯到20世纪前半叶, Johansson于1933年开展了实地测定木质组织呼吸的工作<sup>[9]</sup>。早期研究还包括Geurten(1950)、Kinerson(1975)、Negisi(1975, 1978, 1979)和Linder & Troeng(1980)<sup>[10-15]</sup>的试验工作,测定手段多为离体测定,但离体测量研究受到质疑:受伤可能会导致呼吸速率估计错误。随着测定仪器的改进(尤其是红外气体分析仪)以及影响因素的综合考虑,树干呼吸研究兴起。测定方法主要以活体测定为主,测定精度得以迅速提高,针对不同生态系统的研究先后展开<sup>[16-37]</sup>。木质组织呼吸的野外活体测定,对于理解木质组织呼吸的机理过程和定量估计树干和树枝年释放CO<sub>2</sub>总量具有重要意义。

测定树枝呼吸所采用的仪器设备与树干呼吸测定设备一样,只是需要改造测定室,使之能够密封树枝而不至于伤害树枝。自行设计测定室经常采用锡箔纸覆盖的方法,避免

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直射光线导致测定室温度升高,也可以防止一些幼嫩组织树枝的光合作用。因为树体高大,所以测定树枝呼吸往往用自动测定<sup>[7,38]</sup>,注意事项基本与树干呼吸测定相同。

活体测定和离体测定方法都属于局部CO<sub>2</sub>通量测定法。不同研究者应用局部CO<sub>2</sub>通量测定法所得结果差别很大,甚至相同树种不同个体之间CO<sub>2</sub>通量也有很大差异<sup>[39]</sup>,意味着通量测定具有一定的不确定性。这使研究者探究发生这种现象的原因,并探索用其他方法进行树干呼吸研究。质量平衡法(Mass balance approach)<sup>[39-41]</sup>是近来国外研究者提出的一个测定树干呼吸的新方法。

3种测定方法各有利弊(表1),这样就产生了一个问题,如何对3种方法进行评价?测定结果可否有对比性,尤其是

离体测定的结果能否有应用价值。活体测定是当今研究的主流,能够在树体不受破坏的情况下测定树干呼吸,可信度较高。

目前为止,对于离体方法与野外实体测定方面的对比研究较少,导致综合考虑各种影响因子对树干呼吸进行全面分析非常困难。王文杰等<sup>[42]</sup>对比美国黄松(*Pinus ponderosa*)离体和活体测定的研究发现(选择标准是活体测定温度大致与室内分离测定一致),以树干表面积为基准时,离体测定较活体测定结果平均高74%且差异显著( $P = 0.013$ );而用边材体积为基准时,离体测定平均比Ryan等(1995)<sup>[43]</sup>和Law等(1999)<sup>[44]</sup>的结果高出56倍,但与Carey等(1996)<sup>[45]</sup>测定的结果没有显著差异。因而,离体测定的结果往往导致结果偏高,

表1 树干呼吸研究方法比较

Table 1 Comparison of methods for studying stem respiration.

测定方法 Measuring method	原理 Theory	操作系统 Operation system	优点 Advantage	缺点 Disadvantage	应用实例 Reference
活体测定法 <i>In vivo</i> method	利用CO <sub>2</sub> 红外线测定装置把树干或树枝的一部分或者全部放置于测定室内对其释放CO <sub>2</sub> 速率进行测定 A part of a stem or branch was disposed in the CO <sub>2</sub> IRGA and the changes of CO <sub>2</sub> were measured	开路系统、闭路系统。气体分析仪器多数是红外线分析仪(IRGA),如美国LICOR公司的LI-6262、LI-6400、LI-8100等,CID公司的LCA3或者其他系统,记录数 据一般采用数据存储如Campbell Scientific公司的CR10系列记录仪 Open/close system. Most gas analyzers are IRGAs such as the LI-6262, Li-6400 and LI-8100 made by LICOR, LCA3 by CID and other systems with data storage as CR10 by Campbell Scientific	可以野外实地测定,能够准确代表测定树木的呼吸水平。 根据树干形状,自行设计测定室。可避免由受伤组织引起的呼吸干扰;并可对同一样品进行连续或重复测定,数据准确可靠;操作简便易行 The measurement can be made and stem respiration can be accurately determined in the field. According to stem shape, the chambers are designed to prevent the disturbance from damaged tissues. Continual or repetitive measurement can be easily made with high accuracy	不能够细化树干不同组织的呼吸水平。 闭路系统测定过程中需保证测定室与外界不存在气压差,较小的气压差能够造成较大误差。因室内微气候会发生改变,不适于长期测定,影响测定结果准确性 Respiration from different tissues can not be made accurately. It is necessary to make measurements with no pressure difference between chamber and the ambient atmosphere with close tissues. The minor pressure difference can cause microclimate changes and influence the accuracy	[16-18, 20-26, 34]
离体测定 <i>In vitro</i> method	取下树干或树枝样本,放入定量容器(小瓶)中密封,使用气相色谱仪对瓶内气体浓度进行测定,记录测定时间间隔及样品质量或体积 Putting the stem or branch sample into quantitative vessel and measuring the gas concentration with GC. The measuring time interval and sample mass or volume are logged	可使用IRGA或者静态碱吸收法,也可采用差示扫描热仪(Differential scanning calorimeter),通过呼吸过程中的热量平衡来计算呼吸速率 The respiration rate can be computed by the heat balance during the respiration process with IRGA, static alkaline absorption or differential scanning calorimeter	能够定量分析树干不同组分木质部、韧皮部以及形成层薄壁细胞的呼吸水平 Quantifying the respiration from xylem, phloem and cambium parenchyma cells	测定结果偏高;取样少的情况下,测定精度可能不够;对树干和树枝的破坏性太大,能否真正代表测定部位呼吸水平有待深入研究 It can overestimate the measurement with few samples and low accuracy. It is destructive for stems and branches, and lack of research of sampling respiration as the true one	[27-31]
质量平衡法 Mass balance approach	估测树干内部的CO <sub>2</sub> 通量,即液流中的CO <sub>2</sub> 的储存、运输和扩散 Estimating inner CO <sub>2</sub> fluxes which are the storage, transpiration and diffusion of CO <sub>2</sub> in sapflows	采用CO <sub>2</sub> 微电极直接测定树干液流中的CO <sub>2</sub> 浓度或通过测定树干液流停止流动或相对很低时树干CO <sub>2</sub> 释放通量与液流流动时树干CO <sub>2</sub> 释放通量的差值来间接测定木质部液流中CO <sub>2</sub> 浓度 The CO <sub>2</sub> concentration of stem sap flow can be measured directly by microelectrode or the CO <sub>2</sub> difference between stem CO <sub>2</sub> emission and the of sap flow when the sap flow is stopped or relatively low	提供一个更为精确地估测木本组织呼吸的方法,其结果比单独测定树干CO <sub>2</sub> 释放通量更为合理 Providing a more accurate method for estimating woody tissue respiration and the measurement is more reasonable than that from direct measurement	方法不尽完善,以几种假设条件为前提,这些假设不能直接测得且不同树种各种通量成分有很大差别,会影响估测结果准确性 It is a method with flaws because the measurement is based on hypotheses which can not be measured directly and the significant difference between stem respiration components. The accuracy can be affected by the uncertain factors	[39-41]

但其高出程度尚需要更多的实验对此进行检验. 采用质量平衡方法可观测不同时间和不同条件下决定树干呼吸估测的不同通量成分的动态变化, 但基于释放通量的呼吸估测与用质量平衡方法计算的结果之间差异为1%~76%, 白天测定比夜晚测定具有更大的差别且不同树种间也有差异<sup>[39, 41]</sup>.

应用质量平衡方法进行树干呼吸研究已证明液流中CO<sub>2</sub>浓度对树干呼吸作用以及树干CO<sub>2</sub>释放通量测定的影响. 尽管对二者间关系的研究还不多<sup>[39-41]</sup>, 但这种方法考虑更为全面, 其估测更趋于合理, 今后将会受到越来越多的关注. 因此, 在今后的研究中, 应探索结合使用活体测定法与质量平衡方法, 可以更深入地进行树干呼吸机理研究.

## 2 树干呼吸时空变异及影响因素

树干代表经济成果和长期碳汇, 树干呼吸是森林生态系统碳平衡的重要组成部分. 理解环境生物条件如何影响树干呼吸以及树干呼吸对生态系统总碳损失的贡献对于发展和验证森林生产力模型至关重要<sup>[47]</sup>, 也可为揭示森林生态系统对减缓大气CO<sub>2</sub>浓度变化的作用提供科学依据. 因此, 弄清木质组织呼吸的调控因子是森林经营者和生态学家的兴趣所在.

### 2.1 树干呼吸时空变异

木质组织作为树木的一部分, 其活细胞一年四季进行代谢呼吸<sup>[46]</sup>. 树干呼吸时间变异主要包括树干呼吸速率日变化和季节变化<sup>[24, 48]</sup>, 主要与树干温度、树木生理结构有关<sup>[49]</sup>. 马玉娥等(2007)对树干呼吸的日变化和季节变化进行了详细比较分析<sup>[50]</sup>.

树干呼吸速率随着树干高度增加而增加, 因为树干温度随着树干高度增加而增加且幼嫩部位生理活性比较高, 需要更多的呼吸提供能量<sup>[51]</sup>. 生长状况(形成层活性和实际传

输速率)的不同可部分解释这种现象<sup>[52]</sup>. 自然情况下, 树木个体的内部温度随很多因素的不同而发生变化, 如朝向、高度及树干组织深度等<sup>[17-18, 53]</sup>. 仅在一个方向或者同一高度上测定树干呼吸, 会高估或低估树干呼吸总量. 在利用叶室测定尺度上推单株或树干水平, 利用树干呼吸速率与温度关系, 必须考虑树内空间变异<sup>[17]</sup>. 有几种原因引发树干呼吸空间差异: (1) 木质组织成分差异及沿树干产生木头量将使生长呼吸有差异; (2) 树干内活细胞分布能影响维持呼吸速率<sup>[16-17]</sup>; (3) 树干内碳水化合物运输和储存能引起呼吸速率变异; (4) 液流能传输部分由树干呼吸释放CO<sub>2</sub><sup>[14, 54]</sup>并在树干上部分释放, 但是Edward & Wallschleger (2000)发现液流对树干呼吸影响很小<sup>[55]</sup>; (5) 温度也是影响树干呼吸空间差异的重要因子. 树干温度在冠层上部通常较高, 因为树干更容易接触到阳光且温度变幅更大.

### 2.2 树干呼吸影响因素

木质组织呼吸作为一个复杂的生物学过程, 受多种因素影响, 如温度、湿度、大气CO<sub>2</sub>浓度、土壤养分等外部环境条件<sup>[22, 46, 56-60]</sup>, 树干本身在林冠中所处位置、树干高度、方向(是否受阳光的照射)、树木年龄, 内部因素如液流中CO<sub>2</sub>浓度、维管形成层活动与休眠年循环模式等都会产生影响<sup>[24, 39-41, 48, 61-63]</sup>.

**2.2.1 温度** 与其他呼吸作用一样, 树干呼吸与树干温度密切相关. 在一定的范围内表现为随温度增加而增加, 但增加幅度各异. 不同研究得到了不同的树干呼吸速率和温度间的相互关系模型(表2).

与当前树干温度相比, 树干呼吸速率在某一时刻值与之前(Earlier time)树干温度更加相关密切<sup>[16, 23, 38, 70]</sup>. 树干呼吸速率和树干温度响应时间间距(Time interval)称为时滞“Time lag”, 对于指数关系更适合温度称为延迟温度

表2 树干呼吸速率和温度间的相互关系模型  
Table 2 Models between stem temperature and stem respiration rate

作者 Author	植被类型 Vegetation type	公式 Model	参数意义 Parameter meaning
Vose & Ryan, 2002 <sup>[48]</sup>	白松林 White pine forest	$R_s = R_{15} e^{(T_s-15)}$ $T_s = \{T_s(h-1) + [T_A - T_s(h-1)]\} / 8.5$	$R_s$ : 树干呼吸速率; $R_{15}$ : 15 °C下单位边材呼吸速率; $T_s$ : 边材温度 $R_s$ : Stem respiration rate; $R_{15}$ : Sapwood respiration rate per volume at 15 °C; $T_s$ : Sapwood temperature
Ceschia et al., 2002 <sup>[51]</sup>	水青冈林 <i>Fagus sylvatica</i> L. forest	$R = R_{15} Q_{10}^{(T-10)/10}$	$R_0$ : T为°C通量速率 $R_0$ : Respiration rate at some temperature
Meir & Grace, 2002 <sup>[64]</sup>	热带雨林 Tropical forest	$R = R_0 e^{KT}$	$r_B$ : 平均组织呼吸速率; $M_t$ : 单位地面面积边材体积; $T$ : 组织温度; $T_B$ : 10 °C或者15 °C
Ryan et al., 1997 <sup>[65]</sup>	北方森林 Boreal forest	$R = M_t r_B e^{R(T-T_B)}$	$r_B$ : Mean tissue respiration rate; $M_t$ : Sapwood volum per ground area; $T$ : Tissue temperature; $T_B$ : 10 °C or 15 °C
Bolstad et al., 2004 <sup>[66]</sup>	北部硬木林 Northern hardwood forest	$R = R_{20} Q_{10}^{(T-20)/10}$	$R_{20}$ : 20 °C下单位边材呼吸速率 $R_{20}$ : Sapwood respiration rate per volume at 20°C
Cernusak et al., 2006 <sup>[67]</sup>	热带稀树草原生态系统 Savanna ecosystem	$F = F_R Q_{10}^{(T-T_R)/10}$	$F$ : 测定树干呼吸速率; $F_R$ : 参比温度下预测树干呼吸速率; $T_R$ : 参比温度 $F$ : Measured stem respiration rate; $F_R$ : Stem respiration rate at reference temperature; $T_R$ : Reference temperature
Damesin et al., 2002 <sup>[24]</sup>	欧洲水青冈林 <i>Fagus sylvatica</i> L. forest	$R = R_{10} Q_{10}^{(T-T_B)/10}$	$R_{10}$ : 基础呼吸速率 $R_{10}$ : Basal respiration rate
Curtis et al., 2005 <sup>[68]</sup>	北部硬木林 Northern hardwood forest	$R_s = \beta_0^{\beta_1 x T_s}$	$\beta_0$ : 基础呼吸速率 $\beta_0$ : Basal respiration rate
Yokota & Hagihara 1998 <sup>[69]</sup>	日本扁柏林 <i>Chamaecyparis obtusa</i> forest	$R = R_0 \exp(K\theta)$	

(Lagged temperature). 树干呼吸速率对于树干温度滞后响应尤为重要, 尤其当不能在白天和夜间同时进行测定. 许多研究<sup>[16, 23, 43, 70]</sup>报道树干呼吸速率对于温度变化的滞后响应. Ekland (1990)<sup>[71]</sup>报道树干内CO<sub>2</sub>浓度比外界空气中高10~30倍. 因此, 如果树干和外界空气中CO<sub>2</sub>浓度产生树干呼吸, 需要树干内CO<sub>2</sub>浓度大幅增加以驱动从树干组织到外界空气的CO<sub>2</sub>扩散作用, 当树干温度升高时, 也需要充裕的时间促使CO<sub>2</sub>扩散<sup>[23]</sup>. 另一个引起树干呼吸速率对温度变化滞后响应的原因是树皮短距离测定树干温度不能代表样本树干的温度, 因为树干温度随树干组织位置而变化(深度和方位角)<sup>[17]</sup>. 另一方面, Negisi (1972, 1979)<sup>[12, 14]</sup>指出, 树干细胞呼出的CO<sub>2</sub>, 一部分进入蒸腾液流并被向上载入到木质部液流而不是穿过树皮向外扩散. 这一结果基于日间树干呼吸降低而夜晚树干呼吸增加的假设. 但是, 也有研究未发现日间呼吸速率抑制现象<sup>[18]</sup>.

温度系数 $Q_{10}$ 可以描述树干呼吸对温度升高的敏感性. 树干呼吸 $Q_{10}$ 值中, 频率分布最集中区域是1.5~2.0, 占42%, 而90%以上测定结果在1.0~3.0之间, 中位数为1.91. 但是, 与活体测定相比, 离体测定树干呼吸显著提高了其 $Q_{10}$ 值<sup>[52]</sup>.

**2.2.2 树干液流** 在一些研究中, 测定的树干CO<sub>2</sub>通量速率和温度间存在很好的相关性<sup>[62, 72]</sup>. 但是, 在其他研究中, 测定的CO<sub>2</sub>通量速率和温度间相关性不明显甚至没有发现. Kaipainen等(1998)<sup>[73]</sup>夏季对欧洲赤松(*Pinus sylvestris*)测定的树干CO<sub>2</sub>通量速率和温度日格局间没有相关. Gansert (2004)<sup>[74]</sup>发现在给定温度下, 与夜晚相比, 白桦树枝CO<sub>2</sub>通量速率日间降低, CO<sub>2</sub>通量速率抑制可能解释是液流的影响. 但是, Edwards & Wullschleger<sup>[55]</sup>(2000)发现, 岩栎(*Quercus prinus*)和美国红枫(*Acer rubrum*)树干CO<sub>2</sub>通量速率不随液流日变化而改变, 他们认为CO<sub>2</sub>通量速率抑制可能是实际呼吸速率抑制的表示.

Saveyn等(2007)首次对山毛榉(*Fagus sylvatica*)和栎树幼树(*Quercus robur* L)研究, 发现休眠季树干CO<sub>2</sub>通量速率与温度无关<sup>[75]</sup>. 与暗周期相比, 树干CO<sub>2</sub>通量速率在光周期显著降低. 山毛榉木质部CO<sub>2</sub>浓度呈现与温度无关的变化. 研究对于温度和树干CO<sub>2</sub>通量速率指数关系不符之处解释为液流或者细胞水分含量降低. 同时, 当光周期和暗周期期间树干蒸腾作用差异不显著时, 细胞水分含量减少不可能明显. 这一研究提供其他树干CO<sub>2</sub>通量速率日间抑制的其他可能解释. 其中之一可能是树干部分或者与树皮相连的皮层光合作用可对释放CO<sub>2</sub>再固定.

### 3 维持呼吸年通量

树干呼吸通常包括生长呼吸(Growth respiration, 也称Synthesis or constructive respiration)和维持呼吸(Maintenance respiration, dormant or basal respiration). 生长呼吸( $R_G$ )包括O<sub>2</sub>消耗和CO<sub>2</sub>产生, 提供能量合成新组织. 维持呼吸( $R_M$ )保持或维持现存活细胞正常生命活动代谢. 其能量用于3个过程: (1) 化合物再合成; (2) 维持离子梯度和代谢物; (3) 参与胁迫环境生理适应过程<sup>[76~77]</sup>.

对树干呼吸作用两部分的区分很重要, 因为 $R_G$ 在一年内

变化很大, 其速率随物候学和控制生长的环境因子而变化. 生长速率随温度增加而增大, 但是单位组织产生的 $R_G$ 不受温度影响<sup>[78]</sup>. 相反,  $R_M$ 主要随温度变化, 但 $R_M$ 也随相对生长速率增加而增大<sup>[5]</sup>. 对于树干呼吸而言, 木本植物生长和维持呼吸的研究在几个生物水平上展开, 包括组织<sup>[22, 43, 47, 63, 79~81]</sup>、个体水平<sup>[82]</sup>、林分水平<sup>[83]</sup>. 在了解树干呼吸机理过程方面, 如何准确计算生长呼吸和维持呼吸是关键.

目前区分和计算生长呼吸和维持呼吸基本上有两种方法: 成熟组织法(Mature tissue method)和阶段生长法(Periodic-growth method). 成熟组织法: 假设树木生长休眠期间的呼吸速率代表维持呼吸且呼吸在相同温度下整个季节内保持不变. 一般以冬季的树干呼吸作为维持呼吸, 这样不同季节测定的呼吸值减去维持呼吸就得到生长呼吸, 需要计算维持呼吸的 $Q_{10}$ 值, 以便计算不同月份温度不同情况下的维持呼吸速率. 阶段生长法: 把呼吸测定值或者经过积分后的总量与生长速率和有关细胞维持的参数进行多元回归处理, 直接区分生长呼吸和维持呼吸.

然而, 目前没有统一的公认的准确方法来进行区分, 有研究对不同方法进行了比较, 不同研究者的研究结果也不尽一致. 因测定方法和年通量估算方法而变异很大, 组织维持呼吸年通量范围是0.12~2.55 Mg Cha<sup>-1</sup> year<sup>-1</sup>, 其所占地面上木质呼吸比例波动范围为22.51%~82.50%(表3).

维持呼吸主要受年均温、年降水量、纬度和林龄的显著影响且影响程度各异(表3, 表4). 维持呼吸与年均温和年降水量显著正相关, 与纬度显著负相关, 这与地上木质组织总呼吸相关而与林龄和纬度显著负相关. 维持呼吸取决于环境和组织化学特性, 随温度增加而增大, 因为蛋白质和膜脂在高温下周转更快. 同时, 维持呼吸与林龄显著负相关, 与维持呼吸随相对生长速率增加而增大有关<sup>[5]</sup>. 随林龄增长, 林分随树木个体大小、总光合作用达到恒定值, 而净生物量生产力降低, 因为呼吸作用增加<sup>[84]</sup>.

本研究结论和Kim等(2007)的研究结果<sup>[19]</sup>略有所差异, 其研究发现林分水平维持呼吸与年均温、叶面积指数正相关, 与林龄和纬度负相关, 而本研究未得出与叶面积指数的相关关系, 林分呼吸值在不同研究中差异很大, 因而种间比较难度较大, 因为气候、林分密度、林龄和尺度上推方法不同<sup>[24]</sup>. 研究结果进一步表明, 木质组织维持呼吸可在林分基础参数(位置参数、气候参数、林龄等)上进行粗略估算, 而与植被类型无关.

## 4 结论与展望

研究树干呼吸这一重要生态系统碳收支过程, 可为评价和预测森林生态系统在全球碳平衡中的作用及在全球变化条件下减少生态系统呼吸的不确定性提供科学依据. 虽然树干呼吸研究已经广泛开展, 但在今后的研究中, 还需要作如下考虑:

### 4.1 研究方法的改进与统一

目前国际上对于树干呼吸组分的区分方法仍无统一标准. 采用方法不同给不同研究的比较带来很大难度, 不利于较大时空尺度上的数据整合和模型预测. 因此, 在今后的研

表3 不同森林生态系统树干维持呼吸年通量比较  
Table 3 Annual stem maintenance respiration of different forest ecosystems

树种 Dominant species	林龄 Stand age (year)	纬度 Latitude (°)	年均温 MAT (°C)	降雨量 Precipitation (mm)	基盖度 BA/ m <sup>2</sup> hm <sup>-2</sup>	叶面积 指数 LAI	维持呼吸 $R_M$ / Mg(C) hm <sup>-1</sup> year <sup>-1</sup>	上推基础 Base	文献 References
海滩松 <i>Pinus contorta</i> ssp. <i>latifolia</i>	40	39	2	740	35.2	12.3	0.61	边材体积 Sapwood volume	[79]
海滩松 <i>Pinus contorta</i> ssp. <i>latifolia</i>	65	39	2	740	40.4	12.1	0.74	边材体积 Sapwood volume	[79]
海滩松 <i>Pinus contorta</i> ssp. <i>latifolia</i>	245	39	2	740	44.7	7.7	0.79	边材体积 Sapwood volume	[79]
日本扁柏 <i>Cobtuse</i>	8	35	15	1543			2.4	干重 Dry weight	[83]
红松 <i>Pinus resinosa</i>	31	46	3	804	42.4	6.2	0.7	边材体积 Sapwood volume	[43]
西部铁杉, 花旗松 <i>Tsuga heterophylla</i> , <i>Pseudotsuga menziesii</i>	39	45	9	1320	67	8.7	1.62	边材体积 Sapwood volume	[43]
南湿地松 <i>Pseudotsuga elliotii</i> var. <i>elliotii</i>	24	29	22	1180	26.1	2.2	1.46	边材体积 Sapwood volume	[43]
白栎, 岩栗, 北美红枫 <i>Quercus alba</i> , <i>Quercus prinus</i> , <i>Acer rubrum</i>	75	35	13.3	1400	21.5	5	0.97	边材体积 Sapwood volume	[53]
黑云杉 <i>Picea mariana</i>	150	55		542	32	4.9	0.57	表面积 Surface area	[65]
北美短叶松 <i>Pinus banksiana</i>	63	55		542	17	2.2	0.12	表面积 Surface area	[65]
欧洲山杨 <i>Populus tremuloides</i>	53	55		542	34	2.2	0.42	表面积 Surface area	[65]
黑云杉 <i>Picea mariana</i>	115	53		390	36	5.6	0.48	表面积 Surface area	[65]
北美短叶松 <i>Pinus banksiana</i>	63	53		390	13	2.5	0.17	表面积 Surface area	[65]
欧洲山杨 <i>Populus tremuloides</i>	68	55		390	27	3.3	0.68	表面积 Surface area	[65]
北美短叶松 <i>Pinus banksiana</i>	14	53		390	9.1	2.8	0.21	表面积 Surface area	[65]
欧洲水青冈 <i>Fagus sylvatica</i>	30	48	9.2	820	17.5	5.6	1.54	体积 Volume	[24]
欧洲水青冈 <i>Fagus sylvatica</i>	30	48	9.2	820	17.5	5.6	1.82	表面积 Surface area	[24]
梧桐科, 榆科, 豆科 Sterculiaceae, Ulmaceae, Legumin- oseae		3	25	1520		4.4	2.09	表面积, 体积 Surface area, volume	[64]
赤松 <i>Pinus densiflora</i>	40	34	13.5	1494	29.54		2.55	体积 Volume	[19]
赤松 <i>Pinus densiflora</i>	40	34	13.5	1494	29.54		1.72	表面积 Surface area	[19]

表4 地上木质组织维持呼吸年通量与影响因素间回归方程  
Table 4 Regression models of above-ground woody tissue annual maintenance respiration and influencing factors

影响因素 Influencing factor	回归方程 Regression model	决定系数 $R^2$	样本量 N	P
林龄 Forest age	$Y = -0.0103X + 1.523$	0.201	25	0.025
纬度 Latitude	$Y = -0.039X + 2.793$	0.528	27	<0.0001
年均温 MAT	$Y = 0.070X + 0.686$	0.583	20	<0.0001
年降水量 Precipitation	$Y = 0.002X - 0.188$	0.628	27	<0.0001

究中, 至少在某一特定区域内, 应该采用统一的区分方法标准, 保证大尺度研究的精度。

#### 4.2 观测数据需进一步补充

很多研究<sup>[19, 21, 24, 34, 35, 48, 51, 61]</sup>只提供了一个生长季的数据, 不能得出树干呼吸的年际变化规律。如果用目前的观测数据来进行区域预测存在着精度问题, 尤其是对于树干呼吸及其组分年通量的估算, 缺乏冬季呼吸数据, 这一部分在计算年通量时因其持续时间长不可忽略。

多数研究<sup>[16, 23, 24, 34, 35, 48]</sup>都只探讨了树干呼吸的季节变化, 需要进一步增加空间变异规律和引发原因的探索, 以便对不同森林生态系统的空间变异现象进行更精确的探讨。很多研究<sup>[26, 32, 33, 46, 75]</sup>仅仅针对树干本身, 而地上木质组织呼吸作用还包括树枝、小枝和幼嫩茎干部分, 这些是不可忽略的重要组成部分。

#### 4.3 树干呼吸尺度上推的研究

目前对于树干呼吸及其组分的尺度上推存在很多问题, 目前仍无统一标准。需要开展大量比较研究, 挑选出最佳尺度上推单位、中间转换变量和上推方法, 这样才能便于不同生态系统类型间比较, 尤其是加强阔叶树种的研究。

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