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# 生态学报

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## 目 次

基于生物多样性保护的兴安落叶松与白桦最佳混交比例——以阿尔山林区为例.....	李菁,骆有庆,石娟(4943)
中国能源消费碳排放的时空特征 .....	舒娱琴(4950)
黄土丘陵沟壑区坡面尺度土壤水分空间变异及影响因子 .....	姚雪玲,傅伯杰,吕一河(4961)
新疆艾比湖流域土壤有机质的空间分布特征及其影响因素.....	王合玲,张辉国,秦璐,等(4969)
雅鲁藏布江山南宽谷风沙化土地土壤养分和粒度特征.....	李海东,沈渭寿,邹长新,等(4981)
一株溶藻细菌对海洋原甲藻的溶藻效应.....	史荣君,黄洪辉,齐占会,等(4993)
呻形态对黑藻和竹叶眼子菜有机酸含量的影响.....	钟正燕,王宏镔,王海娟,等(5002)
七项河流附着硅藻指数在东江的适用性评估.....	邓培雁,雷远达,刘威,等(5014)
杭州湾滨海湿地不同植被类型沉积物磷形态变化特征.....	梁威,邵学新,吴明,等(5025)
剪形臂尾轮虫形态的时空变化及其与生态因子间的关系.....	葛雅丽,席贻龙,马杰,等(5034)
太湖流域河流水质状况对景观背景的响应.....	周文,刘茂松,徐驰,等(5043)
荒漠植物白刺属4个物种的生殖分配比较.....	李清河,辛智鸣,高婷婷,等(5054)
臭氧浓度升高对香樟叶片光合色素及抗过氧化的影响及其氮素响应.....	牛俊峰,张巍巍,李丽,等(5062)
不同密度下凤仙花重要形态性状与花朵数的关系.....	田旭平,常洁,李娟娟,等(5071)
五种高速公路边坡绿化植物的生理特性及抗旱性综合评价.....	谭雪红,高艳鹏,郭小平,等(5076)
散孔材与环孔材树种枝干、叶水力学特性的比较研究 .....	左力翔,李俊辉,李秧秧,等(5087)
北京城区行道树国槐叶面尘分布及重金属污染特征 .....	戴斯迪,马克明,宝乐(5095)
南亚热带米老排人工林碳贮量及其分配特征 .....	刘恩,刘世荣(5103)
植物生活史型定量划分及其权重配置方法——以四棱豆生活史型划分为例 .....	赵则海(5110)
半干旱区湿地-干草原交错带边界判定及其变化 .....	王晓,张克斌,杨晓晖,等(5121)
氮肥运筹对晚播冬小麦氮素和干物质积累与转运的影响.....	吴光磊,郭立月,崔正勇,等(5128)
氮肥形态对冬小麦根际土壤氮素生理群活性及无机氮含量的影响.....	熊淑萍,车芳芳,马新明,等(5138)
基于数字相机的冬小麦物候和碳交换监测.....	周磊,何洪林,孙晓敏,等(5146)
黄土高原半湿润区气候变化对冬小麦生长发育及产量的影响.....	姚玉璧,王润元,杨金虎,等(5154)
基于土地破坏的矿区生态风险评价:理论与方法 .....	常青,邱瑶,谢苗苗,等(5164)
基于生态位的山地农村居民点适宜度评价 .....	秦天天,齐伟,李云强,等(5175)
氯虫苯甲酰胺对黑肩绿盲蝽实验种群的影响 .....	杨洪,王召,金道超(5184)
6种植物次生物质对斜纹夜蛾解毒酶活性的影响 .....	王瑞龙,孙玉林,梁笑婷,等(5191)
云南元江芒果园桔小实蝇成虫日活动规律及空间分布格局 .....	叶文丰,李林,孙来亮,等(5199)
重庆市蝴蝶多样性环境健康指示作用和环境监测评价体系构建 .....	邓合黎,马琦,李爱民(5208)
<b>专论与综述</b>	
生态系统服务竞争与协同研究进展 .....	李鹏,姜鲁光,封志明,等(5219)
中国沿海无柄蔓足类研究进展 .....	严涛,黎祖福,胡煜峰,等(5230)
冰雪灾害对森林的影响 .....	郭淑红,薛立(5242)
不同干扰因素对森林和湿地温室气体通量影响的研究进展 .....	杨平,全川(5254)
采石场废弃地的生态重建研究进展 .....	杨振意,薛立,许建新(5264)
<b>研究简报</b>	
基于地统计学和CFI样地的浙江省森林碳空间分布研究 .....	张峰,杜群,葛宏立,等(5275)
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封面图说:秋色藏野驴群——秋天已经降临在海拔4200多米的黄河源区,红色的西伯利亚蓼(生于盐碱荒地或砂质含盐碱土壤)铺满大地,间有的高原苔草也泛出了金黄,行走在上面的藏野驴们顾不上欣赏这美丽的秋色,只是抓紧时间在严冬到来之前取食,添肥增膘以求渡过青藏高原即将到来的漫长冬天。

彩图提供:陈建伟教授 北京林业大学 E-mail: cites.chenjw@163.com

# ACTA ECOLOGICA SINICA Vol. 32 ,No. 16 August ,2012 ( Semimonthly )

## CONTENTS

The optimum mixture ratio of larch and birch in terms of biodiversity conservation:a case study in Aershan forest area .....	LI Jing, LUO Youqing, SHI Juan (4943)
Spatiotemporal characteristics of carbon emissions from energy consumption in China .....	SHU Yuqin (4950)
Spatial patterns of soil moisture at transect scale in the Loess Plateau of China .....	YAO Xueling, FU Bojie, LÜ Yike (4961)
The characteristics of the spatial distribution of soil organic matter and factors influencing it in Ebinur Lake Basin of Xinjiang Autonomous Region, China .....	WANG Heling, ZHANG Huiguo, QIN Lu, et al (4969)
Soil nutrients content and grain size fraction of aeolian sandy land in the Shannan Wide Valley of the Yarlung Zangbo River, China .....	LI Haidong, SHEN Weishou, ZOU Changxin, et al (4981)
Algicidal activity against <i>Prorocentrum micans</i> by a marine bacterium isolated from a HABs area, South China .....	SHI Rongjun, HUANG Honghui, QI Zanhui, et al (4993)
Effects of arsenic speciations on contents of main organic acids in <i>Hydrilla verticillata</i> and <i>Potamogeton malaisanus</i> .....	ZHONG Zhengyan, WANG Hongbin, WANG Haijuan, et al (5002)
Exploration of benthic diatom indices to evaluate water quality in rivers in the Dongjiang basin .....	DENG Peiyan, LEI Yuanda, LIU Wei, et al (5014)
Phosphorus fraction in the sediments from different vegetation type in hangzhou bay coastal wetlands .....	LIANG Wei, SHAO Xuexin, WU Ming, et al (5025)
Spatio-temporal variation of morphometric characteristics of <i>Brachionus forficula</i> in relation to ecological factors .....	GE Yali, XI Yilong, MA Jie, et al (5034)
Response of river water quality to background characteristics of landscapes in Taihu Lake basin .....	ZHOU Wen, LIU Maosong, XU Chi, et al (5043)
Reproductive allocation in four desert species of the genus <i>Nitraria</i> L. ....	LI Qinghe, XIN Zhiming, GAO Tingting, et al (5054)
Effects of elevated ozone on foliar chlorophyll content and antioxidant capacity in leaves of <i>Cinnamomum camphora</i> under enhanced nitrogen loads .....	NIU Junfeng, ZHANG Weiwei, LI Li, et al (5062)
Correlation analysis between floret numbers and important traits of <i>Impatiens balsamina</i> under different planting density .....	TIAN Xuping, CHANG Jie, LI Juanjuan, et al (5071)
Physiological characteristics and comprehensive evaluation of drought resistance in five plants used for roadside ecological restoration .....	TAN Xuehong, GAO Yanpeng, GUO Xiaoping, et al (5076)
Comparison of hydraulic traits in branches and leaves of diffuse- and ring-porous species .....	ZUO Lixiang, LI Junhui, LI Yangyang, et al (5087)
Distribution and heavy metal character of foliar dust on roadside tree <i>Sophora japonica</i> of urban area in Beijing .....	DAI Sidi, MA Keming, BAO Le (5095)
The research of carbon storage and distribution feature of the <i>Mytilaria laosensis</i> plantation in south sub-tropical area .....	LIU En, LIU Shirong (5103)
The novel methods of quantitative classification of plant life cycle forms and weight collocation: taking classification of life cycle forms of <i>Psophocarpus tetragonolobus</i> as an example .....	ZHAO Zehai (5110)
Research on boundary definition and changes of wetland-dry grassland ...	WANG Xiao, ZHANG Kebin, YANG Xiaohui, et al (5121)
Differential effects of nitrogen managements on nitrogen, dry matter accumulation and transportation in late-sowing winter wheat .....	WU Guanglei, GUO Liyue, CUI Zhengyong, et al (5128)
Effects of nitrogen form on the activity of nitrogen bacteria group and inorganic nitrogen in rhizosphere soil of winter wheat .....	XIONG Shuping, CHE Fangfang, MA Xinning, et al (5138)
Using digital repeat photography to model winter wheat phenology and photosynthetic CO <sub>2</sub> uptake .....	ZHOU Lei, HE Honglin, SUN Xiaomin, et al (5146)
Impacts of climate change on growth and yield of winter wheat in the semi-humid region of the Loess Plateau .....	YAO Yubi, WANG Runyuan, YANG Jinhu, et al (5154)
Theory and method of ecological risk assessment for mining areas based on the land destruction .....	CHANG Qing, QIU Yao, XIE Miaomiao, et al (5164)
Suitability evaluation of rural residential land based on niche theory in mountainous area .....	QIN Tiantian, QI Wei, LI Yunqiang, et al (5175)
Effects of chlorantraniliprole on experimental populations of <i>Cyrtorhinus lividipennis</i> ( Reuter ) ( Hemiptera: Miridae) .....	YANG Hong, WANG Zhao, JIN Daochao (5184)
Effects of six plant secondary metabolites on activities of detoxification enzymes in <i>Spodoptera litura</i> .....	WANG Ruilong, SUN Yulin, LIANG Xiaoting, et al (5191)
Daily activity and spatial distribution pattern of the oriental fruit fly, <i>Bactrocera dorsalis</i> ( Diptera: Tephritidae ) in mango orchard, Yuanjiang, Yunnan .....	YE Wenfeng, LI Lin, SUN Lailiang, et al (5199)
The establishment of the indication on environmental health of butterfly and of the environmental monitoring evaluation system in Chongqing .....	DENG Heli, MA Qi, LI Aimin (5208)
<b>Review and Monograph</b>	
Research progress on trade-offs and synergies of ecosystem services: an overview .....	LI Peng, JIANG Luguang, FENG Zhiming, et al (5219)
A review on the balanomorph barnacles in the coastal waters of China .....	YAN Tao, LI Zufu, HU Yufeng, et al (5230)
Effects of ice-snow damage on forests .....	GUO Shuhong, XUE Li (5242)
Greenhouse gas flux from forests and wetlands: a review of the effects of disturbance .....	YANG Ping, TONG Chuan (5254)
Advances in ecology restoration of abandoned quarries .....	YANG Zhenyi, XUE Li, XU Jianxin (5264)
<b>Scientific Note</b>	
Spatial distribution of forest carbon in Zhejiang Province with geostatistics based on CFI sample plots .....	ZHANG Feng, DU Qun, GE Hongli, et al (5275)

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## 臭氧浓度升高对香樟叶片光合色素及 抗过氧化的影响及其氮素响应

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**摘要:**为阐明氮(N)沉降条件下我国亚热带典型常绿树种香樟(*Cinnamomum camphora*)的臭氧(O<sub>3</sub>)胁迫响应特征,以1年生幼苗为试验对象,采用开顶气室(OTC)进行模拟研究。O<sub>3</sub>处理设大气O<sub>3</sub>(AA)、大气O<sub>3</sub>+60 nmol/mol(AA+60)、大气O<sub>3</sub>+120 nmol/mol(AA+120)3个水平;N素以硝酸铵(NH<sub>4</sub>NO<sub>3</sub>)溶液形式施加,施N量设0(N0)、30(N30)、60(N60)(kg·hm<sup>-2</sup>·a<sup>-1</sup>)3个水平。主要考察了叶片膜质过氧化、光合色素、胞质抗坏血酸含量及总抗氧化能力的胁迫响应特征。结果表明:一个生长季(2009年5月15日—2009年9月10日)高浓度O<sub>3</sub>处理导致试验幼苗叶肉细胞膜脂过氧化程度显著加剧,叶绿素a、叶绿素b、类胡萝卜素含量显著降低;N素施加显著提高了叶绿素含量,但未改变细胞膜脂过氧化水平。叶片总抗氧化能力在AA+120处理下显著提高,但未受N施加影响。还原型抗坏血酸含量在N0处理下随O<sub>3</sub>浓度升高而降低;在N30及N60处理下随O<sub>3</sub>浓度升高而增高。施N可通过提高叶片抗坏血酸含量来增强香樟对O<sub>3</sub>升高的适应能力。研究结论可为O<sub>3</sub>与N复合污染下,我国亚热带地区典型常绿树种的保护提供科学参考。

**关键词:**香樟;膜质过氧化;叶绿素;抗坏血酸

## Effects of elevated ozone on foliar chlorophyll content and antioxidant capacity in leaves of *Cinnamomum camphora* under enhanced nitrogen loads

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**Abstract:** Elevated tropospheric ozone (O<sub>3</sub>) and enhanced atmospheric nitrogen (N) deposition exert great impact on the physiology of forest trees. The respective effects of these two pollutants have been studied thoroughly during the past couple of decades. However, little information is available concerning their combined effects on the physiology of subtropical evergreen trees. In the present study, O<sub>3</sub> effects on *Cinnamomum camphora*, a native evergreen tree species, widely distributed in subtropical region, were investigated under enhanced N loads. One-year-old seedlings were adopted and the experiment was carried out in open-top chambers (OTCs). O<sub>3</sub> fumigation regimes were set at ambient air (AA), ambient air plus 60 nmol/mol (AA+60) and ambient air plus 120 nmol/mol (AA+120); N load levels were set at 0 (CK), 30 and 60 kg·hm<sup>-2</sup>·a<sup>-1</sup>, designated as N0, N30 and N60, respectively. Membrane lipid peroxidation, foliar chlorophyll and ascorbic acid contents as well as the total antioxidant capacity were examined after treatments for one growing season (May 5-September 10, 2009). Foliar MDA (malondialdehyde) concentration was significantly enhanced by AA+120 treatment,

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but changed little in AA+60. Neither N30 nor N60 affected foliar MDA concentration significantly. Chlorophyll a content significantly decreased under both AA+60 and AA+120 treatments, and was significantly lower in the latter than in the former. Both N30 and N60 significantly increased chlorophyll a content, and the increment under N60 was significantly greater than that under N30. Chlorophyll b was also significantly increased by both N30 and N60, while was only significantly decreased by AA+120 rather than by AA+60. AA+120, as well as N60, significantly decreased chlorophyll a/b, which, however, was affected by neither AA+60 nor N30. The effects of elevated O<sub>3</sub> and enhanced N on foliar carotenoid content were similar to those on Chlorophyll a content: significant treatment effects (O<sub>3</sub> and N) with significant differences between treatment levels (AA+60 and AA+120, or N30 and N60). Besides, AA+120 significantly increased the total antioxidant capacity, on which, however, the effect of AA+60 was not significant. Significant difference of the total antioxidant capacity was not found either between AA+60 and AA+120, or among the N treatments. There were no significant interactions detected between O<sub>3</sub> and N on foliar MDA, chlorophyll content and the total antioxidant capacity in our study. However, the effects of elevated O<sub>3</sub> on the reduced (ASC) and total ascorbic acid ([ASC+DHA]) content were significantly modified by N loads. Under N0, both AA+60 and AA+120 significantly reduced the foliar ASC content, which, however, was significantly increased by AA+120 under N30 and N60. AA+60 also tended to increase the ASC content under enhanced N, although its effect was not significant. The effects of elevated O<sub>3</sub> on [ASC+DHA] under different N loads were similar to those on ASC, although they were of no statistical significance. Enhanced N loads strengthened the tolerance of *C. camphor* to O<sub>3</sub> through increasing the foliar ASC content.

**Key Words:** *cinnamomum comphra*; membrane lipid peroxidation; chlorophyll; ascorbic acid

地表臭氧(O<sub>3</sub>)浓度升高是全球变化的重要方面,高浓度O<sub>3</sub>对地表植被特别是森林生态系统具有很强的毒害作用<sup>[1]</sup>。工业革命以来,大气O<sub>3</sub>浓度已经升高了36%;目前,全球近1/4的国家和地区面临着夏季对流层60 nmol/mol以上的O<sub>3</sub>威胁<sup>[2]</sup>。虽然近十年来北美和欧洲地表O<sub>3</sub>浓度趋于持平甚至有所下降<sup>[3]</sup>,但以东南亚及非洲为代表的后起工业化地区O<sub>3</sub>浓度将持续上升,对该区及全球生态安全构成严重威胁<sup>[4]</sup>。到2020年,中国中东部大部分地区白天O<sub>3</sub>平均浓度将达到70 nmol/mol<sup>[5]</sup>,小时浓度最大值将超过140 nmol/mol<sup>[6]</sup>。同时,东南亚地区平均氮(N)沉降水平为22 kg·hm<sup>-2</sup>·a<sup>-1</sup>,最大沉降值超过50 kg·hm<sup>-2</sup>·a<sup>-1</sup><sup>[7]</sup>,高于10—20 kg·hm<sup>-2</sup>·a<sup>-1</sup>的森林生态系统N承载阈值<sup>[8]</sup>。过度N输入导致土壤酸化,生态系统营养失衡,生物多样性降低等<sup>[9-11]</sup>。

O<sub>3</sub>主要通过气孔进入植物体内<sup>[12]</sup>,并与叶片内部氧化还原系统发生反应生成超氧阴离子自由基(O<sub>2</sub><sup>-</sup>)、羟自由基(·OH)、过氧化物自由基(ROO·)以及过氧化氢(H<sub>2</sub>O<sub>2</sub>)等一系列活性分子<sup>[13]</sup>。这些活性分子进一步启动或者介导下游氧化裂解<sup>[4]</sup>,并引起膜质过氧化<sup>[14]</sup>、叶绿素降解<sup>[15]</sup>及植物体抗氧化物质如抗坏血酸<sup>[16]</sup>等含量及组成发生变化。这些变化构成植物叶片伤害症状、光合抑制、生物量下降<sup>[17]</sup>等O<sub>3</sub>胁迫的生理基础。另一方面,N施加可以促进冷杉(*Abies fabri*)、冬青栎(*Quercus ilex*)等幼苗胞质氧化抗性增强,叶肉细胞膜脂过氧化程度减轻<sup>[18-19]</sup>;然而,在一项针对不同施N条件下西瓜(*Citrullus lanatus*)O<sub>3</sub>胁迫效应的研究中,Calatayud等发现高N处理显著加剧了O<sub>3</sub>胁迫导致的膜脂过氧化<sup>[20]</sup>。N施加对植物叶片膜脂过氧化的影响因植物种类不同而存在差异。

目前,O<sub>3</sub>对树木胁迫的研究主要集中于暖温带落叶、针叶树种以及地中海常绿硬叶树种等<sup>[21]</sup>。大量试验研究表明,不同树种抵抗O<sub>3</sub>胁迫的能力存在差异,被子植物较裸子植物更为敏感<sup>[22]</sup>,地中海常绿树种较落叶、针叶树种耐性更强<sup>[23]</sup>。国内学者利用开顶气室对O<sub>3</sub>胁迫下银杏(*Ginkgo biloba*)、油松(*Pinus tabuliformis*)、蒙古栎(*Quercus mongolica*)等树种的光合及抗性生理进行了研究<sup>[24-27]</sup>。然而,对于亚热带地区广布常绿树种的O<sub>3</sub>敏感性研究较少,结合考虑该地区高水平的N沉降以及独特的水热等气候条件,认为该区

树种在  $O_3$  胁迫响应机制上具有独特性。本试验以我国亚热带典型常绿树种香樟为研究对象,在人工模拟 N 沉降条件下,测定叶绿素、类胡萝卜素、抗坏血酸含量及总抗氧化能力等,分析  $O_3$  浓度升高对香樟光合色素、抗性生理等的影响,旨在揭示、预测我国长江三角洲地区高水平 N 沉降条件下香樟树种的  $O_3$  胁迫现状和未来趋势,为科学保护该区这一重要树种提供参考。

## 1 材料与方法

### 1.1 试验地点

试验区位于浙江省宁波市天童森林生态系统国家野外科学观测研究站( $29^{\circ}48'N, 121^{\circ}47'E$ ),属典型亚热带季风气候,四季分明,冬季寒冷干燥,夏季温暖湿润。年平均气温 $16^{\circ}C$ ,最暖月7月平均气温 $28.1^{\circ}C$ ,最冷月1月份平均气温 $4.2^{\circ}C$ 。年平均降水为 $1375\text{ mm}$ ,且主要集中在6—8月份。土壤类型为山地红黄壤,土质偏酸,pH值大约在4.4—5.1之间,母质基底为中生代沉积物及侵入性的石英岩和花岗岩。2009年试验期间(5月15日—9月10日),小时平均气温、空气相对湿度分别为 $16^{\circ}C$ 和88%,日均太阳辐射量为 $13.8\text{ MJ}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ ,8h平均(9:00—17:00)  $O_3$ 浓度为 $32.6\text{ nmol/mol}$ ,小时最高浓度为 $156.3\text{ nmol/mol}$ 。

### 1.2 试验处理

试验材料为1年生香樟幼苗,由浙江省嘉兴市桐乡特种苗繁育中心购得,于2009年1月植入容量为5L(高 $15\text{ cm}$ ×直径 $28\text{ cm}$ )的塑料花盆中,栽培基质为当地红黄壤与树皮腐殖质的混合物(体积比1:1)。盆栽幼苗培育于控温温室内,并于2009年4月中旬移到外界大气环境中进行处理前适应。2009年5月10日,选取长势一致的幼苗90株( $15\times 6$ )移植于6个开顶气室(OTC,底面为边长1m的正八边形,高2.4m,塑钢架构,透光率为98.3%的高透性塑料膜)中。每个OTC中15株幼苗分为3组,分别设空白对照(N0)、施N $30\text{ kg}\cdot\text{hm}^{-2}\cdot\text{a}^{-1}$ (N30)、施N $60\text{ kg}\cdot\text{hm}^{-2}\cdot\text{a}^{-1}$ (N60)。N施加分6次进行(5月28日、6月23日、7月7日、7月23日、8月11日、8月27日),以硝酸铵( $\text{NH}_4\text{NO}_3$ )溶液形式浇灌于盆内土壤表层,空白对照浇以等量自来水。 $O_3$ 处理从2009年5月15日开始,持续到2009年9月10日,阴雨天停止熏气, $O_3$ 处理设大气 $O_3$ (AA),大气 $O_3+60\text{ nmol/mol}$ (AA+60),大气 $O_3+120\text{ nmol/mol}$ (AA+120)3个水平,每个 $O_3$ 水平设两个OTC重复。试验期间,水分浇灌充足,不存在干旱胁迫。

### 1.3 指标测定

于2009年9月6日选取冠层顶部相同部位成熟叶片(无明显 $O_3$ 伤害症状)打孔( $0.9\text{ cm}^2$ 叶圆片)取样,叶片在 $4^{\circ}C$ 暗环境下用4mL 95%的乙醇溶液浸泡提取,测定 $664$ 、 $648$ 、 $470\text{ nm}$ 波长吸光度,根据Lichtenthaler<sup>[28]</sup>的修正公式计算叶绿素a、叶绿素b以及类胡萝卜素含量。

丙二醛含量采用硫代巴比妥酸法测定<sup>[29]</sup>。

抗坏血酸含量参照Okamura还原 $\text{Fe}^{3+}$ 的方法测定<sup>[30]</sup>。

总抗氧化能力的测定采用FRAP法<sup>[31]</sup>,以单位鲜重叶片等效 $\text{Fe}^{2+}$ 含量( $\text{mmol/g}$ )表示。

### 1.4 数据分析

所有测定指标均取6次重复,采用SAS软件(Version 9.1.3, SAS Institute, Cary, NC, USA)进行分析。运用单变量方差分析模型检验 $O_3$ 、N以及 $O_3$ 与N交互效应的显著性,验后多重比较采取Tukey法。如果 $O_3$ 与N交互作用不显著,则多重比较分别在两种处理不同水平之间进行;如果 $O_3$ 与N交互作用显著,则考察每一施N水平下不同 $O_3$ 处理之间的差异显著性。数据均满足分布正态及方差齐性要求, $P \leq 0.05$ 认为差异显著。

## 2 结果与分析

### 2.1 $O_3$ 以及N处理对香樟幼苗光合色素含量的影响

结果显示:一个生长季 $O_3$ 以及N处理显著影响了香樟幼苗叶片光合色素含量,然而,两种处理之间不存在明显的交互作用(表1)。与AA处理比,AA+60与AA+120处理导致叶绿素a含量分别下降了12.7%和36.1%,降幅均达到统计显著,且两 $O_3$ 处理之间差异显著。相比于N0处理,N30及N60处理均显著提高了叶绿素a含量,提高幅度分别为5.3%和80.0%,且两个N处理水平之间差异显著。N处理下叶绿素b与叶绿

素 a 具有相同的变化趋势,AA+120 处理显著降低了叶绿素 b 含量,与 AA 处理相比,降幅达 30.9%。相比于 AA 处理及 N0 处理,AA+120 与 N60 处理均显著降低了叶绿素 a 与叶绿素 b 的比值(叶绿素 a/b),对应的下降幅度分别为 6.9% 与 6.4%;AA+60 与 N30 处理导致叶绿素 a/b 较 AA 与 N0 分别下降了 3.9% 和 4.7%,未达到统计显著。叶片类胡萝卜素含量对于 O<sub>3</sub> 与 N 处理的响应类似于叶绿素 a,两种处理效应方向相反,且每种处理两个水平与对照(AA\N0)相比、两个处理水平之间相比均有显著差异(图 1)。

表 1 臭氧(O<sub>3</sub>)、氮(N)以及 O<sub>3</sub>×N 对各观测指标影响显著性Table 1 Significance of the effects of ozone(O<sub>3</sub>),nitrogen(N)and O<sub>3</sub>×N on the examined physiological parameters

测定指标 Physiological parameters	臭氧 O <sub>3</sub>	氮 N	臭氧×氮 O <sub>3</sub> ×N
叶绿素 a Chlorophyll a/( μg/cm <sup>2</sup> )	0.000 **	0.000 **	0.292
叶绿素 b Chlorophyll b/( μg/cm <sup>2</sup> )	0.000 **	0.000 **	0.295
叶绿素 a/b Chlorophyll a/b	0.006 **	0.007 **	0.271
类胡萝卜素 Carotenoid/( μg/cm <sup>2</sup> )	0.000 **	0.000 **	0.623
丙二醛 MDA/( nmol/g)	0.033 *	0.398	0.099
还原型抗坏血酸 ASC/( μmol/g)	0.008 **	0.262	0.000 **
总抗坏血酸 [ASC+DHA]/( μmol/g)	0.499	0.498	0.016 *
总抗氧化能力 FRAP/( mmol/g)	0.004 **	0.870	0.819

\* P<0.05, \*\* P<0.01

## 2.2 O<sub>3</sub> 以及 N 处理对香樟幼苗膜脂过氧化的影响

与 AA 处理相比,AA+120 处理导致香樟幼苗叶片膜质过氧化程度显著加剧,膜脂过氧化产物丙二醛含量升高了 16.1%;然而,AA+60 处理未能显著影响这一过程。N 处理未显著改变香樟叶片膜脂过氧化,O<sub>3</sub> 与 N 处理之间不存在交互作用(图 2、表 1)

## 2.3 O<sub>3</sub> 以及 N 处理对香樟幼苗总抗氧化能力的影响

相比于 AA 处理,AA+120 处理导致香樟幼苗叶片总抗氧化能力显著上升,上升幅度为 19.0%;AA+60 处理下,叶片总抗氧化能力较对照提高了 5.8%,未达到统计显著。AA+60 与 AA+120 处理之间叶片总抗氧化能力差异不显著。N 处理未能显著影响香樟叶片的总抗氧化能力,O<sub>3</sub> 与 N 处理之间交互作用不显著(图 2、表 1)。

## 2.4 O<sub>3</sub> 以及 N 处理对香樟幼苗抗坏血酸含量及组成的影响

不同施 N 水平下,O<sub>3</sub> 处理对香樟幼苗叶片抗坏血酸含量及组成的影响存在差异,O<sub>3</sub> 与 N 处理之间交互作用显著(表 1)。N0 下,O<sub>3</sub> 处理(AA+60 与 AA+120)导致叶片总抗坏血酸含量趋于降低;N30 及 N60 下,O<sub>3</sub> 处理(AA+60 与 AA+120)导致叶片总抗坏血酸含量趋于上升。然而,这些变化趋势均未达到统计显著(图 3)。

还原型抗坏血酸含量在不同 N 水平下受 O<sub>3</sub> 影响变化趋势与总抗坏血酸含量变化相似。N0 下,AA+60 与 AA+120 处理对还原型抗坏血酸含量的降低效应均达到显著水平,与 AA 处理相比,降幅分别为 22.5% 和 20.7%;N 施加条件下,相比于 AA 处理,AA+120 处理显著提高了香樟幼苗叶片还原型抗坏血酸含量,N30 处理下提高了 33.4%,N60 处理下提高了 41.3%;AA+60 处理也有类似效应,但未达到显著水平(图 3)。

## 3 讨论

膜质过氧化被认为是 O<sub>3</sub> 胁迫条件下植物氧化伤害的重要表征<sup>[32]</sup>,丙二醛(MDA)作为膜质过氧化的主要产物之一,广泛用于膜脂过氧化和组织伤害程度的诊断<sup>[33]</sup>。试验结果表明:AA+120 处理导致香樟幼苗叶片膜质过氧化程度显著加剧(图 2)。O<sub>3</sub> 胁迫导致的树木叶片膜质过氧化已经在自然生境下的欧洲山毛榉(*Fagus sylvatica*)和欧洲云杉(*Picea abies*)中得到验证<sup>[34-35]</sup>。然而,本试验中 AA+60 处理并未显著影响香樟叶片膜脂过氧化,说明香樟作为常绿树种具有一定程度的 O<sub>3</sub> 胁迫抗性<sup>[17]</sup>。王效科等<sup>[36]</sup>研究发现:香樟可以 ≥20 μg·g<sup>-1</sup>(干重)·h<sup>-1</sup> 的速率释放异戊二烯。该化合物可与 O<sub>3</sub> 发生反应,稀释叶片边界层 O<sub>3</sub> 浓度,减少气

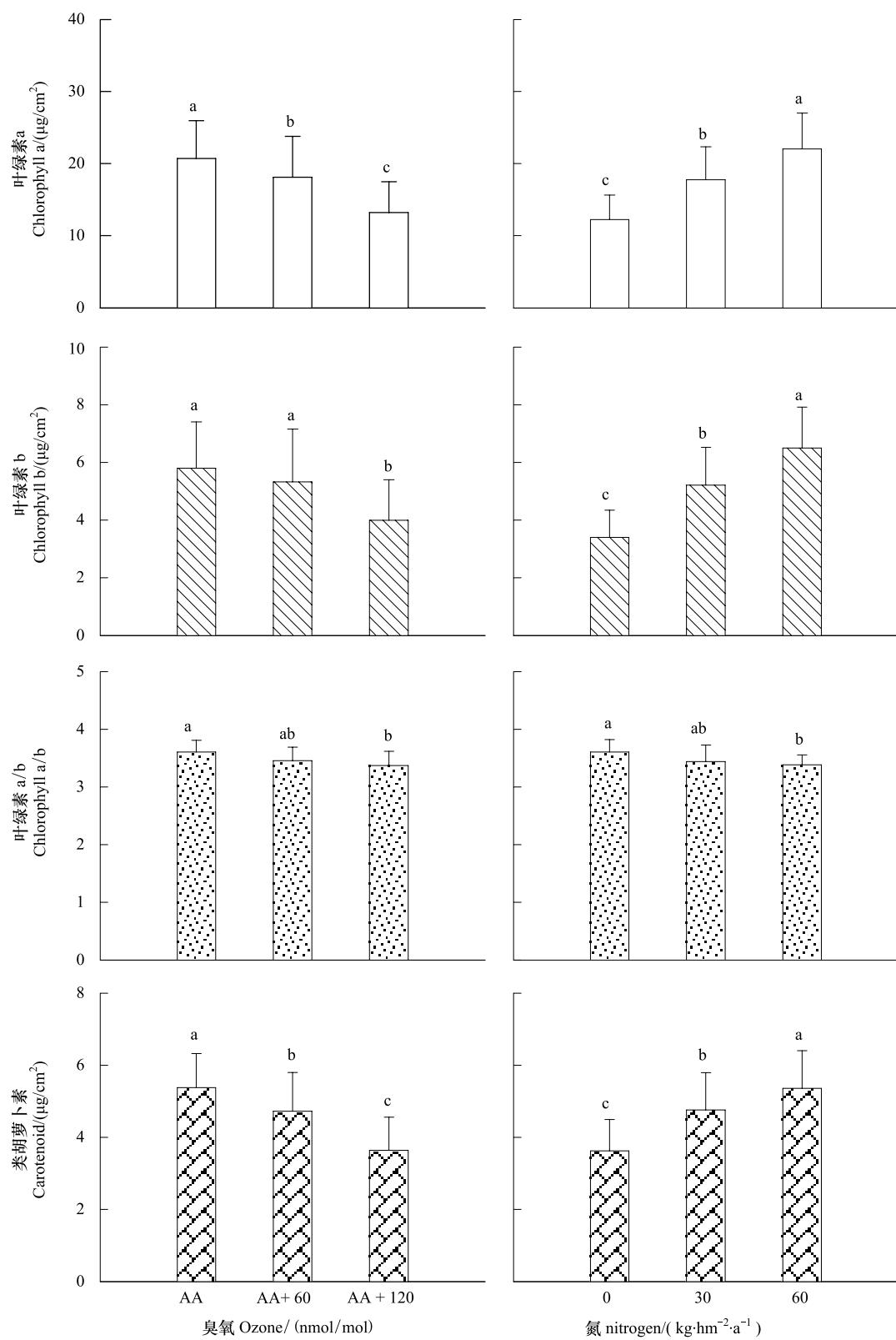


图1 不同臭氧( $O_3$ )与氮(N)处理水平下香樟叶片叶绿素a, 叶绿素b, 叶绿素a/b, 类胡萝卜素含量多重比较, 小写字母a、b、c表示差异显著( $P<0.05$ )

Fig. 1 Multiple comparisons for the foliar chlorophyll a, chlorophyll b, chlorophyll a/b and carotenoid content among different ozone( $O_3$ ) and nitrogen(N) treatment levels. Lowercase letters a, b and c indicate significant differences ( $P<0.05$ )

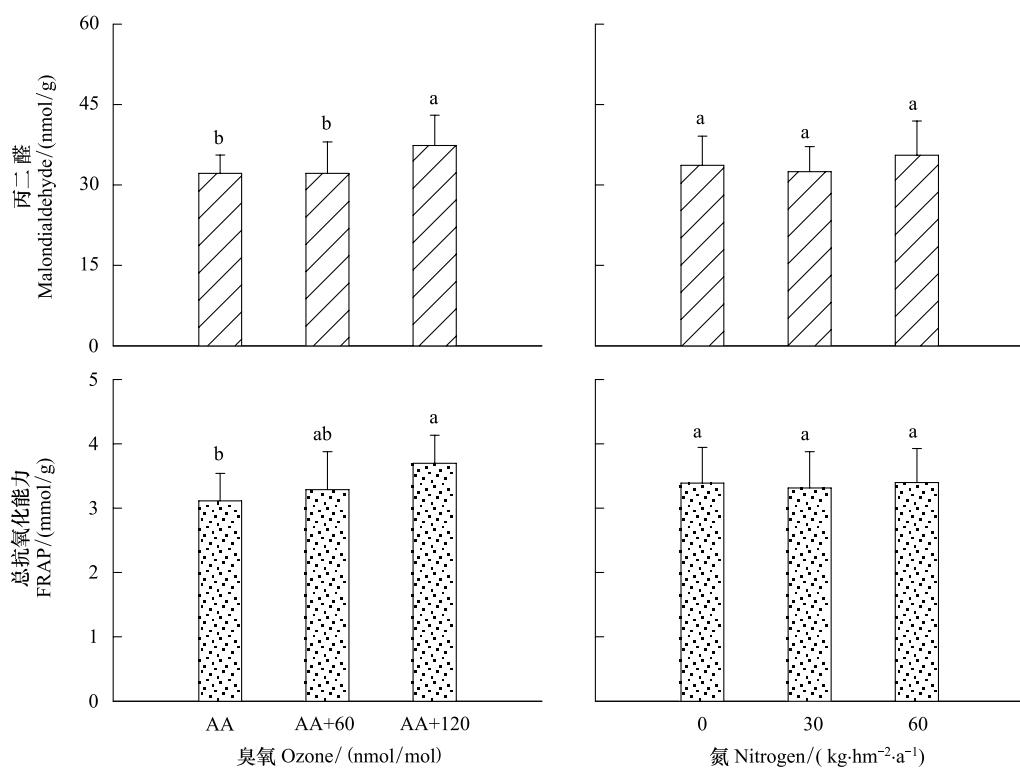


图2 不同臭氧( $O_3$ )与氮(N)处理水平下香樟叶片丙二醛含量及总抗氧化能力多重比较,小写字母a、b、c表示差异显著( $P<0.05$ )

Fig.2 Multiple comparisons for the foliar MDA content and the FRAP capacity among different ozone( $O_3$ ) and nitrogen(N) treatment levels. MDA-Malondialdehyde, FRAP-total antioxidant capacity expressed as  $\mu\text{mol Fe}^{2+} \cdot \text{g}^{-1}$  fresh matter. Lowercase letters a, b and c indicate significant differences( $P<0.05$ )

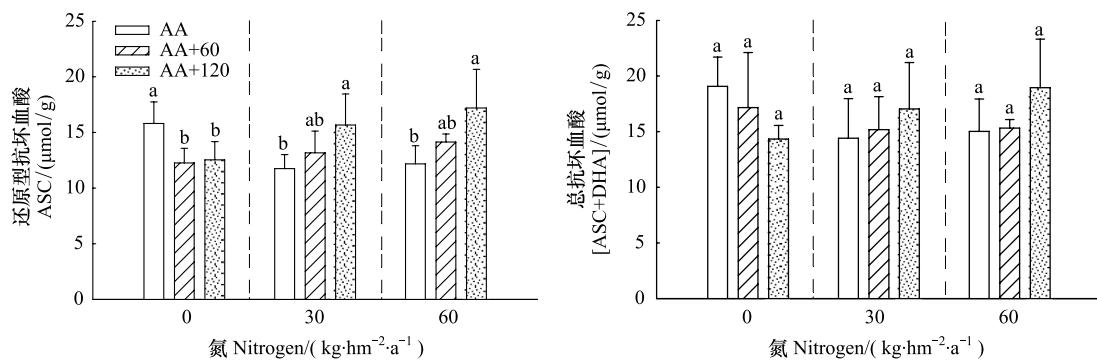


图3 不同施氮(N)水平下臭氧( $O_3$ )胁迫对香樟叶片还原型抗坏血酸(ASC)及总抗坏血酸([ASC+DHA])含量的影响,AA-大气 $O_3$ ,AA+60-大气 $O_3$ +60 nmol/mol,AA+120-大气 $O_3$ +120 nmol/mol,不同字母表示差异显著( $P<0.05$ )

Fig.3 Effect of elevated ozone( $O_3$ ) on the foliar content of ASC and [ASC+DHA] in *Cinnamomum Camphora* seedlings under different nitrogen(N) loads. AA-ambient air, AA+60-ambient air plus 60 nmol/mol, AA+120-ambient air plus 120 nmol/mol. Different letters indicate significant differences( $P<0.05$ )

孔 $O_3$ 通量,进而降低植物 $O_3$ 胁迫<sup>[37]</sup>。N施加能够提高叶片光合色素特别是叶绿素a含量,增强光捕获能力,光能过量捕获可进一步导致过氧离子产生,进而对植物膜脂过氧化具有潜在加剧效应<sup>[38]</sup>。然而,本研究中N施加未显著影响香樟叶片膜脂过氧化,N施加在刺激植物光能捕获的同时,显著促进了香樟叶片光合作用光化学反应过程<sup>[21]</sup>,光化学反应对捕获光能的消耗在一定程度上缓解了后者的氧化胁迫效应(图2)。Zhao等研究发现:环境温度下,N素施加( $250 \text{ kg} \cdot \text{hm}^{-2} \cdot \text{a}^{-1}$ )显著降低了粗枝云杉(*Picea asperata*)幼苗叶片MDA含

量;而在红外加热条件下,施N导致叶片膜脂过氧化显著加剧<sup>[39]</sup>。N施加对树木叶片膜脂过氧化的影响可能与植物生长环境密切有关。

植物体内的抗氧化系统是植物O<sub>3</sub>抗性的基础,能够清除胁迫产生的活性氧及膜脂过氧化的有毒产物,有利于植物的逆境生存<sup>[14]</sup>。抗坏血酸作为植物体内最重要的抗氧化剂,其含量与植物O<sub>3</sub>抗性显著正相关<sup>[40]</sup>。本试验中,O<sub>3</sub>胁迫导致的香樟叶片抗坏血酸含量变化与N素施加有关:N30及N60处理下,O<sub>3</sub>胁迫促使叶片抗坏血酸含量上升,以还原型抗坏血酸含量上升为主,且在AA+120处理下效应达到显著;N0条件下,O<sub>3</sub>胁迫导致叶片总抗坏血酸及还原型抗坏血酸含量均有所下降,且以还原型抗坏血酸含量下降为主,达到统计显著(图3)。该结果一方面论证了还原型抗坏血酸在植物体活性氧清除过程中的重要作用<sup>[41]</sup>;另一方面说明试验中N素的施加能够为O<sub>3</sub>胁迫下植物体抗坏血含量的提高提供必要营养支持<sup>[42]</sup>。N施加对树木氧化抗性的增强效应在常绿硬叶树种冬青栎、针叶树种冷杉中也有报道<sup>[18-19]</sup>。此外,本试验中AA+120处理导致香樟叶片总抗氧化能力显著升高(图2),这可能与抗坏血酸含量的升高有关<sup>[43]</sup>,也可能是胞质中其他类型抗氧化物质如谷胱甘肽(Glutathione)<sup>[4]</sup>等的含量上升导致。

植物体叶绿素含量降低是O<sub>3</sub>胁迫最普遍的效应之一<sup>[44-45]</sup>。本实验中O<sub>3</sub>处理(AA+60以及AA+120)显著降低了香樟幼苗叶片叶绿素a及类胡萝卜素含量(图1),叶绿素b含量在AA+120处理下也呈显著下降(图1)。叶绿素的降解与叶绿体膜的脂质过氧化有关<sup>[46]</sup>,并与核酮糖1,5-二磷酸羧化酶(Rubisco)的降解过程相偶联<sup>[47]</sup>。膜脂过氧化可引起膜通透性改变,活性氧分子通过膜通道或以渗透方式进入叶绿体内,直接作用于叶绿素分子,或通过进攻Rubisco活性位点间接介导叶绿素的降解。此外,本试验结果显示:AA+120与N60处理均显著降低了香樟叶片叶绿素a与叶绿素b含量的比值(图1),叶绿素a/b值的下降意味着叶片的加速衰老<sup>[48]</sup>。另一方面,与O<sub>3</sub>胁迫效应相反,本试验中N施加显著提高了香樟叶片叶绿素a、叶绿素b、及类胡萝卜素的含量,然而,施N未能有效阻止O<sub>3</sub>胁迫导致的叶绿素降解,两种处理之间不存在显著交互作用。这一结论与Watanabe等针对2年生短柄枹栎(*Quercus serrata*)幼苗的研究结论一致<sup>[49]</sup>;Utriainen和Holopainen<sup>[50]</sup>研究了施N条件下欧洲赤松(*Pinus sylvestris*)幼苗的O<sub>3</sub>胁迫效应,结果显示:N施加显著提高了叶片叶绿素及类胡萝卜素含量,然而,N施加对光合色素的促进效应与O<sub>3</sub>抑制效应之间同样不存在显著交互作用。O<sub>3</sub>与N处理对植物光合色素的影响可能受植物体内不同生理机制独立调控。

#### 4 结论

(1) AA+60处理未对香樟叶片膜脂过氧化产生显著影响,香樟较落叶、针叶树种具有较强的O<sub>3</sub>抗性,这可能与其释放的挥发性异戊二烯能够与O<sub>3</sub>反应,对叶片边界层O<sub>3</sub>具有稀释作用有关;施N条件下,AA+120处理导致香樟叶片还原型抗坏血酸含量显著升高,N施加可为O<sub>3</sub>胁迫下抗氧化物的合成提供必要营养支持;AA+120处理导致香樟叶片衰老加速,光合色素含量降低,这可能与叶绿体膜脂质过氧化及核酮糖1,5-二磷酸羧化酶的降解有关;N施加显著增加了香樟叶片光合色素含量,然而施N未能有效缓解O<sub>3</sub>胁迫导致的膜脂过氧化和叶绿素降解。

(2)控制实验条件下充足的水分供给、盆栽对植物根系生长限制以及树木幼苗阶段生长发育的独特生理生长机制等因素可能导致本试验所得结果存在一定偏差,研究结论在推广到自然生境下成熟树木的时候还需结合原位观测进行相关校正。考虑到亚热带地区独特的气候、地理和植被条件,在全球变化的大背景下加强该区树种O<sub>3</sub>胁迫敏感性研究十分必要。

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