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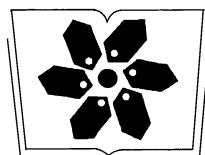
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目 次

中国石龙子母体孕期调温诱导幼体表型:母体操纵假说的实验检测	李 宏,周宗师,吴延庆,等	(7255)
同种或异种干扰对花鼠分散贮藏点选择的影响	申 圳,董 钟,曹令立,等	(7264)
曝气充氧条件下污染河道氨挥发特性模拟	刘 波,王文林,凌 芬,等	(7270)
贵州草海越冬斑头雁日间行为模式及环境因素对行为的影响	杨延峰,张国钢,陆 军,等	(7280)
青藏高原多年冻土区积雪对沼泽、草甸浅层土壤水热过程的影响	常 娟,王根绪,高永恒,等	(7289)
长沙城市斑块湿地资源的时空演变	恭映璧,靖 磊,彭 磊,等	(7302)
基于模型数据融合的千烟洲亚热带人工林碳水通量模拟	任小丽,何洪林,刘 敏,等	(7313)
农田氮素非点源污染控制的生态补偿标准——以江苏省宜兴市为例	张 印,周羽辰,孙 华	(7327)
用 PFU 微型生物群落监测技术评价化工废水的静态毒性	李朝霞,张玉国,梁慧星	(7336)
京郊农业生物循环系统生态经济能值评估——以密云尖岩村为例	周连第,胡艳霞,王亚芝,等	(7346)
基于遥感的夏季西安城市公园“冷效应”研究	冯晓刚,石 辉	(7355)
海南岛主要森林类型时空动态及关键驱动因子	王树东,欧阳志云,张翠萍,等	(7364)
不同播种时间对吉林省西部玉米绿水足迹的影响	秦丽杰,靳英华,段佩利	(7375)
黄土塬区不同品种玉米间作群体生长特征的动态变化	王小林,张岁岐,王淑庆,等	(7383)
密植条件下种植方式对夏玉米群体根冠特性及产量的影响	李宗新,陈源泉,王庆成,等	(7391)
沙地不同发育阶段的人工生物结皮对重金属的富集作用	徐 杰,敖艳青,张璟霞,等	(7402)
增强 UV-B 辐射和氮对谷子叶光合色素及非酶促保护物质的影响	方 兴,钟章成	(7411)
不同产地披针叶茴香光合特性对水分胁迫和复水的响应	曹永慧,周本智,陈双林,等	(7421)
芦芽山林线华北落叶松径向变化季节特征	董满宇,江 源,王明昌,等	(7430)
地形对植被生物量遥感反演的影响——以广州市为例	宋巍巍,管东生,王 刚	(7440)
指数施肥对楸树无性系生物量分配和根系形态的影响	王力朋,晏紫伊,李吉跃,等	(7452)
火烧伤害对兴安落叶松树干径向生长的影响	王晓春,鲁永现	(7463)
山地梨枣树耗水特征及模型	辛小桂,吴普特,汪有科,等	(7473)
两种常绿阔叶植物越冬光系统功能转变的特异性	钟传飞,张运涛,武晓颖,等	(7483)
干旱胁迫对银杏叶片光合系统Ⅱ荧光特性的影响	魏晓东,陈国祥,施大伟,等	(7492)
神农架川金丝猴栖息地森林群落的数量分类与排序	李广良,丛 静,卢 慧,等	(7501)
碱性土壤盐化过程中阴离子对土壤中镉有效态和植物吸收镉的影响	王祖伟,弋良朋,高文燕,等	(7512)
两种绣线菊耐弱光能力的光合适应性	刘慧民,马艳丽,王柏臣,等	(7519)
闽楠人工林细根寿命及其影响因素	郑金兴,黄锦学,王珍珍,等	(7532)
旅游交通碳排放的空间结构与情景分析	肖 潇,张 捷,卢俊宇,等	(7540)
北京市妫水河流域人类活动的水文响应	刘玉明,张 静,武鹏飞,等	(7549)
膜下滴灌技术生态-经济与可持续性分析——以新疆玛纳斯河流域棉花为例	范文波,吴普特,马枫梅	(7559)
高温胁迫及其持续时间对棉蚜死亡和繁殖的影响	高桂珍,吕昭智,夏德萍,等	(7568)
桉树枝瘿姬小蜂虫瘿解剖特征与寄主叶片生理指标的变化	吴耀军,常明山,盛 双,等	(7576)
西南桦纯林与西南桦×红椎混交林碳贮量比较	何友均,覃 林,李智勇,等	(7586)
长沙城市森林土壤 7 种重金属含量特征及其潜在生态风险	方 晰,唐志娟,田大伦,等	(7595)
专论与综述		
城乡结合部人-环境系统关系研究综述	黄宝荣,张慧智	(7607)
陆地生态系统碳水通量贡献区评价综述	张 慧,申双和,温学发,等	(7622)

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封面图说:麋鹿群在过河——麋鹿属于鹿科,是中国的特有动物。历史上麋鹿曾经广布于东亚地区,到 19 世纪时,只剩下在北京南海子皇家猎苑内一群。1900 年,八国联军攻陷北京,麋鹿被抢劫一空。1901 年,英国的贝福特公爵用重金从法、德、荷、比四国收买了世界上仅有的 18 头麋鹿,以半野生的方式集中放养在乌邦寺庄园内,麋鹿这才免于绝灭。在世界动物保护组织的协调下,1985 年起麋鹿从英国分批回归家乡,放养到北京大兴南海子、江苏省大丰等地。这是在江苏省大丰麋鹿国家级自然保护区放养的麋鹿群正在过河。

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

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两种常绿阔叶植物越冬光系统功能转变的特异性

钟传飞^{1,2}, 张运涛¹, 武晓颖³, 王桂霞¹, 董 静¹, 王丽娜¹, 常琳琳¹, 高荣孚^{2,*}

(1. 北京市农林科学院林业果树研究所,北京 100093; 2. 北京林业大学生物科学与技术学院,北京 100083;

3. 中国科学院动物研究所,北京 100101)

摘要:通过叶绿素荧光和P700氧化还原动力学同步测定,研究大叶黄杨(*Euonymus japonicus*)和锦熟黄杨(*Buxus spervirens* L.)的阳生叶和阴生叶在北京地区越冬进程,光系统Ⅱ(PSⅡ)和光系统Ⅰ(PSⅠ)功能转变机制的特异性。结果表明,入冬前0℃以上低温条件下,各叶片PSⅡ有效光量子效率Y(Ⅱ)(Effective quantum yield of PSⅡ)处于同一水平,但阳生叶Y(Ⅰ)(Effective quantum yield of PSⅠ)均高于阴生叶,同时各叶片Fo(Minimal fluorescence)和OJIP水平不完全相同:大叶黄杨两种叶片差异不显著,锦熟黄杨阳生叶显著低于其阴生叶;同步测定P700氧化还原变化表明,两种阴生叶在0—20 ms的P700氧化过程分两个阶段,尤其是锦熟黄杨2 ms后的氧化速率显著降低,而两种阳生叶0—20 ms基本保持同一氧化速率;两种阴生叶的两个光系统量子效率比Y(Ⅰ)/Y(Ⅱ)<1,两种阳生叶Y(Ⅰ)/Y(Ⅱ)=1。入冬后,各类叶片PSⅡ受到不同程度光抑制,而PSⅠ光量子效率Y(Ⅰ)均先增加后减小,Y(Ⅰ)/Y(Ⅱ)发生不同程度增加,Y(Ⅱ)和两个光系统的平衡能力均依次为锦熟黄杨阴生叶>锦熟黄杨阳生叶>大叶黄杨阳生叶>大叶黄杨阴生叶;冬季大叶黄杨阴生叶J相的相对强度高于锦熟黄杨阴生叶,而两种阳生叶OJIP动力学变化几乎消失;同步测定P700氧化还原变化表明,锦熟黄杨阴生叶2 ms即达到Pm(Maximal P700 change),其他叶片0—20 ms保持同一氧化速率,阳生叶Fo、P700氧化速率和Pm均低于阴生叶。返青后,各叶片两个光系统功能逐渐恢复。可见,冬季低温或低温强光逆境会导致阳生叶和阴生叶的两个光系统功能和互动机制发生不同转变。

关键词:大叶黄杨;锦熟黄杨;光系统;越冬;光抑制

Specificity of photosystems function change of two kinds of overwintering broadleaf evergreen plants

ZHONG Chuanfei^{1,2}, ZHANG Yuntao¹, WU Xiaoying³, WANG Guixia¹, DONG Jing¹, WANG Lina¹, CHANG Linlin¹, GAO Rongfu^{2,*}

1 Institute of Forestry and Pomology, Beijing Academy of Agriculture and Forestry Sciences, Beijing, 100093, China

2 College of Biology Science and Technology, Beijing Forestry University, Beijing 100083, China

3 Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, China

Abstract: photoinhibition often occurs in winter for most evergreen plants, which is particularly true in sun leaves. Lots of photoprotective approaches could be induced to prevent from photodestruction for the plants. Photoinhibition and photoprotection mechanisms were studied much more on conifer tree species than broadleaves ones, and more in PSⅡ than PSⅠ. In this paper, two evergreen broadleaved plantstree species (*Euonmymus japonicus* and *Buxus spervirens* L.) under different light environments were studied during winter. The two woody species were introduced from subtropical areas to Beijing. Specificity of both photosystem Ⅱ (PSⅡ) and photosystem Ⅰ (PSⅠ) changes of the two woody species were

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*通讯作者 Corresponding author. E-mail: zhongchuanfei2008@gmail.com

studied using methods of synchro-monitoring chlorophyll fluorescence and P700 redox kinetics.

The results were shown that the low temperature above 0°C didn't inhibit the effective PS II yield $Y(II)$ for each species at the end of October, while Fo and OJIP values of the sun leaves of *Buxus spervirens* L. were lower than those of the shade leaves. Meanwhile P700 oxidization of the sun leaves of the two species kept at the same rate from 0ms to 20ms, but the oxidation rate of the shade leaves of the two species decreased after 2ms, particularly in *Buxus spervirens* L.. Under this case, $Y(I)/Y(II)$ ratio of the sun leaves for both two species were 1, while the values of the shade leaves for both two species of were lower than 1.

During winter, PS II photoinhibition occurred in almost all of the leaves for both species. The order of the $Y(II)$ value from the highest one to the lowest one in winter were as following: shade leaves of *Buxus spervirens* L., sun leaves of *Buxus spervirens* L., shade leaves of *Euonymus japonicus* and sun leaves of *Euonymus japonicus*. Whereas both the relative efficiency of PS I and the ratio of $Y(I)/Y(II)$ increased in winter. Low temperature led to disequilibrium between PS II and PS I of shade leaves of *Euonymus japonicus*, while combined stresses of low temperature and high light led to the same disequilibrium in the sun-leaves of both two species. In the winter OJIP kinetics of sun leaves disappeared, meanwhile that of shade leaves was still active at some extent.

Lots of photoprotective channels could be induced in the overwintering leaves, which could not be consistent in different leaves. State transitions occurred in both of the two species. Nonlinear electron transport maybe more important to *Euonymus japonicus*. The capacity of light harvesting of the sun leaves decreased to decrease the inhibition of photosystem center,. Photoinhibition of PS II was one of the most protective mechanism for the electron transporters in downstream in both of the species in mid-winter. Photoinhibition of the sun leave was much more significant than that of shade leaves. Photoprotection capacity of *Buxus spervirens* L. was much higher than that of *Euonymus japonicus*, which was probably due to the difference in ROS clearing ability under low temperature stress. In conclusion, the degree of photoinhibition and the of photoprotective channels for overwintering leaves in two evergreen broadleaved tree species were different, which leads to the specificity in the photosystems' function.

Key Words: *Euonymus japonicus*; *Buxus spervirens* L.; photosystem; overwintering; photoinhibition

随着城市园林的发展,原产于亚热带的常绿阔叶植物大叶黄杨(*Euonymus japonicus*)和锦熟黄杨(*Buxus spervirens* L.)被引种并广泛应用于我国北方城市绿化,由于抗寒能力的差异,冬季不同类型常绿植物会发生不同程度的光抑制。由于北温带和寒带地区原产的常绿植物以针叶植物为主,越冬光抑制研究相对深入^[1-2],Öquist系统地总结了欧洲赤松越冬过程光保护机制^[1],在冬季气温骤变条件下,尤其是冰点以下低温,常绿针叶植物往往通过增强天线系统热耗散、活性氧清除能力和非线性电子传递能力^[3-5],以及关闭PS II反应中心^[6-11]等各种方式减小过多激发能对光合膜的伤害。当外界气温超出了植物承受的阈值后,就会形成光抑制甚至光破坏。

常绿阔叶植物越冬光温胁迫研究相对较少,前期研究表明,冬季大叶黄杨阳生叶同时遭受低温强光双重胁迫,PS II光抑制比其阴生叶更严重,其热耗散机制与常绿针叶植物不同^[12-14],冬季大多常绿针叶植物PS II天线系统热耗散(NPQ)大幅增强^[1, 15],但原产亚热带的大叶黄杨被引种到北京地区后,冬季NPQ反而减弱^[12-13],可见后者越冬光保护机制具有特殊性。由于研究手段限制,常绿植物越冬光温胁迫研究主要集中在PS II光抑制方面^[1-2],对与PS I的研究较少。本研究将通过同步测定叶绿素荧光和830 nm的吸收^[16-17],探讨两种常绿植物(大叶黄杨和锦熟黄杨)阳生叶和阴生叶越冬进程的PS II和PS I功能的动态转变机制。

1 材料与方法

1.1 试验材料

北京林业大学校园内自然生长在高层建筑物两侧的阴生与阳生的大叶黄杨(*Euonymus japonicus*)和锦

熟黄杨(*Buxus spervirens* L.),选取植株顶层成熟叶片为实验对象。地理位置为:40°N, 116°19' E, 海拔50 m左右, 属暖温带大陆性季风气候。

根据气温波动而进行取样测定, 每次测定时间为9:00, 采用离体方式, 从室外将带叶片的枝条剪下, 插入水中, 暗适应10 min后, 带回室内立即进行测定, 设3次重复。

1.2 测定方法

1.2.1 气温测定

采用HOBO便携式气象站自动记录和BoxCar Pro 4.3软件进行数据处理(美国)。

1.2.2 叶绿素荧光与P700测定

用德国WALZ公司生产的Daul-PAM100叶绿素荧光-P700同步测定系统进行荧光动力学和P700氧化还原动力学同步测定, 分别采用饱和脉冲和快速诱导2种模式进行。

(1) 饱和脉冲模式: 饱和脉冲强度为 $3500 \mu\text{mol photons} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, 800 ms/次, 光化光强度为 $134 \mu\text{mol photons} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, 采样频率为2 ms/点, 测定参数包括实时荧光(F_t)、暗(光)适应后最小荧光 F_0 (F_0')、暗(光)适应后最大荧光 F_m (F_m')、稳态荧光(F_s)、暗(光)适应后P700最大氧化态 P_m (P_m'), P700实时还原态P700 red, 以及通过这几个参数计算得到的PS II最大量子产额 $F_v/F_m = (F_m - F_0)/F_m$ 、PS II有效量子产额 $Y(\text{II}) = (F_m' - F)/F_m'$, 由于供体侧限制引起的PS I非光化学能量耗散的量子产量 $Y(\text{ND}) = 1 - \text{P700red}$, 由于受体侧限制引起的PS I非光化学能量耗散的量子产量 $Y(\text{NA}) = (P_m - P_m')/P_m$, PS I的量子产量 $Y(\text{I}) = 1 - Y(\text{ND}) - Y(\text{NA})$ ^[18-20]。

(2) 快速诱导模式: 饱和脉冲强度为 $3500 \mu\text{mol photons} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, 800 ms, 采样频率10 $\mu\text{s}/\text{点}$, 在测量OJIP快速荧光动力学的同时, 同步测量830 nm吸收, 反映P700氧化还原状态转变, 从而测得PS II和PS I的快速变化^[21-26]。

2 结果与分析

2.1 PS II与PS I光量子效率变化

图1表明, 气温随冬季来临呈波动式降低, 正午日照强度(PAR)亦如此, 日最低气温于2007年11月上中旬降至0℃下, 此时PAR在 $800 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ 以上; 日最高气温于翌年1月上旬降至0℃下; 翌年1月下旬气温达到最低, 日最高和最低气温分别为-4℃和-10℃, 此时PAR达到冬季最低值, 为 $600 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ 左右, 对于低温下的叶片来说仍较强。返青时气温逐渐回升, 日最高和最低气温分别在翌年2月中旬和下旬升至0℃上, PAR也随之升高。

两种常绿阔叶植物 $Y(\text{II})$ 变化趋势(图2)与 F_v/F_m 变化趋势基本一致, 入冬初期(11月上旬前), 两种阴生叶 $Y(\text{II})$ 相对稳定, 而两种阳生叶小幅降低; 11月中下旬气温降至0℃下, 各叶片PS II发生不同程度光抑制(甚至光破坏); 12月下旬锦熟黄杨阳生叶 $Y(\text{II})$ 降至最低, 并保持至1月下旬气温最低时, 其他叶片均在1月下旬降到最低。冬季低温强光双重胁迫使阳生叶PS II光抑制更严重, $Y(\text{II})$ 排序: 锦熟黄杨阴生叶>锦熟黄杨阳生叶>大叶黄杨阴生叶>大叶黄杨阳生叶。返青后, 各类叶片 $Y(\text{II})$ 均随气温回升而升高。

图3表明, 入冬初期, 各叶片PS I相对活性均呈增加趋势, 锦熟黄杨阳生叶波动较大; 12月上中旬至1月下旬, 各叶片 $Y(\text{I})$ 均转变为下降趋势, 除锦熟黄杨阴生叶外, 均降至入冬前水平; 返青后锦熟黄杨阴生叶降低速率减缓, 其他叶片稍有回升。总体上, 阳生叶 $Y(\text{I})$ 高于阴生叶。

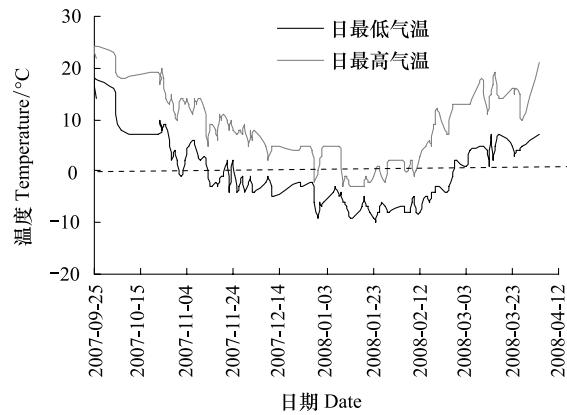


图1 2007—2008年度北京地区越冬进程气温变化

Fig. 1 Air temperature changes from Sep., 2007 to Mar., 2008 in Beijing

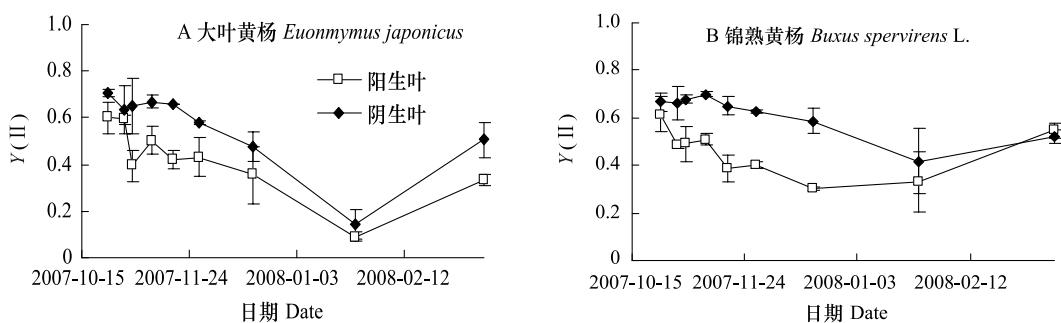


图2 2007—2008年度越冬进程大叶黄杨与锦熟黄杨Y(Ⅱ)变化

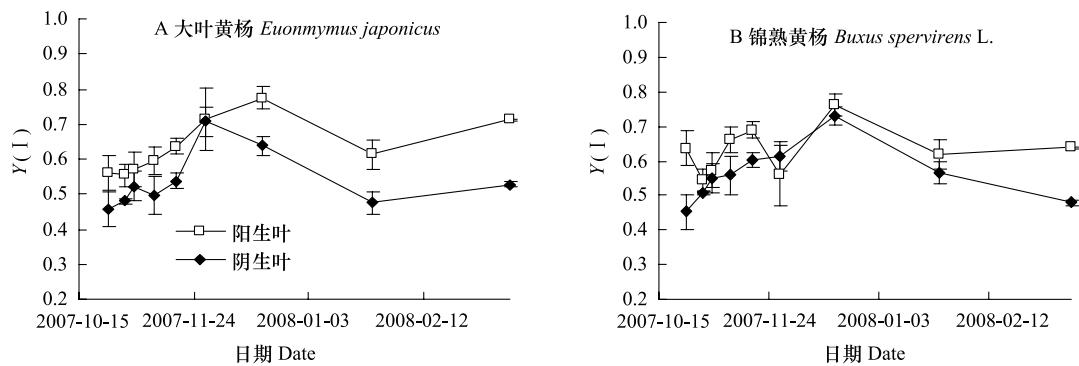
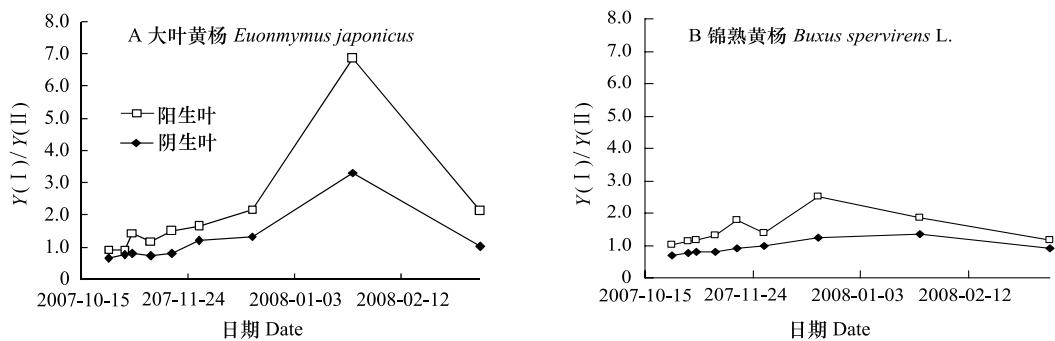
Fig. 2 $Y(II)$'s changes of overwintering *Euonymus japonicus* and *Buxus spervirens L.* from 2007 to 2008

图3 2007—2008年度大叶黄杨与锦熟黄杨越冬进程Y(I)变化

Fig. 3 $Y(I)$'s changes of overwintering *Euonymus japonicus* and *Buxus spervirens L.* from 2007 to 2008

$Y(I)/Y(II)$ 反映PS II与PS I平衡程度,图4表明入冬前,两种阳生叶 $Y(I)/Y(II)$ 处于1左右,说明PS II与PS I平衡相对正常,两种阴生叶稍低于1,说明PS I相对活较低;入冬后,各类叶片 $Y(I)/Y(II)$ 逐渐上升,12月中旬,两种阳生叶 $Y(I)/Y(II)$ 达到2,两种阴生叶升至1左右;之后,气温降至最低,大叶黄杨两种叶片 $Y(I)/Y(II)$ 继续升至最大值,大叶黄杨阳生叶达到7,阴生叶达到3,而锦熟黄杨阳生叶开始下降,其阴生叶仍始终保持1左右。返青后,光系统平衡逐渐恢复,大叶黄杨阳生叶 $Y(I)/Y(II)$ 降到2左右,其他叶片均恢复至1左右。可见,冬季各叶片PS II与PS I功能和平衡性发生了不同转变。

图4 2007—2008年度大叶黄杨与锦熟黄杨越冬进程 $Y(I)/Y(II)$ 变化Fig. 4 $Y(I)/Y(II)$'s changes of overwintering *Euonymus japonicus* and *Buxus spervirens L.* from 2007 to 2008

2.2 PS II、PSI原初反应动力学变化

为了进一步探讨越冬进程中常绿阔叶植物PS II和PS I电子传递动力学的变化,本研究进一步测定了OJIP快速荧光动力学和P700氧化还原动力学的变化。结果表明,入冬前大叶黄杨阳生叶 F_0 与阴生叶接近,

而锦熟黄杨阳生叶 F_o 显著低于阴生叶,入冬后随着气温下降,两种植物的两类叶片 F_o 均随之降低,大叶黄杨下降幅度较大,返青后两种植物 F_o 迅速回升(图 5)。

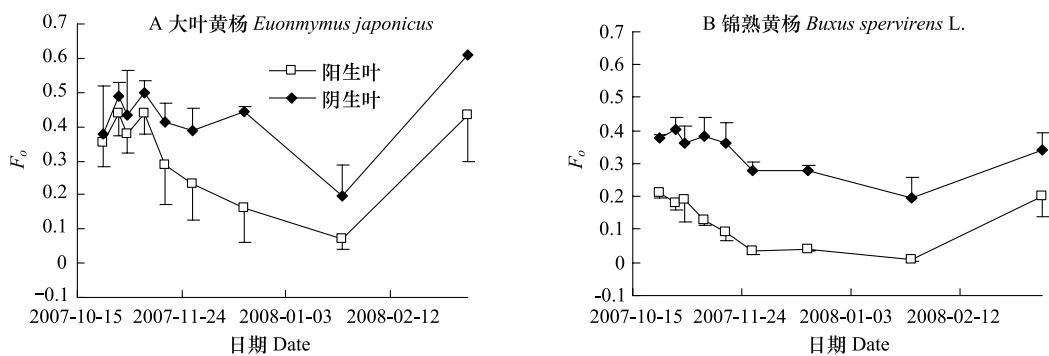


图 5 大叶黄杨与锦熟黄杨越冬进程的 F_o 变化

Fig. 5 F_o changes of overwintering *Euonymus japonicus* and *Buxus spervirens* L. from 2007 to 2008

图 6 表明,入冬前大叶黄杨阴生叶与阳生叶 OJIP 曲线几乎重合,且波动正常,说明 Q_A 到 PQ 库电子传递运转通畅;而锦熟黄杨阳生叶 OJIP 强度显著低于阴生叶,说明全日照条件下,阳生叶对入冬前气温降低(图 1)作出响应,降低了 PS II 电子传递通量。

冬季各叶片 O-P 斜率及 P 峰值均大幅降低,两种阳生叶 OJIP 几乎与时间轴重合,说明 PS II 电子传递通量极低;两种阴生叶仍保持一定波动幅度:锦熟黄杨 JIP 斜率相对较高,说明其 PS II 仍保持一定电子传递通量,而大叶黄杨 J 与 P 相当,说明 $Q_A^- Q_B$ 和 $Q_A^- Q_B^-$ 的还原受阻^[27]。

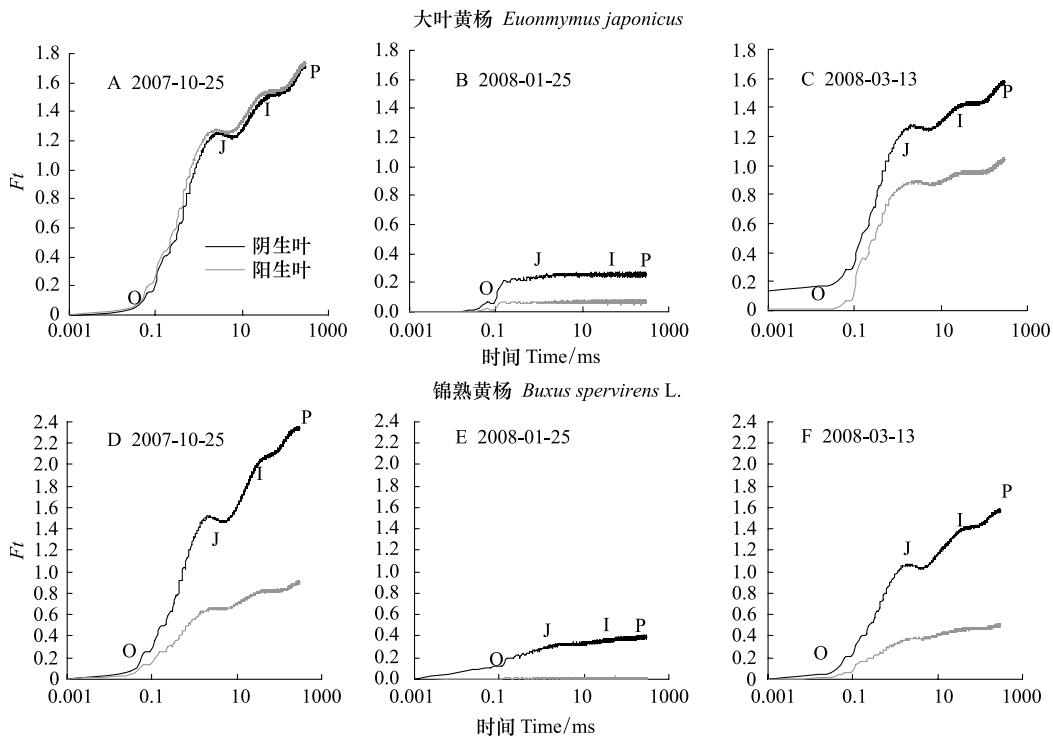


图 6 2007—2008 年度秋冬春大叶黄杨与锦熟黄杨 OJIP 变化

Fig. 6 OJIPs changes of overwintering *Euonymus japonicus* and *Buxus spervirens* L. from 2007 to 2008

返青时两种植物 OJIP 迅速恢复,大叶黄杨阴生叶 O-J 基本恢复到了入冬前水平,阳生叶未完全恢复,二者 JIP 斜率均低于入冬前水平(图 6: C),说明 $Q_A^- Q_B$ 和 $Q_A^- Q_B^-$ 的还原速率未完全恢复;锦熟黄杨两种叶片各相

强度虽未达到入冬前水平,但 JIP 斜率与入冬前接近(图 6: F), 阳生叶 I 相波动幅度小于入冬前,说明 $Q_A^- Q_B^{2-}$ 的还原速率尚未完全恢复^[27]。

图 7 表明, P700 与 OJIP 变化相关联, 入冬前, 两种阴生叶 P700 氧化过程分两个阶段: 0—2ms 快速氧化阶段(与 O-J 相同步), 2—20ms 慢速氧化并达到 P_m 阶段(与 J-I 相同步), 锦熟黄杨阴生叶 2ms 前后氧化速率差异更显著; 而两种阳生叶在 0—20ms 保持同速氧化, 锦熟黄杨阳生叶 P_m 高于其他三者。

冬季, 两种阴生叶 P_m 变化幅度不大, 大叶黄杨 P700 氧化过程与入冬前类似, 锦熟黄杨则在 2 ms 后即达到 P_m , 即氧化速率与重还原速率持平, 说明 PS II 向 PS I 供给电子的能力较强; 两种阳生叶氧化速率及 P_m 均低于入冬前水平, 0—20ms 保持同速, 且低于阴生叶。冬季除了锦熟黄杨阴生叶外, 其他三者 20 ms 后 P700 还原幅度均显著降低, 进一步说明后者 PS II 电子传递通量降低, 导致向 PS I 供给电子能力减弱。

返青后, 各叶片 P700 氧化还原动力学基本恢复到入冬前状态, 两类阴生叶 P_m 强度增加。

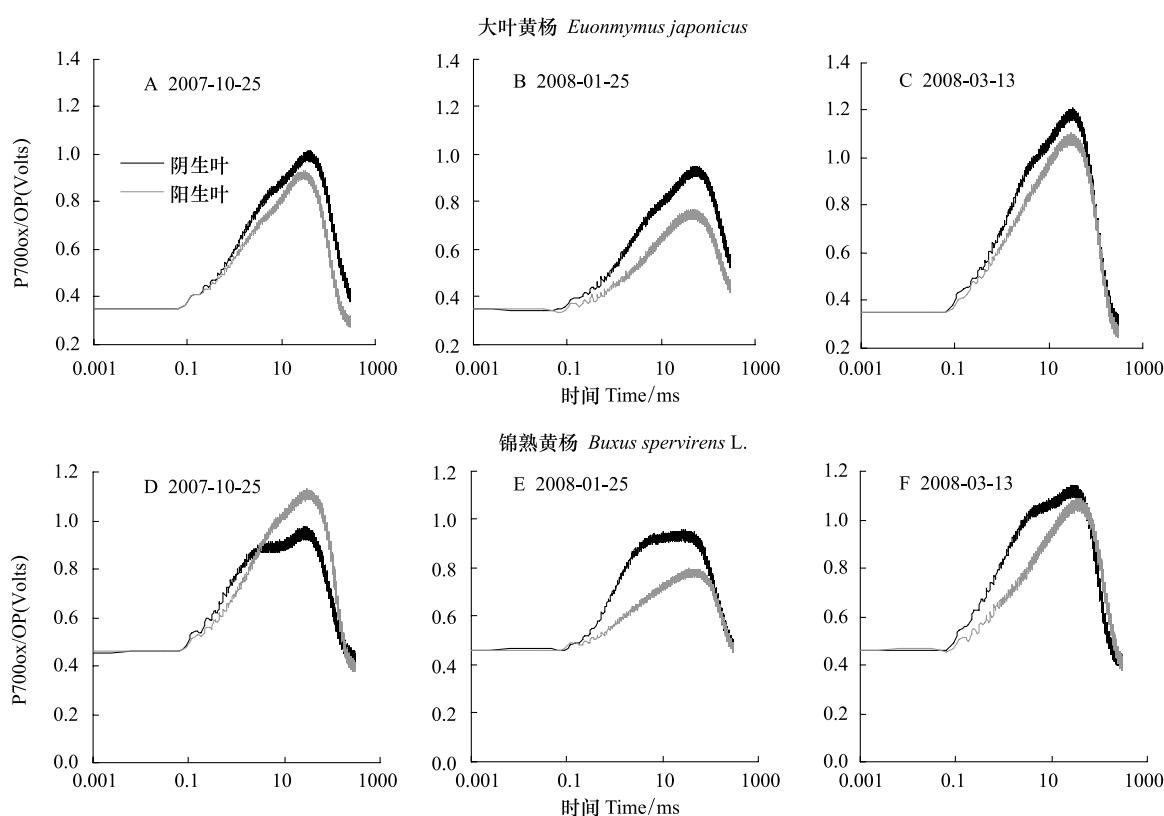


图 7 2007—2008 年度秋冬春大叶黄杨与锦熟黄杨快速 P700 变化

Fig. 7 Fast P700s changes of overwintering *Euonymus japonicus* and *Buxus spervirens* L. from 2007 to 2008

3 讨论

冬季两种阔叶植物阴生叶与阳生叶 PS II 均发生不同程度光抑制(图 2), 这与针叶植物类似^[1], 但两类植物的光保护机制并不相同^[12-15], 对 PS I 功能及其与 PS II 的互动转变机制进行了同步研究, 这在 Daul-PAM100 双通道荧光仪上市前很难实现, 结果表明, 各叶片两个光系统对季节变化的感受和响应机制存在差异。

3.1 阴生叶越冬光系统功能转变机制

入冬前, Adams 等认为冰点以上低温条件下, 常绿植物阴生叶不会发生光抑制^[28-30], 本研究表明, 10 月底两种阴生叶 PS II 虽未发生光抑制(图 6), 但 $Y(I)/Y(II) < 1$ 说明 PS I 遭受一定抑制(图 3, 图 4), 可能是低温钝化碳同化酶活^[13], 导致末端激发压伤害的结果。图 7 结果进一步表明, 此时两种阴生叶 P700 在 2 ms 前后的氧化过程发生了不同转变: 虽然 2ms 与 Q_A^- 还原同步^[27], 但 P700 变化取决于其供体侧与受体侧的共同作

用,OJIP 变化均正常,排除了供体侧差异的可能性(图 6),因此推断两种阴生叶 P700 受体侧存在差异,大叶黄杨可能存在较强的 Mehler 反应^[24, 31-32],导致其 2 ms 后氧化速率仍较高,但仍需进一步研究。

大量研究表明,冬季胁迫会导致大多数常绿植物 PS II 光抑制,并推断会对 PS I 起到光保护作用^[1, 33-34],本研究通过实测两个光系统量子效率发现,入冬后两种阴生叶 PS II 发生不同程度光抑制,大叶黄杨较严重(图 2, 图 6),而 Y(I) 不但未降低,反而呈现上升趋势,说明 PS II 光抑制对其下游产生光保护的同时,发生了状态转变^[35-36],从而调节激发能的分配模式。

当气温继续降低时,两种阴生叶 PS I 活性相继开始下降(图 3),虽然二者 Y(I) 的转变不同步,但均在 Y(II) 降至 0.6 时发生,暗示着这可能是低温胁迫下,PS II 对 PS I 光保护的关键值。深冬时,大叶黄杨阴生叶 Y(I)/Y(II) 突然升至 3,表明 PS I 非线性电子传递加强,而锦熟黄杨两个光系统仍保持较强平衡能力(图 4)。OJIP 与 P700 的结果则进一步说明,此时两种阴生叶 PS II 与 PS I 间电子传递动力学发生不同转变,虽然锦熟黄杨两个光系统均遭受光抑制,但仅是电子通量降低,其电子传递动力学仍较正常,而大叶黄杨 PS II 受体侧电子传递受阻,PS I 受体侧非线性电子传递加强。

由此可见,两种植物应对冬季温度胁迫的方式和能力不同,锦熟黄杨适应能力较强,很可能与其在低温下 POD、SOD 和 CAT 活性升高^[37],活性氧清除较强有关。

3.2 阳生叶越冬光系统功能转变机制

越冬过程,低温强光双重胁迫,导致两种阳生叶的两个光系统功能发生了更多元化的转变。

入冬前,感受 10 月下旬冰点以上低温后,锦熟黄杨阳生叶即作出了响应,Fo 和 OJIP 强度显著降低,叶色变褐,但 Y(II) 仍较高,说明其阳生叶通过降低天线系统捕光能力,减小 PS II 反应中心供体侧激发压,因此,其 P700 供体侧电子通量被降低,导致其 Pm 高于其他叶片(图 7),这可能也是导致其阳生叶 P700 氧化过程与其阴生叶不同的主要原因。而这种低温对大叶黄杨和亚高山常绿针叶植物的天线系统影响不大^[38]。可见,不同种植物阳生叶对同一环境变化的感受机制不同。

入冬后,两种阳生叶 PS II 电子传递活性相继降低(图 6),这与以往研究一致^[12-15],其中锦熟黄杨对初冬低温较敏感,但其 Y(II) 最低值高于大叶黄杨,再次说明其适应能力较强。深冬时,两种阳生叶与其阴生叶 Y(II) 差异随气温降低而减小(图 2),则说明温度逐渐成为 PS II 胁迫的主要因素。

Y(I) 结果(图 3)表明阳生叶也发生了与阴生叶类似的状态转变^[35-36];Y(I)/Y(II) 结果(图 4)表明,冬季低温强光双重胁迫,使大叶黄杨 PS I 非线性电子传递速率^[34]大于其阴生叶,并使锦熟黄杨也发生了一定 PS I 非线性电子传递;冬季两种阳生叶 Fo 均显著低于阴生叶,则说明降低天线系统捕光能力,可能是阳生叶另一主要光保护方式。在阳生叶 PS II 光抑制较严重导致 P700 供体侧还原能力较低的情况下,两种阳生叶 P700 氧化速率和 Pm 均低于各自阴生叶,说明阳生叶 P700 受体侧可能发生了较强的环式电子传递。

总之,低温强光双重胁迫导致阳生叶比阴生叶 PS II 光抑制更严重,状态转变和非线性电子传递速率更强,且可能以环式电子传递为主,同时减小天线系统也是阳生叶主要光保护方式之一。锦熟黄杨感受低温的能力、光系统自我保护和平衡能力均比大叶黄杨强。冬季光保护机制的多元化程度较高,可能是导致阔叶植物能量耗散机制与针叶植物不同的主要原因。

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ACTA ECOLOGICA SINICA Vol. 32 ,No. 23 December ,2012(Semimonthly)
CONTENTS

Maternal thermoregulation during gestation affects the phenotype of hatchling Chinese skinks (<i>Eumeces chinensis</i>) : testing the maternal manipulation hypothesis	LI Hong, ZHOU Zongshi, WU Yanqing, et al (7255)
Effects of conspecific and interspecific interference competitions on cache site selection of Siberian chipmunks (<i>Tamias sibiricus</i>)	SHEN Zhen, DONG Zhong, CAO Lingli, et al (7264)
Characterization of ammonia volatilization from polluted river under aeration conditons: a simulation study	LIU Bo, WANG Wenlin, LING Fen, et al (7270)
Diurnal activity patterns and environmental factors on behaviors of Bar-headed Geese <i>Anser indicus</i> wintering at Caohai Lake of Guizhou, China	YANG Yanfeng, ZHANG Guogang, LU Jun, et al (7280)
Impacts of snow cover change on soil water-heat processes of swamp and meadow in Permafrost Region, Qinghai-Tibetan Plateau	CHANG Juan, WANG Gengxu, GAO Yongheng, et al (7289)
Spatial-temporal changes of urban patch wetlands in Changsha, China	GONG Yingbi, JING Lei, PENG Lei, et al (7302)
Modeling of carbon and water fluxes of Qianyanzhou subtropical coniferous plantation using model-data fusion approach	REN Xiaoli, HE Honglin, LIU Min, et al (7313)
Ecological compensation standard for controlling nitrogen non-point pollution from farmland: a case study of Yixing City in Jiang Su Province	ZHANG Yin, ZHOU Yuchen, SUN Hua (7327)
Static toxicity evaluation of chemical wastewater by PFU microbial communities method	LI Zhaoxia, ZHANG Yuguo, LIANG Huixing (7336)
Emergy evaluation of an agro-circulation system in Beijing suburb: take Jianyan village as a case study	ZHOU Liandi, HU Yanxia, WANG Yazhi, et al (7346)
Research on the cooling effect of Xi'an parks in summer based on remote sensing	FENG Xiaogang, SHI Hui (7355)
The dynamics of spatial and temporal changes to forested land and key factors driving change on Hainan Island	WANG Shudong, OUYANG Zhiyun, ZHANG Cuiping, et al (7364)
Impact of different sowing dates on green water footprint of maize in western Jilin Province	QIN Lijie, JIN Yinghua, DUAN Peili (7375)
The dynamic variation of maize (<i>Se a mays L.</i>) population growth characteristics under cultivars-intercropped on the Loess Plateau	WANG Xiaolin, ZHANG Suiqi, WANG Shuqing, et al (7383)
Effect of different planting methods on root-shoot characteristics and grain yield of summer maize under high densities	LI Zongxin, CHEN Yuanquan, WANG Qingcheng, et al (7391)
Heavy metal contaminant in development process of artificial biological Soil Crusts in sand-land	XU Jie, AO Yanqing, ZHANG Jingxia, et al (7402)
Effects of enhanced UV-B radiation and nitrogen on photosynthetic pigments and non-enzymatic protection system in leaves of foxtail millet (<i>Setaria italica</i> (L.) Beauv.)	FANG Xing, ZHONG Zhangcheng (7411)
Photosynthetic response of different ecotype of <i>Illicium lanceolatum</i> seedlings to drought stress and rewetting	CAO Yonghui, ZHOU Benzhi, CHEN Shuanglin, et al (7421)
Seasonal variations in the stems of <i>Larix principis-rupprechtii</i> at the treeline of the Luya Mountains	DONG Manyu, JIANG Yuan, WANG Mingchang, et al (7430)
Influence of terrain on plant biomass estimates by remote sensing: a case study of Guangzhou City, China	SONG Weiwei, GUAN Dongsheng, WANG Gang (7440)
Effects of exponential fertilization on biomass allocation and root morphology of <i>Catalpa bungei</i> clones	WANG Lipeng, YAN Ziyi, LI Jiyue, et al (7452)
Effects of fire damages on <i>Larix gmelinii</i> radial growth at Tahe in Daxing'an Mountains, China	WANG Xiaochun, LU Yongxian (7463)
A model for water consumption by mountain jujube pear-like	XIN Xiaogui, WU Pute, WANG Youke, et al (7473)
Specificity of photosystems function change of two kinds of overwintering broadleaf evergreen plants	ZHONG Chuanfei, ZHANG Yuntao, WU Xiaoying, et al (7483)

-
- Effects of drought on fluorescence characteristics of photosystem II in leaves of *Ginkgo biloba* WEI Xiaodong, CHEN Guoxiang, SHI Dawei, et al (7492)
- Numerical classification and ordination of forest communities in habitat of Sichuan Snub-nosed Monkey in Hubei Shennongjia National Nature Reserve LI Guangliang, CONG Jing, LU Hui, et al (7501)
- Impact of inorganic anions on the cadmium effective fraction in soil and its phytoavailability during salinization in alkaline soils WANG Zuwei, YI Liangpeng, GAO Wenyan, et al (7512)
- Photosynthetic adaptability of the resistance ability to weak light of 2 species *Spiraea* L. LIU Huimin, MA Yanli, WANG Baichen, et al (7519)
- Fine root longevity and controlling factors in a *Phoebe Bournei* plantation ZHENG Jinxing, HUANG Jinxue, WANG Zhenzhen, et al (7532)
- Analysis on spatial structure and scenarios of carbon dioxide emissions from tourism transportation XIAO Xiao, ZHANG Jie, LU Junyu, et al (7540)
- The hydrological response to human activities in Guishui River Basin, Beijing LIU Yuming, ZHANG Jing, WU Pengfei, et al (7549)
- Socio-economic impacts of under-film drip irrigation technology and sustainable assessment: a case in the Manas River Basin, Xinjiang, China FAN Wenbo, WU Pute, MA Fengmei (7559)
- Effects of pattern and timing of high temperature exposure on the mortality and fecundity of *Aphis gossypii* Glover on cotton GAO Guizhen, LÜ Zhaozhi, XIA Deping, et al (7568)
- Physiological responses of *Eucalyptus* trees to infestation of *Leptocybe invasa* Fisher & La Salle WU Yaojun, CHANG Mingshan, SHENG Shuang, et al (7576)
- Carbon storage capacity of a *Betula alnoides* stand and a mixed *Betula alnoides* × *Castanopsis hystrix* stand in Southern Subtropical China: a comparison study HE Youjun, QIN Lin, LI Zhiyong, et al (7586)
- Distribution and ecological risk assessment of 7 heavy metals in urban forest soils in Changsha City FANG Xi, TANG Zhijuan, TIAN Dalun, et al (7595)
- Review and Monograph**
- The relationship between humans and the environment at the urban-rural interface: research progress and prospects HUANG Baorong, ZHANG Huizhi (7607)
- Flux footprint of carbon dioxide and vapor exchange over the terrestrial ecosystem: a review ZHANG Hui, SHEN Shuanghe, WEN Xuefa, et al (7622)

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E-mail: shengtaixuebao@rcees.ac.cn 网 址: www.ecologica.cn

编辑部主任 孔红梅

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shengtaixuebao@rcees.ac.cn

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