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模拟增温对黄河三角洲滨海湿地非生长季土壤呼吸的影响

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摘　要　冬季土壤呼吸能释放生长季所固存的碳, 因而在陆地碳循环中占有重要地位。随着全球气候变暖, 平均地表温度将升高0.3–4.8 ℃, 且冬季增温更加明显, 而温度的升高会促进更多CO_2的释放。另外, 滨海湿地地下水位浅, 淡咸水交互作用明显, 增温能引起土壤表层盐分升高, 从而影响土壤呼吸。该研究以黄河三角洲滨海湿地为研究对象, 采用红外辐射加热器模拟增温, 研究了该地区非生长季土壤呼吸的日动态及季节动态, 同时探讨了土壤呼吸对环境因子的响应机制。结果显示: 日动态中, 增温与对照的土壤呼吸速率变化趋势一致, 为单峰曲线; 在平均日变化中, 整个非生长季不同处理的土壤呼吸速率无显著差异, 而土壤温度和土壤盐分均为增温大于对照, 并且土壤呼吸峰值时间均比土壤温度提前。季节动态中, 整个研究期分为非盐分限制阶段(2014年11月–2015年2月中旬)和盐分限制阶段(2015年2月中旬–2015年4月)。在整个非生长季, 土壤呼吸速率无显著差异; 在非盐分限制阶段, 当10 cm土壤温度升高4.0 ℃时, 土壤呼吸速率显著提高22.9%, 而土壤呼吸温度敏感性系数(Q_{10})与对照相比有所降低; 在盐分限制阶段, 尽管土壤温度升高3.3 ℃, 土壤呼吸速率却降低了20.7%, 这可能是由于增温引起了土壤盐分的升高, 同时由增温引起的土壤含水量的升高在一定程度上也限制了土壤呼吸, 而此阶段增温对Q_{10}无显著影响。因此, 在滨海湿地中, 增温除了直接影响土壤温度, 还可通过影响土壤水盐状况来影响土壤呼吸, 进而影响滨海湿地土壤碳库。

关键词　增温; 土壤呼吸; 非生长季; 土壤盐分含量; 滨海湿地; 黄河三角洲

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Effects of elevated temperature on soil respiration in a coastal wetland during the non-growing season in the Yellow River Delta, China

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Abstract

Aims　Winter soil respiration plays a crucial role in terrestrial carbon cycle, which could lose carbon gained in the growing season. With global warming, the average near-surface air temperatures will rise by 0.3 to 4.8 °C. Winter is expected to be warmer obviously than other seasons. Thus, the elevated temperature can significantly affect soil respiration. The coastal wetland has shallow underground water level and is affected by the fresh water and salt water. Elevated temperature can cause the increase of soil salinity, and as a result high salinity can limit soil respiration. Our objectives were to determine the diurnal and seasonal dynamics of soil respiration in a coastal wetland during the non-growing season, and to explore the responses of soil respiration to environmental factors, especially soil temperature and salinity.

Methods　A manipulative warming experiment was conducted in a costal wetland in the Yellow River Delta using the infrared heaters. A complete random block design with two treatments, including control and warming, and each treatment was replicated each treatment four times. Soil respiration was measured twice a month during

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the non-growing season by a LI-8100 soil CO_2 efflux system. The measurements were taken every 2 h for 24 h at clear days. During each soil respiration measurement, soil environmental parameters were determined simultaneously, including soil temperature, moisture and salinity.

Important findings The diurnal variation of soil respiration in the warming plots was closely coupled with that in the control plots, and both exhibited single-peak curves. The daily soil respiration in the warming was higher than that in the control from November 2014 to January 2015. Contrarily, from March to April 2015. During the non-growing seasons, there were no significant differences in the daily mean soil respiration between the two treatments. However, soil temperature and soil salt content in the warming plots were significantly higher than those in the control plots. The non-growing season was divided into the no salt restriction period (November 2014 to middle February 2015) and salt restriction period (middle February 2015 to April 2015). During non-growing season, soil respiration in the warming had no significant difference compared with that in control. During the no salt restriction period, soil respiration in the warming was 22.9% ($p < 0.01$) greater than the control when soil temperature at 10 cm depth in warming was elevated by 4.0 °C compared with that in control. However, experimental warming decreased temperature sensitivity of soil respiration (Q_{10}). During salt restriction period, soil warming decreased soil respiration by 20.7% compared with the control although with higher temperature (3.3 °C), which may be attributed to the increased soil salt content (Soil electric conductivity increased from 4.4 $ds \cdot m^{-1}$ to 5.3 $ds \cdot m^{-1}$). The high water content can limit soil respiration in some extent. In addition, the Q_{10} value in the warming had no significant difference compared with that in control during this period. Therefore, soil warming can not only increase soil respiration by elevating soil temperature, but also decrease soil respiration by increasing soil salt content due to evaporation, which consequently regulating the soil carbon balance of coastal wetlands.

Key words elevated temperature; soil respiration; non-growing season; soil salt content; coastal wetland; Yellow River Delta

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土壤呼吸作为陆地生态系统碳循环的重要环节(Raich & Schlesinger, 1992), 是陆地生态系统碳释放的主要途径, 可达总释放量的2/3 (Davidson *et al*., 2006)。全球气候变暖会促进土壤呼吸(Fang & Moncrieff, 2001; Fouche *et al*., 2014), 进而使大气CO_2浓度增加, 在陆地生态系统和大气之间产生一个强烈的正反馈作用(Cox *et al*., 2000; Davidson *et al*., 2000), 使全球变暖的情况更趋严重(Peterjohn *et al*., 1994; Carney *et al*., 2007)。模拟研究表明, 2016–2035年全球平均地表温度将升高0.3–0.7 ℃, 2018–2100年将升高0.3–4.8 ℃ (IPCC, 2013)。在全球尺度上, 冬季和春季增温速度较快, 而夏季和秋季的增温速率明显低于冬季和春季以及年平均增温速率(Nagato & Tanakab, 2012)。北半球高纬度和高海拔地区温度升幅更大, 而且冬季被认为是增温幅度最大的季节(IPCC, 2013)。近50年中, 中国年、季的全国平均气温均表现出显著增高趋势, 而冬季和春季地表增温最为显著, 其中冬季增幅最大, 为0.03 $℃ \cdot a^{-1}$ (蔡福等, 2006)。因此, 研究增温特别是冬季增温对土壤呼吸的影响对正确评估全球变化背景下的陆地生态系统碳循环具有重要意义。

野外自然条件下的增温实验是研究全球变化重要的信息来源(徐振峰等, 2010), 是研究全球变暖与陆地生态系统相互关系的一个主要方法(牛书丽等, 2007; Hoeppner & Dukes, 2012; Hou *et al*., 2013), 不仅能够获取气候变暖对生态系统影响的直接证据, 还可以解释陆地生态系统对气候变化响应的内在机制(Hou *et al*., 2013)。目前, 有关全球变暖对陆地生态系统影响的增温装置主要有被动增温和主动增温两类。其中, 红外辐射器能更真实有效地模拟全球变暖, 对土壤无物理干扰, 也不改变小气候状况, 是现有的模拟增温的理想装置, 近年来被广泛应用于森林、草地、苔原等生态系统(牛书丽等, 2007)。增温影响微生物或根系的代谢活性从而提高了土壤呼吸速率(Saleska *et al*., 1999; Berger *et al*., 2004), 大多数研究表明增温明显促进了土壤呼吸(Lin *et al*., 2001; Wan *et al*., 2007; Zhou *et al*., 2007; Xia *et al*., 2009; Wang *et al*., 2014)。然而, 也有研究表明随着

温度的升高, 土壤呼吸速率出现降低的趋势(Pajari, 1995; Saleska *et al*., 1999; Melillo *et al*., 2002; Yin *et al*., 2013)或不变(Wan *et al*., 2007), 这可能是因为土壤有限的活性碳库(Oechel *et al*., 2000; Giardina & Ryan, 2000; Rustad *et al*., 2001; Melillo *et al*., 2002; Eliasson *et al*., 2005)和土壤呼吸温度适应性的存在(Luo *et al*., 2001)。

湿地生态系统在全球碳收支平衡中扮演着重要角色(Huntingford *et al*., 2009)。一方面, 湿地具有较高的初级生产力, 因而具有较强的固碳能力(Gorham, 1991)。另一方面, 全球变暖背景下, 温度升高促进土壤有机碳分解, 可能会使湿地碳库由碳汇变为碳源(孔雨光等, 2009)。然而, 与其他生态系统类型相比, 增温对湿地生态系统土壤呼吸的研究相对较少。同时, 目前土壤呼吸测定大多集中在生长季, 对年土壤呼吸量的估算大多基于非生长季土壤呼吸为0的假设(Grogan & Jonasson, 2006)。然而已有研究表明土壤呼吸是全年性的过程, 非生长季土壤呼吸不仅不为0, 而且能占到年土壤呼吸总量的14%–30% (Jones, 1999), 同时冬季会释放生长季固存碳的50%甚至更多(Oechel *et al*., 2000; Brooks *et al*., 2004; Monson, 2005), 是区域碳收支非常重要的组成部分(Wickland *et al*., 2001; Schimel *et al*., 2006; Han *et al*., 2012), 能够显著地影响生态系统的碳平衡(Hubbard *et al*., 2005; Wang *et al*., 2014)。因此, 研究模拟增温对非生长季土壤呼吸很有必要。同时, 湿地生态系统典型样地一般都分布在偏远地区, 且非生长季观测期间易受雪霜以及低温条件的限制, 环境条件恶劣, 因此相关的研究开展得并不多, 是湿地生态系统碳通量研究的薄弱环节。

滨海湿地作为湿地生态系统的重要类型, 其地下水位浅且受淡咸水交互作用(Fan *et al*., 2011; Zhong & Du, 2013), 温度升高增强土壤水分蒸发, 带动浅层地下水可溶性盐向地表输送(Yao & Yang, 2010; Zhang *et al*., 2011), 从而引起土壤表层盐分的变化, 而盐分的升高会影响土壤呼吸(Wichern *et al*., 2006; Yang *et al*., 2009; Setia *et al*., 2011), 然而关于温度、盐分是如何影响滨海湿地土壤呼吸的, 目前还没有明确结论。因此本研究选取黄河三角洲滨海湿地为研究对象, 采用红外辐射加热器模拟土壤增温, 对非生长季(2014年11月–2015年4月)的土壤呼吸速率、土壤温湿度和土壤盐分等进行监测。分析增温对非生长季土壤呼吸日变化及季节变化的影响, 并探讨土壤呼吸对土壤温度、盐分变化的响应机制, 可为了解未来气候变暖对土壤碳循环的影响规律提供基础数据和理论依据。

1　材料和方法

1.1　试验地概况

研究区位于山东省东营市的中国科学院黄河三角洲滨海湿地生态试验站(37.76° N, 118.99° E)。该研究区属于温带半湿润大陆性季风气候, 阳光充足, 四季分明, 雨热同期。年平均气温为12.9 ℃, 最高气温41.9 ℃, 最低气温–23.3 ℃, 年降水量为550–640 mm (Han *et al*., 2014), 70%降水集中于5–9月, 降水量的季节和年际变化较大, 年蒸发量为1 962 mm (Han *et al*., 2013)。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(Nie *et al*., 2009)。主要的植被为芦苇(*Phragmites australis*)、盐地碱蓬(*Suaeda salsa*)、柽柳(*Tamarix chinensis*)和白茅(*Imperata cylindrical* var. *major*)。

1.2　实验设计

试验采用随机区组设计, 设置增温和对照2个处理, 每个处理设置4个重复, 每个重复的小区面积为3 m × 4 m, 区间距为3 m。样方面积2 m × 3 m, 小区与样方之间预留0.5 m的缓冲区。采用MRM-2420型红外辐射器(Kalglo Electronics, Bethlehem, USA)对试验小区进行模拟增温, 此装置的红外能量与太阳能量性质相同, 但是不包含紫外线。加热和不加热小区随机分布, 红外线辐射加热灯(长160 cm, 宽15 cm)额定功率为100 $W \cdot m^{-2}$, 非生长季对4支加热灯进行24 h持续供电(220 V)。每个加热管均通过供电发热, 各自具有独立的电源控制开关, 并由漏电保护总开关控制其开启和关闭。红外线辐射加热灯的长边方向为南北方向, 架设在每个小区东西方向的中间处, 加热灯距地面的高度为1.75 m, 加热仪顶部架设倒V字形的反光设备, 避免小区边缘因距离加热仪较远而导致地面受热不均。在非增温样地的中央正上方, 悬挂一个与加热灯大小和形状完全一致的“假灯”, 以去除加热灯对地表的遮阴作用。

1.3　土壤呼吸及环境因子测定

采用便携式土壤呼吸分析仪((LI-8100, LI-COR, Lincoln, USA)测定土壤呼吸速率。实验开始前期,

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在每个小区平坦的中心位置永久设置1个聚氯乙烯(PVC)土壤呼吸环。土壤呼吸环一端削薄，埋入土中，露出地面2–3 cm，并尽可能不扰动地表的凋落物。安装完毕，待受扰动的土壤稳定后开始测量。整个测量时期(2014年11月–2015年4月)，测量频率为每2周一次，每次测定时段为7:00到第二天7:00，每隔2 h测定一次。10 cm土壤温度、湿度、盐度采用5TE传感器(Decagon, Washington, USA)进行测量，数据采集使用Em50 (Decagon, Washington, USA)，数据采集频率为每30 min一次。

1.4 数据分析

采用单因素方差分析和最小显著差异法检验土壤呼吸、10 cm土壤温度、湿度、盐度的日变化及季节变化。所有统计分析用SPSS 17.0统计软件完成，置信区间为95%，显著性水平$\alpha = 0.05$。所有的图均在SigmaPlot 10.0中完成。

土壤呼吸速率与土壤温度进行指数回归，采用指数模型：

$$y = ae^{bt} \tag{1}$$

式中：y为土壤呼吸；a为温度为0 ℃时的土壤呼吸；b为温度反应系数；t为温度。

Q_{10}值通过下式确定：

$$Q_{10} = e^{10b} \tag{2}$$

b为温度反应系数。

2 研究结果

2.1 增温对土壤呼吸和环境要素日变化的影响

不同处理下土壤呼吸日动态变化趋势一致，均表现出单峰曲线形式，且白天土壤呼吸速率变化大，夜间变化小(图1)，整个测量时间内(2014年11月–2015年4月)，早上开始迅速上升，到中午以后迅速下降，在夜晚变化较为稳定。增温处理的最大值和最小值范围分别为0.34–1.68 $\mu mol \cdot m^{-2} \cdot s^{-1}$和0.09–0.59 $\mu mol \cdot m^{-2} \cdot s^{-1}$；对照的最大值和最小值范围分别为0.22–1.94 $\mu mol \cdot m^{-2} \cdot s^{-1}$和0.08–0.90 $\mu mol \cdot m^{-2} \cdot s^{-1}$。

比较增温处理与对照发现，在不同测量日期，土壤呼吸速率在测定的各个时间段有差异。2014年11月到2015年1月底，土壤呼吸基本表现为增温处理大于对照；2015年2月则表现为白天增温样地的土壤呼吸大于对照，夜晚则相反；之后，从2015年3月到2015年4月基本表现为对照大于增温处理。增温处理和对照出现峰值的时间也存在差异。在12次日动态中，增温处理与对照峰值时间一致的有5次，滞后的也有5次，而在2014年12月有2次增温处理比对照提前。

对上述12次测得的日变化数据求取平均值得到图2。一昼夜内，增温和对照处理的土壤呼吸速率均表现为单峰曲线。土壤呼吸的最大值均出现在13:00 (增温0.75 $\mu mol \cdot m^{-2} \cdot s^{-1}$，对照0.73 $\mu mol \cdot m^{-2} \cdot s^{-1}$)；最小值均出现在1:00 (增温0.28 $\mu mol \cdot m^{-2} \cdot s^{-1}$，对照0.29 $\mu mol \cdot m^{-2} \cdot s^{-1}$)(图2A)。土壤呼吸速率的变化与10 cm土壤温度的变化趋势一致，但是其峰值时间(11:00)较土壤温度的峰值时间(17:00)提前。10 cm土壤温度增温(9.2 ℃)显著高于对照(6.1 ℃)，而土壤呼吸速率却无显著差异($p = 0.123$)，这可能是由于增温使土壤盐分升高(土壤电导率由4.4 $ds \cdot m^{-1}$升高到5.3 $ds \cdot m^{-1}$)，从而影响了土壤呼吸对土壤温度升高的响应(图2)。

2.2 增温对土壤呼吸和环境要素季节变化的影响

整个非生长季，土壤呼吸的季节变化趋势与10 cm土壤温度的变化趋势相一致。在2015年1月达到最小值(增温处理0.20 $\mu mol \cdot m^{-2} \cdot s^{-1}$，对照0.13 $\mu mol \cdot m^{-2} \cdot s^{-1}$)，之后升高，在4月底达到最高(增温0.94 $\mu mol \cdot m^{-2} \cdot s^{-1}$，对照1.21 $\mu mol \cdot m^{-2} \cdot s^{-1}$)。整个非生长季，土壤温度始终为增温处理高于对照，而土壤呼吸速率在2015年2月中旬以前为增温处理高于对照，之后则相反，这与土壤水分、盐分出现大幅度升高的时间点相一致。因此，可以将整个非生长季划分为两个阶段：非盐分限制阶段，从2014年11月初到2015年2月中旬；盐分限制阶段，从2015年2月中旬到2015年4月底(图3)。

利用单因素重复测量方差分析，得到图4。在整个生长季，土壤呼吸速率无显著差异($p = 0.077$)。在非盐分限制阶段，增温处理的土壤呼吸速率比对照显著提高了22.9% ($p < 0.01$)，而此阶段的10 cm土壤含水量(增温48.0%，对照45.5%)和土壤盐分(土壤电导率增温4.7 $ds \cdot m^{-1}$，对照4.5 $ds \cdot m^{-1}$)均无显著差异($p = 0.099$, $p = 0.556$)，而10 cm土壤温度为增温处理显著高于对照($p < 0.005$)(图4)。因此，在这一阶段，10 cm土壤温度是影响土壤呼吸速率的主要因子。在盐分限制阶段，土壤盐分增温显著高于对照($p < 0.05$)，尽管10 cm土壤温度依旧为增温显著大于对照(增温比对照高3.3 ℃，$p < 0.05$)，但是增温处理的土壤呼吸速率(0.49 $\mu mol \cdot m^{-2} \cdot s^{-1}$)显著降低了20.7% ($p =$

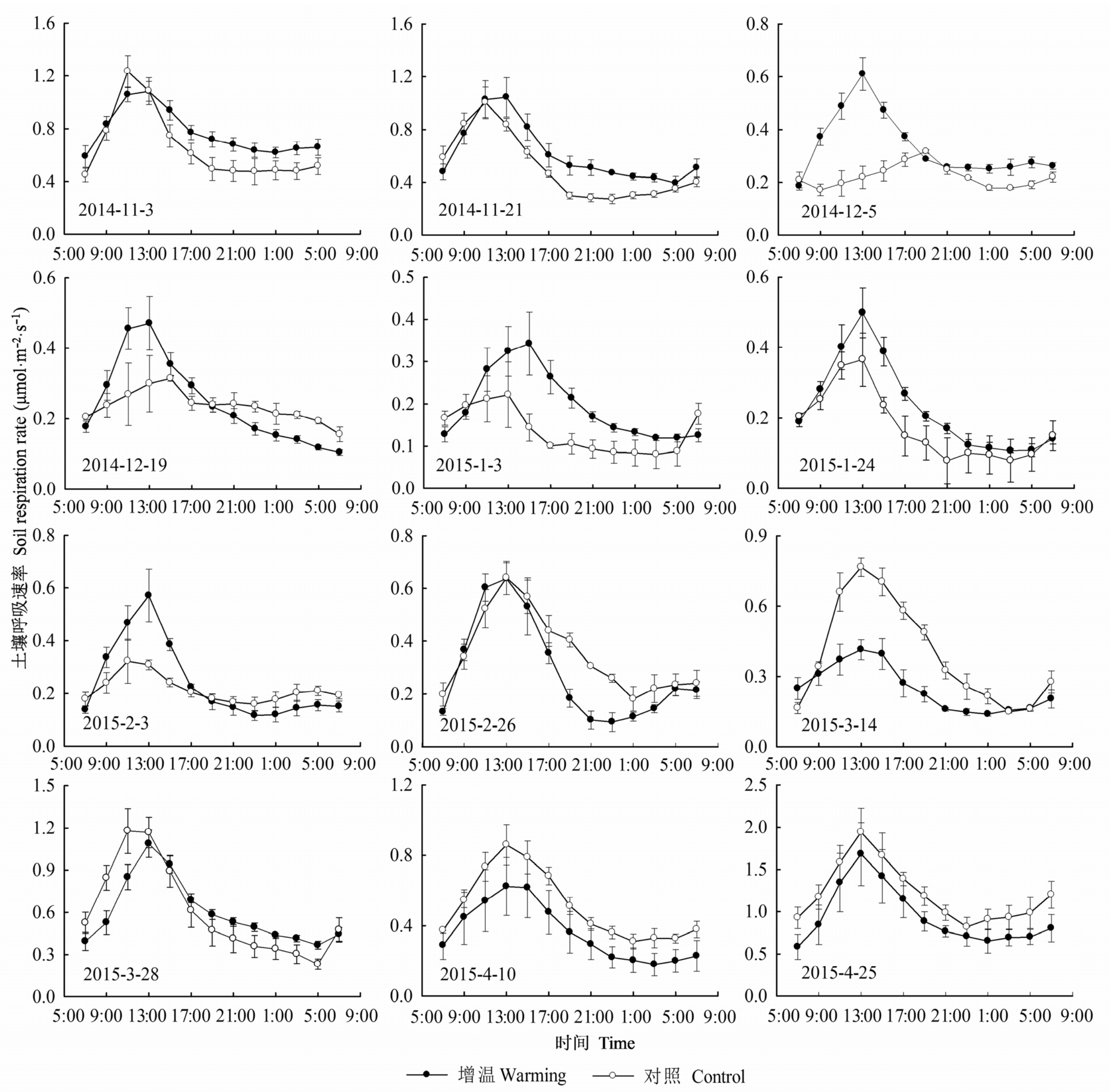

图1　增温和对照处理下土壤呼吸速率日动态(平均值±标准误差)。

Fig. 1　Diurnal variation of soil respiration rate under warming and control treatments (mean ± *SE*).

0.046)(图4)。在这一阶段, 土壤含盐量提高的同时也伴随着土壤含水量的显著增加, 与干旱生态系统不同, 在这个生态系统中平均土壤含水量都在40%以上, 水分并不是一个限制因子, 相反可能会在一定程度上对土壤呼吸产生抑制作用, 因此这一阶段影响土壤呼吸速率的主要因子为土壤盐分, 但是土壤含水量在一定程度上限制了土壤呼吸。

因此, 非盐分限制阶段, 增温处理和对照处理土壤盐分均较低, 且无显著差异($p > 0.05$), 土壤温度是土壤呼吸的主要控制因素, 因此增温处理下的土壤呼吸速率显著高于对照($p < 0.05$)。而在盐分限制阶段, 由于增温样地蒸发增强, 使得地下水向上运输, 从而使其土壤盐分和土壤水分含量显著增高($p < 0.05$)。此时, 土壤盐分是限制土壤呼吸速率的主要因子, 而高的土壤水分含量也在一定程度上降低了土壤呼吸速率使得增温处理显著低于对照($p < 0.05$)。

2.3　增温处理对土壤呼吸温度敏感性的影响

对每次测量的土壤呼吸速率与10 cm土壤温度进行指数回归分析(表1), 结果表明: 增温处理和对

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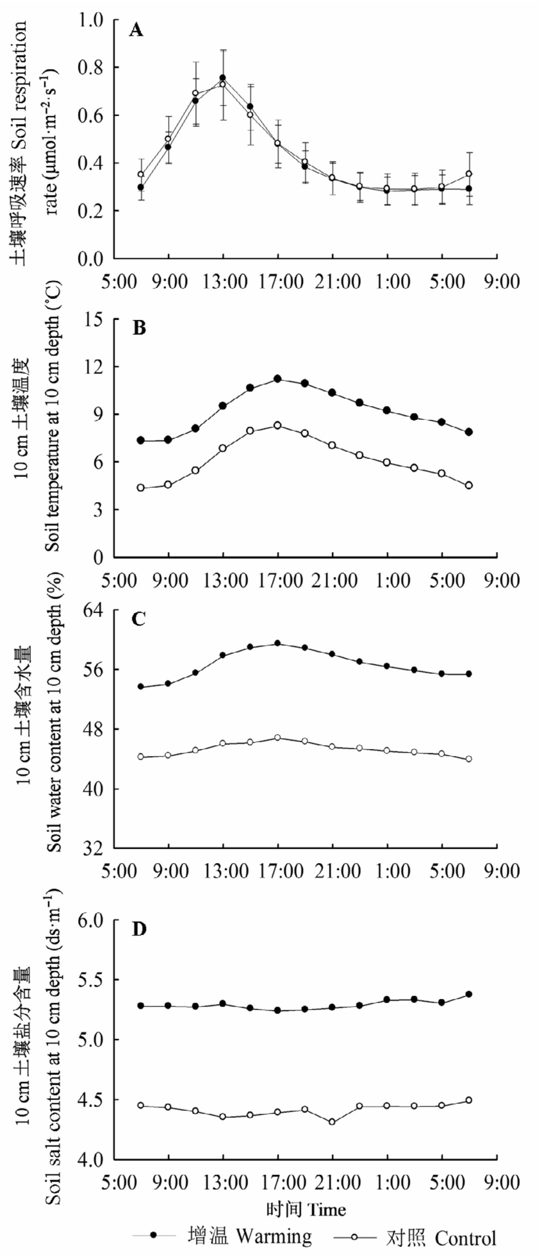

图2 增温和对照处理土壤呼吸速率(**A**)、10 cm土壤温度(**B**)、土壤水分含量(**C**)、土壤电导率(**D**)的日动态(平均值±标准误差)。

Fig. 2 Average diurnal variation of soil respiration rate (**A**), soil temperature (**B**), soil water content (**C**), and soil salt content (**D**) at 10 cm depth under warming and control treatments (mean ± *SE*).

照下的土壤呼吸速率与10 cm土壤温度都呈显著的指数相关关系。在非盐分限制下，Q_{10}值基本表现为增温处理小于对照，说明增温处理降低了土壤呼吸速率的温度敏感性。而在盐分限制下，增温处理和对照处理的Q_{10}分别为1.07–1.23和1.08–1.23，无显著差异，说明在此阶段，增温处理对土壤呼吸温度敏感性无影响。

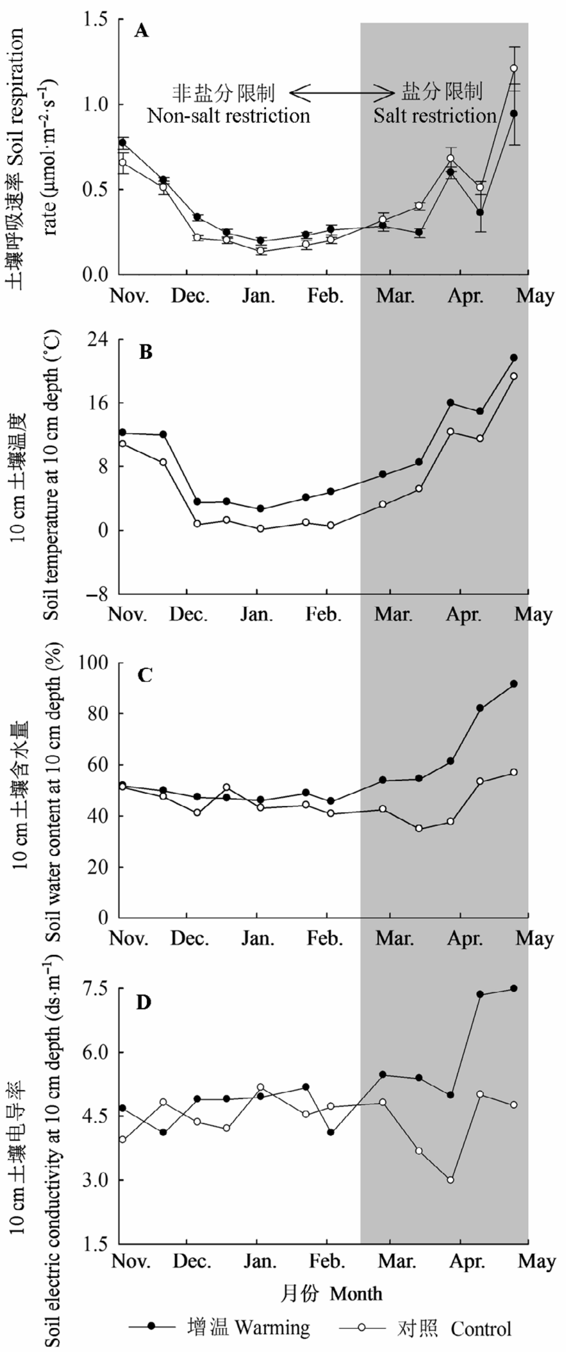

图3 增温和对照处理下土壤呼吸速率(**A**)、10 cm土壤温度(**B**)、土壤水分含量(**C**)、土壤电导率(**D**)的季节动态(白色区域表示非盐分限制阶段，灰色区域表示盐分限制阶段)。

Fig. 3 Seasonal variation of soil respiration rate (**A**), soil temperature (**B**), soil water content (**C**), and soil electric conductivity (**D**) at 10 cm depth under warming and control treatments (White expresses non-salt restriction period, gray expresses salt restriction period).

3 讨论

3.1 增温处理对非生长季土壤呼吸速率的影响

本研究发现，在非盐分限制阶段，黄河三角洲

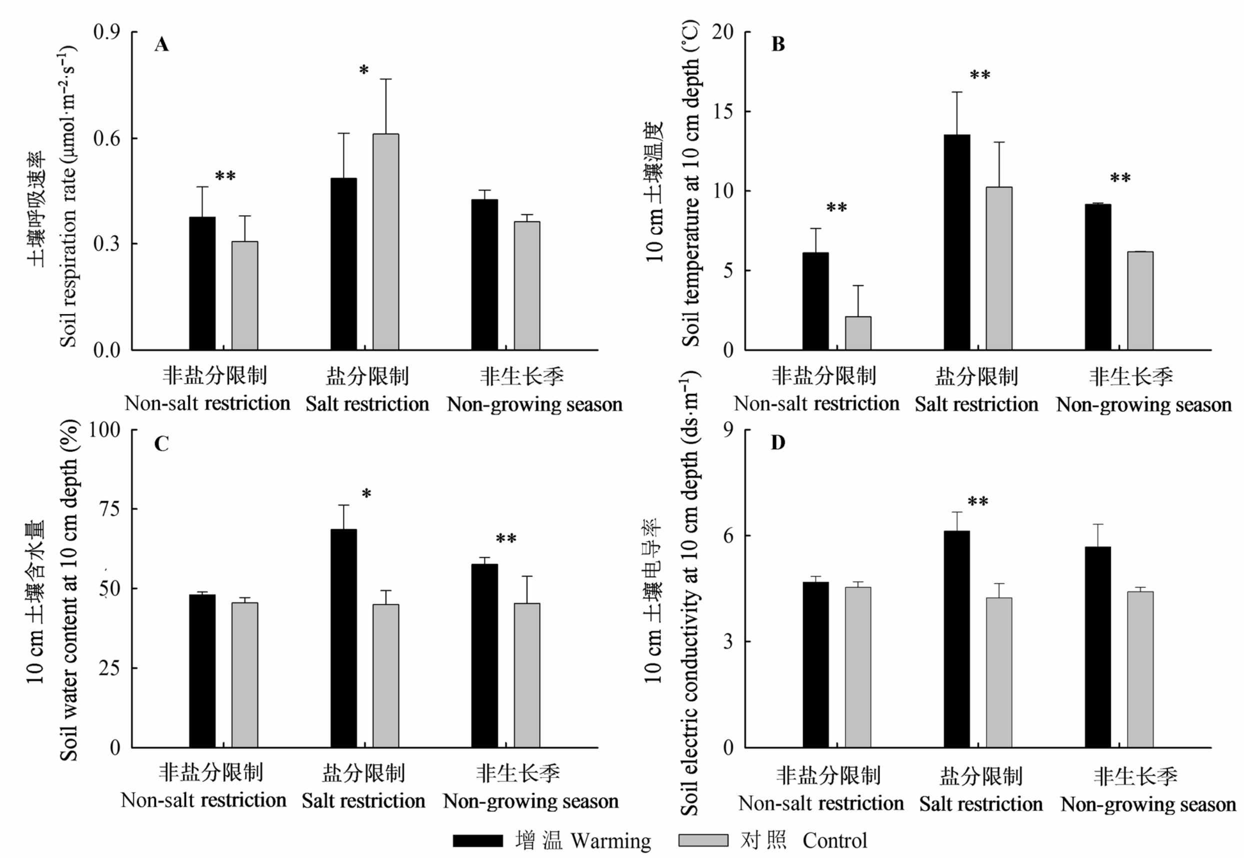

图4 增温对非盐分限制阶段、盐分限制阶段和整个非生长季土壤呼吸速率(**A**)、10 cm土壤温度(**B**)、土壤含水量(**C**)、土壤电导率(**D**)的影响(平均值±标准误差)。*, $p < 0.05$; **, $p < 0.01$。

Fig. 4 Soil respiration rate (**A**), soil temperature (**B**), soil water content (**C**), and soil electric conductivity (**D**) at 10 cm depth of non-salt restriction period, salt restriction period and non-growing season under warming and control treatments (mean ± *SE*).

表1 不同日期土壤呼吸速率与土壤温度间关系模型$SR = a \times \exp(b \times t)$的参数及$Q_{10}$值

Table 1 Parameter of relational model ($SR = a \times \exp(b \times t)$) between soil respiration rate and soil temperature and the Q_{10} value on different dates

阶段 Period	日期 Date	*a*		*b*		Q_{10}		R^2		*p*	
		增温 Warming	对照 Control	增温 Warming	对照 Control	增温 Warming	对照 Control	增温 Warming	对照 Control	增温 Warming	对照 Control
非盐分限制阶段 Non-salt restriction period	11-1	0.316	0.117	0.059	0.137	1.06^{*}	1.15	0.79	0.63	<0.01	<0.01
	11-21	0.040	0.151	0.097	0.102	1.10	1.11	0.66	0.63	0.06	0.04
	12-6	0.147	0.082	0.146	0.775	1.16^{**}	2.17^{**}	0.66	0.54	<0.01	<0.01
	12-19	0.044	0.139	0.435	0.674	1.54^{*}	1.96^{*}	0.85	0.74	<0.01	<0.01
	1-3	0.044	0.908	0.453	0.305	1.57	1.36	0.71	0.74	<0.01	0.03
	1-24	0.040	0.138	0.293	0.219	1.34	1.24	0.72	0.74	<0.01	0.02
	2-3	0.074	0.042	0.144	0.122	1.15	1.13	0.71	0.68	<0.01	0.06
盐分限制阶段 Salt restriction period	2-26	0.055	0.094	0.168	0.205	1.18	1.23	0.50	0.52	0.02	0.02
	3-14	0.028	0.102	0.206	0.203	1.23	1.23	0.55	0.66	0.03	0.02
	3-28	0.071	0.045	0.117	0.169	1.12	1.18	0.74	0.95	<0.01	<0.01
	4-10	0.065	0.133	0.106	0.099	1.11	1.10	0.88	0.52	<0.01	<0.01
	4-28	0.176	0.316	0.065	0.062	1.07	1.06	0.75	0.62	<0.01	0.01

Q_{10}, 土壤呼吸温度敏感性。*a*、*b*表示拟合参数。*, $p < 0.05$; **, $p < 0.01$。

Q_{10}, temperature sensitivity of soil respiration. *a*, *b* represents the parameters of model fitting.

芦苇湿地土壤温度升高4.0 ℃, 土壤呼吸速率显著增加22.9% (图3)。这与许多学者的观点相一致。在暖温带锐齿针叶林中, 温度升高1.75 ℃时, 土壤呼吸速率增加23.1% (刘彦春, 2013); 当温度升高6.73 ℃时, 岷江上游华山松(*Pinus armandi*)林冬季土壤呼吸提高31.4% (熊沛等, 2010), 同时在北美高草草

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原的控制加热对比试验中也得到了类似结论(Wan *et al*., 2007; Zhou *et al*., 2007); 并且Wang等(2014)通过Meta分析总结了50个陆地生态系统增温对土壤呼吸速率的影响, 结果是土壤温度平均增加2 ℃, 土壤呼吸速率提高12%。因此, 土壤温度是影响土壤呼吸速率的关键因子(Ruehr & Buchmann, 2010)。

众多学者认为是由于温度升高影响了微生物的代谢活性, 从而提高了土壤呼吸速率(Saleska *et al*., 1999; Berger *et al*., 2004)。冬季植物根系呼吸显著减少, 土壤呼吸主要是微生物的呼吸(Schindlbacher *et al*., 2007; Ruehr & Buchmann, 2010)。增温一方面会增加土壤无机氮库(Luo *et al*., 2001; Rustad *et al*., 2001; Melillo *et al*., 2002), 而无机氮库的增加在一定程度上弥补了冬季活性养分的缺失, 从而促进了微生物的生长; 另一方面, 增温能够提高土壤微生物和酶的活性(Bokhorst *et al*., 2010), 从而提高土壤中CO_2的释放速率。有研究发现, 冬季的土壤呼吸平均能释放掉生态系统在生长季所固存碳的50% (Brooks *et al*., 2004), 在此情况下, 温度的升高将进一步导致土壤向大气排放更多CO_2。因此, 气候变化引起的冬季土壤呼吸速率的升高可能会显著降低高海拔、高纬度生态系统的碳储量(Melillo *et al*., 2002)。

然而, 也有研究表明, 土壤呼吸与增温的关系并没有固定的反应模式, 土壤呼吸速率随着土壤温度的升高也可能会降低(Pajari, 1995; Saleska *et al*., 1999)或者不变(Wan *et al*., 2007)。本研究中, 整个非生长季增温对土壤呼吸速率无显著影响, 并且在盐分限制阶段, 增温使土壤呼吸速率降低(图3)。这与以下研究结果相似: 美国Harvard森林在试验前6年, 温度升高使CO_2通量平均增加了28%, 而在后4年, 温度升高对土壤呼吸的影响明显降低(Melillo *et al*., 2002); 长江口崇明东滩围垦湿地生态系统中, 非生长季温度升高0.66 ℃时, 土壤呼吸速率降低了16% (Zhong & Du, 2013)。

这是由于土壤活性碳库是有限的, 当这部分碳释放消耗后, 增温不再刺激土壤呼吸(Melillo *et al*., 2002); 同时, 随着温度的进一步升高或较高温度持续时间的延长, 呼吸底物的有效性降低(Atkin & Tjoeller, 2003; Bradford *et al*., 2008; Yuste *et al*., 2010), 从而降低了土壤呼吸温度敏感性, 进而减缓土壤呼吸随温度升高而增加的量(Jarvis & Linder, 2000; Giardina & Ryan, 2000; Oechel *et al*., 2000; Luo *et al*., 2001; Rustad *et al*., 2001; Melillo *et al*., 2002; Eliasson *et al*., 2005); 而且, 长期增温可能改变了土壤酶的活性和微生物的种群结构, 从而使土壤呼吸速率降低(Grogan & Jonasson, 2005; Bradford *et al*., 2008; Hartley *et al*., 2008); 此外, 因增温引起的其他生态因子的变化也能引起土壤呼吸速率的降低(陈全胜等, 2003a), 这样导致的结果是潜在地减弱了增温-土壤呼吸-大气CO_2浓度这个环节的正反馈(Luo *et al*., 2001)。

3.2 增温处理对土壤呼吸温度敏感性的影响

本研究中, 在非盐分限制阶段, 增温使得土壤呼吸温度敏感性降低(表1), 这与众多研究的结果相一致。土壤呼吸的温度敏感性随着土壤温度的升高而下降(Janssens & Pilegaard, 2003; Wan *et al*., 2007; Zhou *et al*., 2007; Zhong & Du, 2013)。北美高草草原没有加温的实验点的Q_{10}值显著高于加温的实验点的Q_{10}值(Luo *et al*., 2001; Wan *et al*., 2007; Zhou *et al*., 2007); 当温度升高幅度在1.8–3.1 ℃时, 芬兰东部北方针叶林土壤呼吸温度敏感性降低了2.7%–12.2% (Niinisto *et al*., 2004); 中国长江口崇明岛盐沼湿地非生长季温度升高0.2 ℃, 土壤呼吸温度敏感性降低13.2% (Zhong & Du, 2013)。

增温降低土壤呼吸温度敏感性有以下几个原因。首先, 增温造成土壤碳库中活性碳的快速耗竭, 从而使得土壤呼吸对温度变化不再敏感(Kirschbaum, 1995; Giardina & Ryan, 2000); 其次, 增温促使土壤活性碳库向钝性或缓性(保护性)碳库转移(Hartley & Ineson, 2008), 这样土壤微生物可利用的活性碳源减少, 进而导致土壤呼吸的温度敏感性降低; 再次, 在温度较高时, 对土壤呼吸有贡献的微生物的数量达到一定程度(Janssens & Pilegaard, 2003), 温度变化对其难以产生影响。

另外, 在盐分限制阶段, 增温对土壤呼吸温度敏感性无显著影响。本研究中, 从2015年2月中旬以后, 影响土壤呼吸速率的主导因子发生变化, 进入了以盐分为主导因子的盐分限制阶段(图3; 表1)。土壤呼吸底物主要来源于土壤有机质和植物分泌物及残留物(Konnerup *et al*., 2014), 盐分输入增加了土壤中可溶性有机碳的可利用性(Liu & Lee, 2007), 从而提高了底物的有效性, 而底物有效性越高, 土壤呼吸温度敏感性越低(Atkin & Tjoelker, 2003; Bradford *et al*., 2008; Yuste *et al*., 2010), 而温度的

升高降低土壤呼吸温度敏感性。两者共同作用下可能会使Q_{10}值无明显变化。

3.3 土壤盐分含量对土壤呼吸的影响

增温不仅能直接影响土壤呼吸, 也能通过影响土壤盐分进而影响土壤呼吸。黄河三角洲滨海湿地咸淡水交互作用明显, 且地下水位浅(Fan *et al*., 2011; Zhong & Du, 2013), 当土壤温度升高时, 土壤水分的蒸发加速, 从而促进了地下咸水向土壤表面的输送(Wichern *et al*., 2006; Setia *et al*., 2011), 导致的结果是土壤表层盐分含量高。因此, 盐度也可能是影响滨海湿地CO_2产生与排放的重要环境因子(仝川等, 2011)。本研究中, 在盐分限制阶段, 增温处理下土壤盐分抑制了滨海湿地土壤呼吸速率(图3)。很多研究表明, 随着土壤含盐量的增加, 土壤呼吸速率呈现下降的趋势(Setia *et al*., 2010; Wong *et al*., 2010; Hugler & Sievert, 2011; Yan *et al*., 2013)。例如, 海水入侵淡水潮汐沼泽时, 高盐度水平下土壤CO_2产生速率随着盐度的升高而减小(Marton *et al*., 2012); 长江口滩涂土壤呼吸呈现出近岸水体年平均盐度越高, 土壤呼吸速率越低的趋势, 即距海越近土壤呼吸速率越小(聂明华等, 2011); 珠江三角地区近陆红树林湿地CO_2排放通量显著高于近海红树林湿地, 这可能是由土壤盐分的差异性引起的(Chen *et al*., 2010); 当土壤盐分含量比对照高出4倍时, 南澳大利亚莫纳托湿地土壤呼吸速率降低20% (Hasbullah & Petra, 2015)。另外, 盐分还可能导致土壤碳源、汇的转化, 例如美国Nueces三角洲湿地在土壤含水量较高、土壤盐度较低的情况下表现为吸收CO_2, 而在土壤含水量较低、土壤盐度较高的情况下则表现为排放CO_2 (Heinsch *et al*., 2004)。

盐分影响着微生物异养呼吸作用, 从而改变土壤呼吸速率。一方面, 盐分抑制土壤微生物活性, 使得土壤呼吸随盐度的升高而降低(Wichern *et al*., 2006; Wong *et al*., 2008; Iwai *et al*., 2012; 李凤霞等, 2012); 同时, 高的含盐量会降低微生物数量(Garcia & Hernandez, 1996; Pattnaik *et al*., 2000; Pivnickova *et al*., 2010; Kiehn *et al*., 2013)以及微生物群落的多样性(Baldwin *et al*., 2006); 并且, 高盐度能使微生物生理形态发生明显变化, 从而使其分解有机质的能力受到强烈影响(Thottathil *et al*., 2008), 微生物受到盐分的影响时, 一般能通过自身的渗透压调节机制来平衡细胞内的渗透压, 而在高的渗透压条件下, 微生物耗氧速率增加, 但耗氧速率的增加不是为了有机物的降解, 而是为了能够抵御高盐环境对微生物所产生的伤害(Pankhurst *et al*., 2001; Rietz & Haynes, 2003; 崔有为等, 2004; Thottathil *et al*., 2008)。另一方面, 多数土壤水解酶与氧化还原酶类活性均随盐渍化的水平升高而明显下降(Rietz & Haynes, 2003; 张建锋等, 2005), 低盐分对酶的活性有促进作用, 而高盐分条件下其活性反而下降(Yan *et al*., 2013)。

3.4 土壤水分含量对土壤呼吸的影响

土壤水分含量也是影响土壤呼吸的因子, 而影响土壤水分变化的因素有很多, 包括气温、降水、土壤质地以及地下水供应等(马柱国等, 2000)。本研究中, 在盐分限制阶段, 增温引起土壤含盐量提高的同时也伴随着土壤含水量的显著增加, 这与苔原生态系统的研究结果相一致: 土壤温度增加1.73 ℃时, 土壤水分含量增加了9.0% (Wang *et al*., 2014)。与以往大多数研究结果相反。这主要是由黄河三角洲滨海湿地的特点决定的。土壤水分来源一方面是大气降水, 另一方面是地下水补给。在非生长季, 大气降水少, 温度的升高加速了土壤水分蒸发, 而蒸发是地下水向上移动的驱动力; 此外, 由于冬季温度低, 土壤易冻, 增温能够加速解冻, 从而使其土壤水分含量高于对照。与干旱生态系统不同, 在本研究生态系统中平均土壤含水量都在40%以上, 水分并不是一个限制因子, 但是其可能会与土壤盐分产生协同作用, 在一定程度上对土壤呼吸产生抑制。首先, 土壤水分直接参与生物的生理过程, 土壤水分在过低或过高的水平下都会限制微生物的呼吸作用(Gaumont-Guay *et al*., 2006)。其次, 土壤水分主要通过影响酶和基质的扩散、O_2在土壤中的传输来影响土壤呼吸(杨毅等, 2011)。当水分含量过高时, 虽然酶和可利用基质的含量充足, 但土壤孔隙被水填充, 限制了土壤呼吸所需O_2的传输, 并且这种通气性较差和厌氧的环境能够降低微生物呼吸(杨毅等, 2011)。

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