

臭氧与干旱对植物复合影响的研究进展

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摘要 地表臭氧(O₃)浓度和干旱频率的持续增加成为限制植物生长的重要因素。O₃通过气孔扩散进入植物组织内部, 产生并积累活性氧(ROS)自由基, 促发细胞程序性死亡。干旱破坏植物抗氧化系统对ROS的解毒和修复功能, 导致ROS累积。两种胁迫对植物的影响都是积累ROS并引发氧化胁迫, 使植物的光合作用和生理代谢机能受到限制, 最终阻碍植物生长, 导致生物量降低。然而, O₃和干旱胁迫对植物的复合效应可能是协同加重植物损伤, 也可能是拮抗减轻植物伤害, 二者的交互影响存在复杂的作用过程。一方面, O₃引起气孔响应滞后甚至失灵, 使植物对于两种胁迫的响应变得迟钝, 进而加重植物的蒸散失水和O₃毒害。另一方面, 干旱使植物气孔关闭, 从而降低对O₃的吸收量和水分蒸发, 但长期干旱限制CO₂的吸收, 最终导致植物的生长受限。植物的响应过程不仅取决于两种胁迫作用的先后次序和持续时间, 而且受到植物本身生理代谢差异的影响。该文结合国内外研究, 从气孔、光合碳代谢、抗氧化系统和生长发育等方面阐述了O₃和干旱胁迫对植物代谢调节和生长发育的复合影响, 并提出了未来研究的发展方向。

关键词 臭氧; 干旱; 交互; 植物; 响应

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Interactive effects of ozone and drought stress on plants: A review

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Abstract

Ground-level ozone (O₃) and drought are two key factors limiting plant growth. O₃ can enter into the plant tissue through the stomata, then causing the formation of reactive oxygen species (ROS) which inspires programmed cell death. Drought usually induces the accumulation of ROS due to damage to antioxidant systems of plants. The effects of two kinds of stress on plants are similar due to the accumulation of ROS, resulting in reduced photosynthesis rate and physiological metabolism, eventually decreased plant growth and biomass. Nevertheless, O₃ and drought interacts synergistically to accumulate detrimental effects or antagonistically to reduce harmful effects. Actually, it is complex interactive process between O₃ and drought. On the one hand, O₃ triggers stomatal sluggishness or even dysfunction, which exacerbates water transpiration of leaves, water loss from plants and further O₃ phytotoxicity. On the other hand, drought induces stomatal closure, and thus protecting plants against the O₃ influx and evaporation of water. However, prolonged drought could limit the uptake of CO₂ and thus result in reduced plant growth. The response of plants to both O₃ and drought not only depends on the occurring sequence and duration of any factor but also rely on the difference in physiological metabolism of the plant itself. The interactive effects of O₃ and drought on stomatal characteristics, photosynthetic carbon mechanism, antioxidant response and growth development are reviewed in this paper and the aspects to be further studied are also suggested.

Key words O₃; drought; interaction; plant; response

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21世纪快速的都市化、工业化和交通运输使地表臭氧(O₃)浓度逐渐增加, 世界各地出现不同程度

的O₃污染。其中, 英国、法国、德国、瑞士和意大利等多个欧洲国家持续10天的O₃浓度都超过了90

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$\text{nmol}\cdot\text{mol}^{-1}$ (ICP Vegetation, 2011), 亚洲和拉丁美洲等快速发展中国家的 O_3 平均浓度也超过 $40 \text{ nmol}\cdot\text{mol}^{-1}$ (Matyssek *et al.*, 2014)。在中国人口密集的特大城市(如北京、上海、广州等) O_3 浓度超过 $100 \text{ nmol}\cdot\text{mol}^{-1}$ (Chang & Lee, 2006; Li *et al.*, 2011), 预计到2100年, 全球大部分地区的年平均 O_3 浓度将达到 $40 \text{ nmol}\cdot\text{mol}^{-1}$ 以上, 夏季北半球地区甚至将超过 $70 \text{ nmol}\cdot\text{mol}^{-1}$ (Sitch *et al.*, 2007)。地表 O_3 作为具有植物毒性的空气污染物, 对自然植物种群、作物和森林的危害被广泛关注(Matyssek & Innes, 1999; Ashmore, 2005; Matyssek *et al.*, 2012)。长时间暴露于 O_3 下的敏感植物会出现表现可见的叶片伤害症状(Mills *et al.*, 2011; Feng *et al.*, 2014), 并伴随光合速率下降(Dizengremel, 2001; Renaut *et al.*, 2009; Wittig *et al.*, 2009), 生长缓慢及早衰(Matyssek & Sandermann, 2003), 进而削弱植物的抗逆性、竞争力和适应力, 最终降低碳汇潜力(Miller & McBride, 1999; Karnosky *et al.*, 2007; Edwards & Zak, 2011), 对生态系统的结构、功能和碳循环产生长远影响。现有的 O_3 污染可导致森林树种生物量损失达10%, 农作物产量的损失为5.3%–17.5% (Broadmeadow, 1998; Feng & Kobayashi, 2009)。至2030年, 全球农作物因 O_3 的影响年经济损失将高达170–350亿美元 (Avnery *et al.*, 2011)。

随着人口增长以及农业、能源和工业部门的扩增, 对水的需求也迅猛增加, 近年来不断发生的大规模密集干旱事件在欧洲、非洲、亚洲、澳大利亚、南美洲、中美洲和北美洲产生了广泛影响(Comte, 1998; Schubert *et al.*, 2004; Dai, 2011)。1950–2010年中国平均每年的受灾面积达到了 $21.6 \times 10^6 \text{ hm}^2$ (邱海军等, 2013)。干旱对植物的影响表现为: 降低气孔导度、影响水分蒸散(Sadras & Milroy, 1996; Bréda *et al.*, 2006), 改变叶片光系统组分含量(Anjum *et al.*, 2003), 损害光合反应器官(Fu & Huang, 2001), 降低卡尔文循环的酶活性(Monakhova & Chernyadèv, 2002), 使植物的细胞分裂和增长受损(Nonami, 1998), 限制叶片的数量, 缩减叶片的伸张, 降低比叶面积(Abrams *et al.*, 1994), 从而限制植物生长, 最终导致产量降低(Schuppler *et al.*, 1998; Monakhova & Chernyadèv, 2002; Kaya *et al.*, 2006)。中国在2006–2011年间, 由干旱造成的直接经济损失达到1 150亿元(中国水利部, 2006–2010;

国家统计局, 2007–2012)。气候变化导致的干旱使全球森林在2000–2009年间减少了5.5亿T净初级生产力(Zhao & Running, 2010)。

政府间气候变化专门委员会(IPCC, 2013)报告指出由气候变化导致的环境因素改变对生物体系有直接、间接以及交互的影响。在植物旺盛生长的时期, 充足的光照和高温往往导致 O_3 浓度爆发性的升高, 并常常伴随着干旱的发生, 从而使得植物同时受到高浓度 O_3 和干旱的双重胁迫(Matyssek *et al.*, 2010)。

目前, O_3 和干旱对植物的影响存在如下有争议的结论: 一方面, O_3 引起的气孔滞后效应加重了植物在干旱胁迫下的水分蒸散损失, 从而对植物产生协同伤害(Grulke *et al.*, 2003b; Karnosky *et al.*, 2005); 另一方面, 干旱诱导气孔关闭, 限制进入叶片的 O_3 剂量, 起到保护植物的拮抗作用, 降低了 O_3 伤害(Panek & Goldstein, 2001; Panek *et al.*, 2002; Grünhage & Jager, 2003; Dizengremel *et al.*, 2013); 也有一些研究显示二者胁迫下植物并不受交互作用的影响(Le Thiec *et al.*, 1994; Wittig *et al.*, 2009)。在 O_3 暴露下, 干旱对植物的保护作用仅限于叶片水平, 但对整株植物而言, 干旱的伤害大于 O_3 的伤害(Alonson *et al.*, 2014; Pollastrini *et al.*, 2014)。此外, 由于 O_3 刺激糖基酶类基因表达促进了葡聚糖代谢, 而干旱则是抑制其代谢, 导致两种胁迫下上述代谢过程并没有受到影响(Iyer *et al.*, 2013), 减轻了植物在交互作用下所受到的伤害。因此, O_3 和干旱对植物的伤害不仅取决于 O_3 进入细胞的量(Heath, 1994), 而且与植物通过酶类和非酶类反应去除氧自由基的能力(Manderscheid *et al.*, 1991)及自身防御和修复过程的活跃度有关(Sandermann, 1996)。

深入了解 O_3 和干旱复合胁迫下植物的生长响应机制对于理解陆地生态系统应对气候变化至关重要。本文总结了2000–2016年间 O_3 和干旱交互作用对植物影响的研究(表1)。发表的文章中, 欧美国达到71.0%, 而中国只占14.6%。虽然中国早在1974年就由王勋陵和陈庆诚提出了 O_3 污染对植物的伤害, 但是由于20世纪90年代国家治理的重点主要放在一次污染物上, O_3 作为二次污染物直到2013年才被环保部门纳入城市的空气质量监测指标。而国内 O_3 和干旱复合胁迫对植物影响的研究始于Xu等(2007)对冬小麦(*Triticum aestivum*)的研究。鉴于前人在 O_3 (如许宏等, 2007; 寇太记等, 2009)或干旱

表1 2000–2016年间O₃与干旱对复合植物影响的研究列表

Table 1 A list on the combined effects of ozone and drought on plants between 2000 and 2016

植物类型 Plant type	植物种类 Plants species	树龄(年) Tree-age (year)	实验方法 Experimental method	O ₃ 处理 O ₃ treatment (nmol·mol ⁻¹)	干旱处理 Drought treatment	研究内容 Research content	参考文献 Reference
草本 Herbaceous	冬小麦 <i>Triticum aestivum</i>	–	温室 Greenhouse	80	SWC 60%, 45%, 35%	叶片O ₃ 吸收与产量 Leaf ozone uptake and grain yield	Khan & Soja, 2003
	冬小麦 <i>Triticum aestivum</i>	–	OTC	125	SWC 35%–40%	生理生长 Physiology and biochemistry	Xu <i>et al.</i> , 2007
	冬小麦 <i>Triticum aestivum</i> , 圆锥小麦 <i>Triticum turgidum</i> ssp. <i>durum</i>	–	OTC	83	SWC 42%	生理生化、产量 Physiology and biochemistry, grain yield	Biswas & Jiang, 2011
	春小麦 <i>Triticum aestivum</i> , <i>Triticum durum</i>	–	OTC	AA + 50	40%对照SWC 40% SWC of control	抗氧化系统 Antioxidant defense systems	Herbinger <i>et al.</i> , 2002
	大豆 <i>Glycine max</i>	–	OTC	0.70 × AA, 60	–0.8MPa黎明前叶片水势 – 0.8 MPa Pre-dawn leaf water potential	蒸散 Evapotranspiration	Rana <i>et al.</i> , 2012
	菜豆 <i>Pharosalus vulgaris</i>	–	GC	48, 87, 150	SWC 6%–15%	气孔 Stomata	Hoshika <i>et al.</i> , 2013
	番茄 <i>Lycopersicon esculentum</i>	–	大田 Field	AA, AA + 80	18%–33%田间持水量 18%–33% Field capacity	果实自由基含量 Radical contents in fruit	Pirker <i>et al.</i> , 2003
	<i>Leontodon hispidus</i>	–	GC	70	50%田间持水量 50% Field capacity	脱落酸(ABA)作用机制 Mechanisms of action of abscisic acid	Wilkinson & Davies, 2009
	<i>Medicago runcatula</i>	–	GC	70	以测定量灌溉 Adding measured amounts of water	生理生化、分子 Physiological, biochemical and molecular response	Iyer <i>et al.</i> , 2013
	烟草 <i>Nicotiana tabacum</i>	–	GC	200	适当灌溉 With holding water from the plants	分子(DHAR表达) Molecular (dehydroascorbate reductase overexpressing)	Eltayeb <i>et al.</i> , 2006
常绿、落叶乔木 Evergreen and deciduous trees	欧洲云杉 <i>Picea abies</i> , <i>Fagus sylvatica</i>	50; 60	开放式熏 气系统 A free-air fumigation system	2 × AA	NE (2年不同气候) NE (Climatic variation in two years)	地下影响(土壤呼吸、 根系生物量) Belowground effects (soil respiration, fine-root bio- mass)	Nikolova <i>et al.</i> , 2010
	欧洲云杉 <i>Picea abies</i> , <i>Fagus sylvatica</i>	–	NE	AA	NE (两种树分别12个和4 个不同地点) NE (12 and 4 different site conditions were used, respectively)	规模性生长关系 Size-growth relationship	Pretzsch & Dieler, 2011
	阿巴拉契亚山脉南部 森林 Southern Appa- lachian forest	成熟林 Mature forest trees	NE	AA	NE (3个不同地点在2–3年 的不同气候) (Three sites over 2–3 years)	生长和液流速率 Growth and sap flow velocity	McLaughlin <i>et al.</i> , 2007
常绿乔木 Evergreen trees	欧洲云杉 <i>Picea abies</i>	4	OTC	37	胁迫期停止灌溉 The irrigation system was turned off during the dry periods	叶肉细胞显微结构 Microscopic structures of meso- phyll cells	Kivimäenpää <i>et al.</i> , 2001
	欧洲云杉 <i>Picea abies</i>	2–5	OTC	26–30, 25–29, 29–33	以土壤水势确定灌溉水量 Watered by the soil water potential	叶绿素、养分和生长 Chlorophyll, mineral nutrients and growth	Wallin <i>et al.</i> , 2002
	欧洲云杉 <i>Picea abies</i>	2–5	OTC	1.5 × AA	以土壤水势确定灌溉水量 Watered by the soil water potential	叶片细胞结构 Cell structural changes in the needles	Kivimäenpää <i>et al.</i> , 2003
	<i>Abies veitchii</i>	6	GC	50	土壤水势6.19–30.96 kPa; 30.96–97.98 kPa Soil water potential 6.19–30.96 kPa; 30.96–97.98 kPa	生长 Growth	Feng & Shi- mizu, 2005
	<i>Abies concolor</i>	2; 53	OTC, NE	52, 30–35	0, 10%, 25%, 50%的年降 水量减少 0, 10%, 25%, 50% Reduc- tions in total annual pre- cipitation	模型模拟胁迫下生长 Simulation growth by model under stress	Retzlaff <i>et al.</i> , 2000
	<i>Pinus halepensis</i>	2	OTC	69	50%对照灌溉水量 Half the water supplied to control	叶片抗氧化酶类 Antioxidative enzymes in needles	Alonso <i>et al.</i> , 2001
	<i>Pinus halepensis</i>	4	GC	300	以叶片水势和气体交换临 界值确定灌水量 Characterized by very low leaf water potential and gas exchange values	叶片生理 Physiological response of needles	Manes <i>et al.</i> , 2001

表1 (续) Table 1 (continued)

植物类型 Plant type	植物种类 Plants species	树龄(年) Tree-age (year)	实验方法 Experimental method	O ₃ 处理 O ₃ treatment (nmol·mol ⁻¹)	干旱处理 Drought treatment	研究内容 Research content	参考文献 Reference
常绿乔木 Evergreen trees	<i>Pinus halepensis</i>	3	GC	200	100%–50%缓慢水分散失 (中度); 以黎明前叶片水 势确定灌溉水量(重度) From 100% to 50% of the water loss by evapotranspi- ration (mild); watered by pre-dawn needle water potential (intensity)	叶片酶(PEPC) Phosphoenolpyruvatecarboxylase in needles	Fontaine <i>et al.</i> , 2003
	<i>Pinus halepensis</i>	2	OTC	AA + 40	50%对照灌溉水量 Half the water supplied to control	生理生化补偿过程 Compensation processes in physiology and biochemistry	Inclan <i>et al.</i> , 2005
	<i>Quercus ilex</i>	3	气候室 Climatic chambers	250	20 mL水每间隔一周灌溉 20 mL of water per plant every week	生理响应 Physiological responses	Vitale <i>et al.</i> , 2008
	<i>Quercus ilex</i> ssp. <i>ilex</i> , 长角豆 <i>Ceratonia</i> <i>siliqua</i>	1	OTC	37; 57	50%对照灌溉次数 Half the watered times to control	生理生化 Physiology and biochemistry	Ribas <i>et al.</i> , 2005
	<i>Quercus ilex</i> ssp. <i>ilex</i> , <i>Q. ilex</i> ssp. <i>ballota</i>	1–2	OTC	31; 49	50%对照灌溉水量 Half the water supplied to control	气体交换、生长和生物量 Gas exchange, growth and bio- mass	Alonso <i>et al.</i> , 2014
	西黄松 <i>Pinus ponderosa</i>	6–8	NE	40–70	NE	O ₃ 和碳吸收 O ₃ and carbon uptake	Panek & Gold- stein, 2001
	西黄松 <i>Pinus ponderosa</i>	40	NE	58–60, 64–67, 80	黎明前木质部水势<–1.2 MPa Xylem potentials <–1.2 MPa at predawn	碳获取 Carbon acquisition	Grulke <i>et al.</i> , 2002
	西黄松 <i>Pinus ponderosa</i>	5–7	NE	53	NE (2年不同气候) NE (Climatic variation in two years)	O ₃ 暴露度量参数 O ₃ exposure metrics parameters	Panek <i>et al.</i> , 2002
	西黄松 <i>Pinus ponderosa</i>	7	NE	AA	NE (4个不同地点) NE (Four sites)	吸收模型参数 uptake modeling	Parameters for O ₃ Panek, 2004
	海南蒲桃 <i>Syzygium</i> <i>hainanense</i> , 糖胶树	当年 Current year	OTC	75	40%–50%土壤相对含水量 40%–50% Relative soil water content	光合生理 Photosynthetic physiology	Hao <i>et al.</i> , 2014
落叶乔木 Deciduous trees	长芒杜英 <i>Elaeocarpus</i> <i>apiculatus</i> , 壳菜果 <i>Mytilaria laosensis</i> , 黧 蒴锥 <i>Castanopsis fissa</i> 醉香含笑 <i>Michelia</i> <i>macclurei</i> , 樟 <i>Cinnamomum cam-</i> <i>phora</i> , 红花荷 <i>Rhodoleia championii</i> , 壳菜果 <i>Mytilaria</i> <i>laosensis</i>	当年 Current year	OTC	150	50%对照灌溉次数 Half the watered times to control	荧光生理 Chlorophyll <i>a</i> fluorescence	Li <i>et al.</i> , 2015
	醉香含笑 <i>Michelia</i> <i>macclurei</i> , 樟 <i>Cinnamomum cam-</i> <i>phora</i> , 红花荷 <i>Rhodoleia championii</i> , 壳菜果 <i>Mytilaria</i> <i>laosensis</i>	1	OTC	20	两天一次灌溉 Watered once in two days	根、茎、叶和总生物量及根茎比 Root biomass, stem biomass, leaf biomass, total biomass and root/shoot ratio	Ye <i>et al.</i> , 2014
	<i>Fagus crenata</i>	3	GC	60	70%对照灌溉水量 70% Water supplied to control	叶片物候和芽抗寒性 Leaf phenological characteristics and bud frost hardiness	Yonekura <i>et al.</i> , 2004
	<i>Fagus crenata</i>	3	GC	60	70%对照灌溉水量 70% Water supplied to control	叶片抗氧化系统 Leaf antioxidative systems	Watanabe <i>et al.</i> , 2005
	<i>Fagus sylvatica</i>	60	NE	2 × AA	NE (3年不同气候) NE (Climatic variation in three years)	生理生化 Physiology and biochemistry	Löw <i>et al.</i> , 2006
	<i>Fagus sylvatica</i>	60	NE	2 × AA	NE (2年不同气候) NE (Climatic variation in two years)	细根抗氧化物 Antioxidants in fine roots	Haberer <i>et al.</i> , 2008
	<i>Fagus sylvatica</i>	–	NE	AA	NE (9个不同地点) NE (Nine sites)	日生长 Daily growth	Kuehn <i>et al.</i> , 2015
	<i>Fagus sylvatica</i> , 夏栎 <i>Quercus robur</i> , 辽杨×中东杨 <i>Popu-</i> <i>lus maximowiczii</i> × <i>P. berolinensis</i>	1	OTC	0.95 × AA	50%田间持水量 50% Field capacity	生长和生理响应 Growth and physiological re- sponses	Pollastrini <i>et al.</i> , 2010
	岳桦 <i>Betula ermanii</i>	2	GC	50	土壤水势 6.19–30.96 kPa, 30.96–97.98 kPa Soil water potential 6.19–30.96 kPa, 30.96–97.98 kPa	生长、生理生化 Growth、 physiology and biochemistry	Shimizu & Feng, 2007
	元宝槭 <i>Acer truncatum</i>	1	OTC	102–147	40%–50%田间持水量 40%–50% Field capacity	气孔响应 Stomatal response	Wen <i>et al.</i> , 2014
	元宝槭 <i>Acer truncatum</i>	1	OTC	102–147	40%–50%田间持水量 40%–50% Field capacity	生长和生理 Growth and physi- ology	Li <i>et al.</i> , 2015

表1 (续) Table 1 (continued)

植物类型 Plant type	植物种类 Plants species	树龄(年) Tree-age (year)	实验方法 Experimental method	O ₃ 处理 O ₃ treatment (nmol·mol ⁻¹)	干旱处理 Drought treatment	研究内容 Research content	参考文献 Reference
落叶乔木 Deciduous trees	辽杨×中东杨 <i>Populus maximowiczii</i> × <i>P. berolinensis</i>	当年 Current year	OTC	0.95 × AA	150 mL水每天灌溉 150 mL of water a day	不同冠层叶绿素荧光 Chlorophyll <i>a</i> fluorescence along a crown	Desotgiu <i>et al.</i> , 2012
	辽杨×中东杨 <i>Populus maximowiczii</i> × <i>P. berolinensis</i>	当年 Current year	OTC	0.95 × AA	150 mL水每天灌溉 150 mL water a day	光合、生长和同位素 Photo-synthesis, growth and stable isotope	Pollastrini <i>et al.</i> , 2013
	欧洲山杨×银白杨 <i>Populus tremula</i> × <i>P. alba</i>	当年 Current year	GC	CF + 120	SWC 35%	生理、蛋白质组 Physiological and proteomic	Bohler <i>et al.</i> , 2013
	辽杨×中东杨 <i>Populus maximowiczii</i> × <i>P. berolinensis</i>	当年 Current year	OTC	44–53	60%, 20%对照灌溉水量 60%, 20% Water respect to control	生理生化、生长和同位素 Physiological and biochemistry, biomass and isotope	Pollastrini <i>et al.</i> , 2014

OTC, 开顶气室; AA, 环境浓度; CF, 过滤空气; NF, 未过滤空气; CF/NF+, 过滤/未过滤空气再加一定浓度臭氧; GC, 生长室; NE, 自然生长环境; SWC, 土壤含水量。

OTC, open top chamber; AA, ambient air; CF, charcoal-filtered air; NF, non-filtered air; CF/NF+, charcoal-filtered/non-filtered air + extra ozone; GC, growth chamber; NE, natural environment; SWC, soil water capacity.

(如孙梅霞等, 2004; 田汉勤等, 2007; 杨帆等, 2007) 单因子胁迫对植物的影响方面已有大量阐述, 本文在总结国内外O₃和干旱复合影响的研究理论和结果的基础上, 深入探讨此两种胁迫交互作用条件下植物的响应机制及响应过程, 旨在明确植物如何应对由气候变化导致的O₃和干旱两种胁迫, 同时指出未来需要侧重的研究方向。

1 臭氧和干旱对植物的复合影响

1.1 植物的气孔导度响应

气孔是植物体与外界环境进行气体交换的门户, 通过控制CO₂和水分对蒸腾、光合、呼吸等重要生理过程进行调节, 也是诸如O₃等气体污染物进入植物的主要通道。气孔调节的首要功能是平衡与碳收支相关的水分消耗(Cowan, 1978)。植物应对O₃和干旱胁迫的最初防御门户就是气孔。O₃在通过气孔进入植物的同时伴随水汽的蒸发, 气孔关闭的响应机制理论上会保护植物抵抗这两种胁迫, 形成物理防御抵制O₃吸收和水汽的散失(图1)。渐进式(progressive)的土壤干旱阻碍了植物对O₃的吸收(Panek *et al.*, 2002; Matyssek *et al.*, 2006)。Ciais等(2005)的结果显示, 即使O₃浓度在增加了40%的严重胁迫下, 由于初夏的干旱迫使气孔关闭, 植物对O₃的吸收仍低于潮湿年份的平均吸收值。据此一些田间限制性灌溉的保护措施也在实际中得到应用。例如古巴农民在预防夏季O₃浓度升高对作物的毒害方面, 通过提前1–2天控制对叶类作物(莴苣(*Lactuca sativa*)和烟草(*Nicotiana tabacum*))的灌溉, 成功地降低了O₃带来的伤害(ICP Vegetation, 2011)。然而, 此种方法

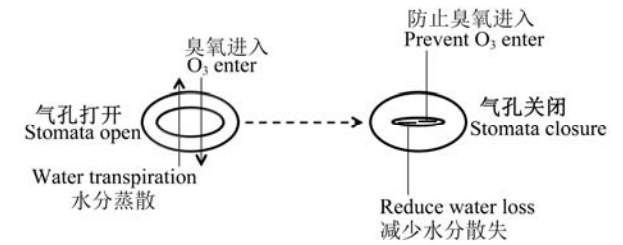


图1 气孔在臭氧与干旱胁迫下的调节。
Fig. 1 Regulation of the stomata under the condition of O₃ and drought.

仅针对一些在干旱胁迫下表现出诸如气孔关闭和叶表面积减少的品种才是有效的(ICP Vegetation, 2011)。在大气和土壤都潮湿的环境中, 即使暴露在低浓度O₃下, 通过气孔进入到植物的O₃通量也是较高的; 而在水分缺乏的环境中, 即使在高浓度O₃条件下, 干旱诱导的气孔关闭仍极大地限制了植物对O₃的吸收(Retzlaff *et al.*, 2000; Paoletti, 2006)。而且干旱对气孔导度和O₃吸收的限制有记忆效应(memory-effects) (Karlsson *et al.*, 2000)。可见气孔内在行为机制的改变可能是为了降低O₃胁迫引起的植物细胞壁木质化和膜损伤(Heath & Taylor, 1997; Maier-Maercker, 1998)。但干旱条件下的气孔关闭虽然降低了植物对O₃的吸收, 同时也限制了植物对CO₂的吸收(Panek & Goldstein, 2001), 进而影响植物生长。气孔的响应(关闭)也并不是始终如一的(Wittig *et al.*, 2007), 如O₃诱发的气孔反应滞后(sluggish)(Paoletti & Grulke, 2010; Hoshika *et al.*, 2012, 2014; Dumont *et al.*, 2013)所导致的气孔关闭缓慢(Pearson & Mansfield, 1993; Karlsson *et al.*, 1995)或气孔导度增大(Oksanen, 2003), 降低了气孔

在干旱条件下对蒸腾的抑制, 从而扰乱了植物对水分亏缺的响应(Hoshika *et al.*, 2014), 导致O₃和干旱交互作用下植物的伤害加重(Retzlaff *et al.*, 2000; Pollastrini *et al.*, 2010)。这种气孔在时间上的滞后效应与植物物种品种(Paoletti & Grulke, 2010; Hoshika *et al.*, 2012)、胁迫的程度(Hoshika *et al.*, 2012)及季节的变化有关(Hoshika *et al.*, 2014)。

O₃和干旱交互作用下, 干旱诱导的气孔关闭被认为是保护植物免受O₃伤害的防御措施。干旱条件下种植园的西黄松(*Pinus ponderosa*)也显示O₃伤害的短期保护效应(Panek & Goldstein, 2001)。然而, 这一现象尚未得到普遍证实。尽管干旱诱导的气孔关闭降低了植物对O₃的吸收, 但干旱胁迫同时也增加了叶片的自由基(Buckland *et al.*, 1991; Biehler & Fock, 1996), 使植物受到伤害, 因而干旱和O₃的复合胁迫对植物可能是有害的(Heber *et al.*, 1995)。自然环境中O₃与干旱对气孔的交互作用取决于品种(Pell *et al.*, 1993; Ribas *et al.*, 2005; Biswas & Jiang, 2011; Wagg *et al.*, 2012)、胁迫出现次序(Bohler *et al.*, 2013)、胁迫程度(Le Thiec *et al.*, 1994)、一天内胁迫的时段(Le Thiec *et al.*, 1994)、植物的生长期(Alonso *et al.*, 2001; Skärby *et al.*, 1998)以及季节的变化(Pell *et al.*, 1993)。对O₃敏感的冬小麦品种, 在O₃和干旱的交互作用下显示出对O₃的抗性; 然而另一抗性品种(*Triticum turgidum* ssp. *durum*)则丧失了对O₃的抗性(Biswas & Jiang, 2011)。两种胁迫发生的次序对交互作用也至关重要(Le Thiec *et al.*, 1994; Bohler *et al.*, 2013)。如果干旱发生在O₃胁迫之前, 干旱首先促发气孔导度关闭, 进而保护了随后发生的O₃对植物的伤害。有实验证实O₃暴露下的*Leontodon hispidus*施用外源脱落酸(ABA)后, 渐进的干旱胁迫会降低气孔导度(Wilkinson & Davies, 2009), 通过干旱影响气孔对ABA的敏感性和离子泵, 降低了细胞的膜损伤(Torsethaugen *et al.*, 1999), 减轻了植物的伤害程度。而当干旱发生在O₃胁迫之后, 因ABA诱导的气孔关闭被O₃诱导植物释放的乙烯引起的气孔缓慢响应所抑制(Tanaka *et al.*, 2005), 导致的气孔滞后效应加重了干旱对植物的伤害(Wilkinson & Davies, 2009)。但也有科学家指出干旱诱导的ABA对气孔在O₃胁迫下的敏感程度的影响仍未明确(Wilkinson & Davies, 2010)。

综上所述, 植物的气孔响应取决于发生胁迫的

时期和两种胁迫交互作用的强度: 如果是O₃首先损害气孔调节, 那么植物对O₃和干旱胁迫的抗性将减弱; 如果干旱先于O₃发生, 则可能通过调节气孔关闭而使植物免受O₃伤害。然而干旱的这种保护作用也可能因叶片的气孔关闭阻碍CO₂固定而受到限制, 最终严重影响整株植物的生长。

1.2 植物光合碳代谢响应机制

光合碳代谢中二磷酸核酮糖羧化酶(Rubisco)是C₃植物碳固定的关键酶, 同时也是植物光呼吸的关键酶。O₃通过降低Rubisco酶活性、酶亚基丰度(Brendley & Pell, 1998; Pelloux *et al.*, 2001)影响植物的生理功能, 并导致净光合速率、最大羧化速率以及气孔导度的降低(Guidi *et al.*, 2001; Morgan *et al.*, 2003; Biswas & Jiang, 2011)。在卡尔文循环中一些氧化还原调节酶类(如Rubisco活化酶、果糖-1,6-二磷酸酶、景天庚酮糖-1,7-二磷酸酶和核酮糖-5-磷酸激酶)在O₃胁迫下受到抑制而导致其丰度降低(Bohler *et al.*, 2007, 2010, 2013), 使卡尔文循环被激活。土壤因有效水分减少而降低光合速率也主要是因为Rubisco活性的降低(Bota *et al.*, 2004), 进而导致植物的生长受限(Huang & Fu, 2000)。Rubisco对胁迫的响应往往因植物品种不同和环境的改变而不同。如水分胁迫下烟草的Rubisco酶类受到抑制降低了Rubisco活性(Parry *et al.*, 2002), 而夏栎(*Quercus robur*)的Rubisco活化酶增加导致Rubisco降解(Sergeant *et al.*, 2011), *Pinus halepensis*的Rubisco和Rubisco活化酶转录的丰度及蛋白含量则并未改变(Pelloux *et al.*, 2001)。在O₃与干旱的交互作用下, 因两种胁迫各自对植物Rubisco的影响不同和植物本身生长阶段的不同, 表现出更加复杂多变的结果: 复合胁迫下杨树(*Populus tremula* × *P. alba*) Rubisco的降解是增加的, 但并不显著, 而且与干旱相比O₃的影响更强(Bohler *et al.*, 2013)。O₃对*P. halepensis* Rubisco的影响在植物生长后期也可能强于干旱, O₃胁迫下Rubisco活性降低, 但是干旱无持续的显著作用, 使复合胁迫下Rubisco活性降低(Pelloux *et al.*, 2001)。但也有结果显示*P. halepensis*的Rubisco活性并未因O₃而改变, 而是因干旱显著降低, 使两种胁迫下Rubisco活性显著降低(Gerant *et al.*, 1996)。

光合碳代谢的磷酸烯醇丙酮酸羧化酶(PEPc)对固定CO₂有重要作用(Hatch *et al.*, 1969), 而且PEPc活性增强可激发三羧酸循环保持氮代谢运行的补偿

机制(Tietz & Wild, 1991)。PEPc活性的变化不仅取决于胁迫时间,而且因品种变化而不同。例如有实验证实干旱条件下豌豆(*Pisum sativum*)和*Arachis pintoi*中的PEPc活性是增强的(Sharma & Nisha, 1993; Fedina & Popova, 1996),棉花(*Gossypium hirsutum*)中PEPc活性表现出降低的趋势(Pandey *et al.*, 2001),而*P. halepensis*中PEPc的活性、数量和转录都无显著改变(Fontaine *et al.*, 2003)。在高浓度O₃下,植物叶片的PEPc活性是增加的(Landolt *et al.*, 1994; Lutz *et al.*, 2000; Inclan *et al.*, 2005),但也可能随时间改变而发生变化。Fontaine等(2003)就指出三年生*P. halepensis*的PEPc活性只有在O₃暴露后期才是增加的,同时O₃和干旱交互作用下生长后期的PEPc活性也是增加的,但是比单独O₃的影响低。也有结果显示O₃和干旱复合胁迫对二年生*P. halepensis*的PEPc活性无影响(Inclan *et al.*, 2005)。因此,PEPc的活性因植物品种,胁迫发生时间、持续时间以及两种胁迫的作用强度不同而不同。

叶绿体电子传递链中, O₃使光合系统和三磷酸腺苷(ATP)酶的一些亚基显著降低(Bohler *et al.*, 2007, 2011),而植物对O₃伤害的抵御与O₃通量有关(Dizengremel *et al.*, 2008)。干旱加强植物气孔关闭,限制了O₃的吸收,使气体交换受限,但同时也影响了ATP酶(Tezara *et al.*, 1999; Flexas *et al.*, 2002),限制了光合电子传递速率(Vitale *et al.*, 2008)。O₃诱导铁氧还蛋白-NADP⁺-氧化还原酶在胁迫初期快速增加(Bohler *et al.*, 2013),这与氧化胁迫下植物的响应一致(Dizengremel *et al.*, 2008, 2009; Heath, 2008)。但在长期的O₃胁迫下铁氧还蛋白-NADP⁺-氧化还原酶会由于防御体系超负荷而降低,一直降低的光合系统亚基也可能是由叶绿体中ATP和NADPH累积引起,导致卡尔文循环活力降低,而这些都未在干旱胁迫中发现。O₃和干旱交互作用下引起卡尔文循环中的蛋白质含量降低,这与O₃单独胁迫的结果相似,但影响程度较低,并未产生显著的改变(Bohler *et al.*, 2013)。可见, O₃和干旱对植物光合碳代谢的影响与品种和胁迫强度及实际的环境状况有关,目前尚缺乏复合胁迫下相关蛋白质组调控机理研究。

1.3 植物抗氧化系统响应机制

植物受到胁迫时,细胞内部需要复杂的调控体系,包括活性氧(ROS)的信号传导、产生及清除来控制其受到的毒害作用。因此,植物进行氧化应激平

衡ROS的活性和抗氧化系统的能力至关重要。O₃和干旱胁迫对植物的影响最主要是诱导氧化应激的不同, O₃会进入叶片内部并迅速转换为ROS,导致氧化胁迫(Rao *et al.*, 2000; Ernst *et al.*, 2012),虽然严重的干旱也可导致氧化胁迫(Foyer & Noctor, 2000),但干旱胁迫下的植物应激更多是利用ROS作为内部产生信号的分子(Yao *et al.*, 2013)。因此, O₃胁迫下ROS会不断累积,而在干旱胁迫下ROS只是作为逆境胁迫的响应因子存在于叶绿体中。双重胁迫诱导大量ROS产生,使许多细胞成分(如细胞液、蛋白质、碳水化合物、核酸等)受到氧化伤害,进而激发了与防御有关的蛋白进行的解毒作用(Pääkkönen *et al.*, 1998),其中高活性的清除氧化伤害的酶类保护了植物免受胁迫伤害(Asada, 1997; Pasqualini *et al.*, 2001)。

抗坏血酸-谷胱甘肽(AsA-GSH)循环通过调节氧化还原反应防御ROS的伤害,是植物细胞中主要的抗氧化途径。植物会通过抗氧化物质的结合消除ROS的毒害,例如存在于叶绿体、细胞质、线粒体和过氧化物酶体中的一些抗氧化物质,如抗坏血酸盐、谷胱甘肽、维生素a、超氧化物歧化酶(SOD)和过氧化氢酶(CAT)以及AsA-GSH循环途径中抗坏血酸过氧化物酶(APX)、单脱水抗坏血酸还原酶(MDAR)、脱氢抗坏血酸还原酶(DHAR)和谷胱甘肽还原酶(GR)等构成细胞器中重要的抗氧化防御体系,防止过氧化氢(H₂O₂)的产生(Potters *et al.*, 2002)。Iyer等(2013)证实由于还原型AsA和GSH的增加, O₃和干旱复合胁迫下ROS的水平与无胁迫对照相近。干旱增加了*Fagus crenata*叶片的GSH含量,提高了抗性机制,减轻了植物受到的O₃伤害(Watanabe *et al.*, 2005)。O₃暴露下植物的APX、CAT、SOD等抗氧化酶类的活性和(或)丰度是增加的(Alonso *et al.*, 2001),且干旱条件下植物的GR和SOD也是增加的(Alonso *et al.*, 2001; Huseynova *et al.*, 2014),而与O₃和干旱的单独胁迫相比,两者交互作用下抗氧化酶类反而是降低的,从而推断两种胁迫的累积作用破坏了植物的防御体系(Wellburn *et al.*, 1996; Alonso *et al.*, 2001)。因此,植物对O₃与干旱的去氧化响应取决于两种胁迫诱导产生的抗氧化分子和酶类的多少。但目前仍缺乏转录水平与AsA-GSH循环中基因调控的蛋白酶活性的相关性研究(Creissen & Mullineaux, 2002; Iyer *et al.*, 2013)。

AsA是AsA-GSH循环中一种主要的抗氧化剂,

直接与羟基自由基、超氧化物和单线态氧反应,在光合作用调节中也起重要作用(Noctor & Foyer, 1998),并作为电子供体将 H_2O_2 还原为水,而AsA的生成需要NADPH的还原力,同时Rubisco活性降低,PEPC活性升高。质外体系统(质外体AsA和APX)是对氧化伤害的第一层防御体系(Luwe *et al.*, 1993; Sanmartin *et al.*, 2003)。植物对 O_3 的敏感性也与叶片组织AsA的氧化还原态有关(Conklin & Barth, 2004; Chen & Gallie, 2005)。另外,AsA也是植物细胞质、叶绿体、液泡、线粒体和质外体中主要的氧化还原缓冲剂(Potters *et al.*, 2002; Pignocchi *et al.*, 2003)。总AsA水平降低了由ROS对细胞造成的伤害程度,与植物的耐旱性有重要关系,而DHAR的活性增加与干旱胁迫的程度也有关(Sofa *et al.*, 2005)。干旱条件下,细胞质和叶绿体中的AsA发挥重要的解毒作用,且主要取决于植物的种类(Mittler & Zilinskas, 1994; Zhang & Kirkham, 1996)。欧洲云杉(*Picea abies*)针叶中总AsA含量因 O_3 胁迫而增加,同时干旱胁迫使其质外体AsA也显著增加,且在共同胁迫下两者都是显著增加的(Kronfuß *et al.*, 1998)。因此, O_3 和干旱复合胁迫可能增加了还原力,同时促进了氧化胁迫下植物的防护作用。

抗氧化系统在植物对 O_3 和干旱胁迫的抗性中发挥重要的作用, O_3 增加了抗氧化物的浓度和抗氧化酶的活性(Alonso *et al.*, 2001; Herbinger *et al.*, 2005)且增强了抗氧化系统相关的基因表达(Gupta *et al.*, 2005)。虽然AsA含量与植物的抗性密切相关,如烟草中DHAR过量表达也证实了增加的AsA含量增强了其对 O_3 和干旱的抗性(Chen & Gallie, 2005; Eltayeb *et al.*, 2006),但也有研究指出两种白车轴草(*Trifolium repens*)质外体中的AsA含量差异无法说明 O_3 的抗性差异(D'Haese *et al.*, 2005)。干旱胁迫也增加了植物叶片抗氧化物质的浓度或改变其氧化还原态(Šircelj *et al.*, 2005; Talbi *et al.*, 2015)。然而当干旱达到一定程度时,抗氧化物的活性却降低,从而使植物受到伤害(Quartacci & Navari-Izzo, 1992; Zhang & Kirkham 1994; Alonso *et al.*, 2001)。因此, O_3 和干旱胁迫下植物的抗氧化响应是多变的,因植物品种、胁迫时间及胁迫强度各异,其内在的作用机制也需进一步明确。

1.4 植物的生长响应

O_3 和干旱对不同植物的器官、组织和细胞具有

不同程度的氧化伤害,当胁迫达到一定程度时,首先伤害敏感植物的叶片,进而限制整株植物的生长。两种胁迫下叶片的表现伤害症状则各有特征。 O_3 引起叶片坏疽斑块和不规则的褪绿、萎黄斑点,而干旱引起叶片同质和渐进的变色,同时伴有叶片的发育不良和卷曲下垂(Bohler *et al.*, 2013)。 O_3 和干旱交互作用下的植物则并不表现为一致的加重伤害。与单独胁迫下的植物相比,双重胁迫可能减弱(Showman, 1991; Iyer *et al.*, 2013)或者加重(Bohler *et al.*, 2013)叶片受伤害的表型特征。因此,叶片的不同伤害症状表现可能是由于病斑的产生与胁迫诱导ROS大量生成并引发植物自身调节抗氧化系统有关,不一定是气孔吸收 O_3 所致(Grulke *et al.*, 2003a)。这也表明 O_3 和干旱的相互作用对植物的影响在表观上和形态学上可能是相似的或累积的。但即使 O_3 和(或)干旱胁迫下植物未表现出明显可见的叶片伤害症状,其生长最后也可能受到限制(Shimizu & Feng, 2007)。

O_3 和干旱都会引起光合速率的降低并由此影响净 CO_2 的固定(Flexas *et al.*, 2002; Wittig *et al.*, 2007; Biswas & Jiang, 2011),而在 O_3 胁迫之后发生的干旱加重了对植物净同化率和光合效率的伤害(Grulke *et al.*, 2002),导致生物量降低。生物量的降低包括种子质量和数量的降低(Flexas *et al.*, 2002; Biswas & Jiang, 2011),且 O_3 和干旱同时发生对植物生物量降低是累积效应(Biswas & Jiang, 2011)。不同的植物对胁迫的响应是不同的,且干旱对植物的影响可能更大。水分胁迫对夏栎的伤害影响并不明显,对欧洲山毛榉甚至没有影响,但降低了杨树(*Populus maximowiczii* × *P. berolinensis*)的生长,包括茎粗和生物量,而且 O_3 和干旱的交互作用加剧了对杨树叶绿素荧光参数和生长的伤害(Pollastrini *et al.*, 2010)。即使高浓度 O_3 促进土壤呼吸,增加了细根的生长,但是在干旱胁迫下欧洲云杉根系的生长仍然受到限制,而山毛榉却未有此现象,可能对云杉而言干旱更占主导地位(Nikolova *et al.*, 2010)。在德国克兰茨贝格的森林实验点也证实干旱的影响可能更大。 O_3 对山毛榉树的影响也因水分亏缺而大大降低,对茎粗和整个茎杆体积增量的有害影响很大程度上是因干旱造成的(Matyssek *et al.*, 2010)。

综上所述, O_3 和干旱的交互作用不仅依赖于植物本身和外部环境因素,而且依赖于两种胁迫的强

度以及发生的先后次序。尽管干旱诱导的气孔导度降低限制了 O_3 的吸收,但 O_3 被视作是一种附加的胁迫,改变了植物的生理,增加了氧化胁迫,引起抗氧化物的累积(Alonso *et al.*, 2001),从而植物更易受到其他环境胁迫(如干旱、病虫害、升温等)的伤害。而且,即使干旱初期可以保护植物抵御 O_3 伤害,但是这种保护作用也只限于短期内的叶片水平,长期的气孔关闭必将影响碳同化,导致生物量降低。由于干旱直接作用于植物的根部,影响到同化物的运输和分配,而 O_3 攻击的直接位点是植物的叶片,因此可能导致干旱对植物的伤害比 O_3 对植物的伤害更严重。同时,持续的土壤水分亏缺也使植物更易受到其他胁迫(如风、生物危害)的伤害,而长期的 O_3 胁迫也使树木更易受到干旱的伤害(Matyssek *et al.*, 2006)。

2 总结和展望

近地层 O_3 浓度升高和干旱这两种胁迫在自然界中是相随发生的。其复合作用常常引起累积效应。干旱引起的气孔关闭或许可以减少植物对 O_3 的吸收,并由此降低 O_3 的毒害作用。然而在水分胁迫期气孔关闭的保护作用也可能会受到 O_3 干扰,加重植物的伤害程度。因此两种胁迫的复合影响是由多种因素共同决定的。

O_3 和干旱交互作用因胁迫发生的先后次序而不同,植物对 O_3 的累积暴露阈值可归因于不同阶段生理的改变或是干旱发生的时间。 O_3 胁迫先于干旱发生时,气孔的延迟关闭加重干旱条件下的水分损失,使 O_3 能持续毒害植物。反之,干旱胁迫先于 O_3 发生时,干旱引起的气孔关闭形成最首要的自然屏障,抵御了 O_3 的进入。如常年生长在干旱环境中的地中海常绿植物可能延续了它们逐渐产生的内在的 O_3 抗性(Nali *et al.*, 2004)。当植物在 O_3 胁迫之前就曾有过其他胁迫时,植物在适应环境变化时附加了额外的负担, O_3 的伤害是累加的,对植物造成不可逆的永久伤害。总之,不管是单独的胁迫还是两者结合,都会因品种、 O_3 通量、抗氧化能力、敏感性、发生时间、生长期等不同引起植物对 O_3 和干旱的响应差异。

目前的文献报道 O_3 和干旱交互作用对植物的影响研究大多局限在光合、生理及生长指标等中观尺度上,但不同的研究方法和对象对于两种胁迫因

子的交互作用对植物内在机制的影响方面尚无明确结论。因此,未来的研究需要运用一些先进的分子生物学技术和手段更加系统深入地研究光合碳代谢过程中蛋白相互作用的调节及抗氧化内在机制,识别单因子胁迫与复合胁迫对植物生长的影响。同时包含更多的研究区域,更全面的物种响应,更集中的全球变化下多因子胁迫对植物抗性机制的研究,以便获得更加接近真实环境的实验结果。同时延长实验研究的时间,以便于更加明确植物对胁迫的短期和长期响应。生物信息学方法和高通量技术(如转录组学、蛋白质组学和代谢组学等)的应用可更加直观地阐释两种胁迫下植物的内在响应机制。将此类高新技术应用到室内高频率模拟和大田长周期接近自然的实验,对于进一步了解复合胁迫对植物生长的影响将会有更深的突破。由此,在明确 O_3 和干旱胁迫下植物的响应机理基础上,通过基因工程改进不同植物品种抗氧化胁迫酶类的表达,进而增强植物的抗性,以适应未来的多变气候。

自然界的植物是多样性的,面对的胁迫是多重的,但实验研究往往无法囊括不同品种、不同生长阶段以及多重胁迫的影响。最终的实验结果了解到的仅是局限于某一物种、某一生长期(幼树或成熟大树)对某一特定胁迫的响应。未来的研究方向是将个体的响应扩展至生态系统的尺度,并整合各种环境因素下的实验结果进行meta分析,在充分考虑到各种环境因素的交互作用对生态系统组成和功能影响的基础上,建立更加完善的生态系统模型,降低未来预测全球陆地生态系统碳、氮、水和养分循环变化时的不确定性。同时,在模型模拟基础上分析并确立不确定性的关键区域,进行多变量预测植物的气孔响应,并在长期的田间实验基础上,评价植物在复杂自然环境下的生长,进而准确模拟气孔对 O_3 和干旱的响应,这对于研究 O_3 和干旱复合胁迫环境下植物对水分利用的影响至关重要。

未来的研究需要将自然环境中的多因素胁迫结合,集成多因子交互作用的区域模型,并使用分子生物学的研究方法和技术手段对植物进行更微观的研究集成,从而全面地揭示植物对多因子环境胁迫的响应,并进行抗性品种的培育和改进风险评估。

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参考文献

- Abrams MD, Kubiske ME, Mostoller SA (1994). Relating wet and dry year ecophysiology to leaf structure in contrasting temperate tree species. *Ecology*, 75, 123–133.
- Alonso R, Elvira S, Castillo FJ, Gimeno BS (2001). Interactive effects of ozone and drought stress on pigments and activities of antioxidative enzymes in *Pinus halepensis*. *Plant, Cell & Environment*, 24, 905–916.
- Alonso R, Elvira S, González-Fernández I, Calvete H, García-Gómez H, Bermejo V (2014). Drought stress does not protect *Quercus ilex* L. from ozone effects: Results from a comparative study of two subspecies differing in ozone sensitivity. *Plant Biology*, 16, 375–384.
- Anjum F, Yaseen M, Rasul E, Wahid A, Anjum S (2003). Water stress in barley (*Hordeum vulgare* L.). II. Effect on chemical composition and chlorophyll contents. *Pakistan Journal of Agricultural Sciences*, 40(1–2), 45–49.
- Asada K (1997). The role of ascorbate peroxidase and monodehydroascorbate reductase in H_2O_2 scavenging in plants. *Oxidative Stress and the Molecular Biology of Antioxidant Defenses*, 34, 715–735.
- Ashmore MR (2005). Assessing the future global impacts of ozone on vegetation. *Plant, Cell & Environment*, 28, 949–964.
- Avnery S, Mauzerall DL, Liu JF, Horowitz LW (2011). Global crop yield reductions due to surface ozone exposure: 2. Year 2030 potential crop production losses and economic damage under two scenarios of O_3 pollution. *Atmospheric Environment*, 45, 2297–2309.
- Biehler K, Fock H (1996). Evidence for the contribution of the Mehler-peroxidase reaction in dissipating excess electrons in drought-stressed wheat. *Plant Physiology*, 112, 265–272.
- Biswas DK, Jiang GM (2011). Differential drought-induced modulation of ozone tolerance in winter wheat species. *Journal of Experimental Botany*, 62, 4153–4162.
- Bohler S, Bagard M, Oufir M, Planchon S, Hoffmann L, Jolivet Y, Hausman J-F, Dizengremel P, Renaut J (2007). A DIGE analysis of developing poplar leaves subjected to ozone reveals major changes in carbon metabolism. *Proteomics*, 7, 1584–1599.
- Bohler S, Sergeant K, Hoffmann L, Dizengremel P, Hausman J-F, Renaut J, Jolivet Y (2011). A difference gel electrophoresis study on thylakoids isolated from poplar leaves reveals a negative impact of ozone exposure on membrane proteins. *Journal of Proteome Research*, 10, 3003–3011.
- Bohler S, Sergeant K, Jolivet Y, Hoffmann L, Hausman J-F, Dizengremel P, Renaut J (2013). A physiological and proteomic study of poplar leaves during ozone exposure combined with mild drought. *Proteomics*, 13, 1737–1754.
- Bohler S, Sergeant K, Lefevre I, Jolivet Y, Hoffmann L, Renaut J, Dizengremel P, Hausman J-F (2010). Differential impact of chronic ozone exposure on expanding and fully expanded poplar leaves. *Tree Physiology*, 30, 1415–1432.
- Bota J, Medrano H, Flexas J (2004). Is photosynthesis limited by decreased Rubisco activity and RuBP content under progressive water stress? *New phytologist*, 162, 671–681.
- Bréda N, Huc R, Granier A, Dreyer E (2006). Temperate forest trees and stands under severe drought: A review of eco-physiological responses, adaptation processes and long-term consequences. *Annals of Forest Science*, 63, 625–644.
- Brendley BW, Pell EJ (1998). Ozone-induced changes in biosynthesis of Rubisco and associated compensation to stress in foliage of hybrid poplar. *Tree Physiology*, 18, 81–90.
- Broadmeadow M (1998). Ozone and forest trees. *New Phytologist*, 139, 123–125.
- Buckland SM, Price AH, Hendry GAF (1991). The role of ascorbate in drought-treated *Cochlearia atlantica* Poved. and *Armeria maritima* (Mill.) Willd. *New Phytologist*, 119, 155–160.
- Chang SC, Lee CT (2006). Ozone variations through vehicle emissions reductions based on air quality monitoring data in Taipei City, Taiwan, from 1994 to 2003. *Atmospheric Environment*, 40, 3513–3526.
- Chen Z, Gallie DR (2005). Increasing tolerance to ozone by elevating foliar ascorbic acid confers greater protection against ozone than increasing avoidance. *Plant Physiology*, 138, 1673–1689.
- Ciais P, Reichstein M, Viovy N, Granier A, Ogee J, Allard V, Aubinet M, Buchmann N, Bernhofer C, Carrara A, Chevallier F, de Noblet N, Friend AD, Friedlingstein P, Grunwald T, Heinesch B, Keronen P, Knohl A, Krinner G, Loustau D, Manca G, Matteucci G, Miglietta F, Ourcival JM, Papale D, Pilegaard K, Rambal S, Seufert G, Soussana JF, Sanz MJ, Schulze ED, Vesala T, Valentini R (2005). Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature*, 437, 529–533.
- Comte DL (1998). Weather highlights around the world. *Weatherwise*, 51(2), 26–31.
- Conklin PL, Barth C (2004). Ascorbic acid, a familiar small molecule intertwined in the response of plants to ozone, pathogens, and the onset of senescence. *Plant, Cell & Environment*, 27, 959–970.
- Cowan IR (1978). Stomatal behaviour and environment. *Advances Botanical Research*, 4, 117–228.
- Creissen GP, Mullineaux PM (2002). The molecular biology of the ascorbate-glutathione cycle in higher plants. In: Inzé D, Montagu MV eds. *Oxidative Stress in Plants*. Taylor & Francis, Abingdon, UK. 247–270.
- Dai A (2011). Drought under global warming: A review. *Climate Change*, 2(1), 45–65.
- Desotgiu R, Pollastrini M, Cascio C, Gerosa G, Marzuoli R, Bussotti F (2012). Chlorophyll a fluorescence analysis

- along a vertical gradient of the crown in a poplar (Oxford clone) subjected to ozone and water stress. *Tree Physiology*, 32, 976–986.
- D'Haese D, Vandermeiren K, Asard H, Horemans N (2005). Other factors than apoplastic ascorbate contribute to the differential ozone tolerance of two clones of *Trifolium repens* L. *Plant, Cell & Environment*, 28, 623–632.
- Dizengremel P (2001). Effects of ozone on the carbon metabolism of forest trees. *Plant Physiology and Biochemistry*, 39, 729–742.
- Dizengremel P, Jolivet Y, Tuzet A, Ranieri A, Le Thiec D (2013). Integrative leaf-level phytotoxic ozone dose assessment for forest risk modelling. *Developments in Environmental Science*, 13, 267–288.
- Dizengremel P, Le Thiec D, Bagard M, Jolivet Y (2008). Ozone risk assessment for plants: Central role of metabolism-dependent changes in reducing power. *Environmental Pollution*, 156, 11–15.
- Dizengremel P, Le Thiec D, Hasenfratz-Sauder MP, Vaultier MN, Bagard M, Jolivet Y (2009). Metabolic-dependent changes in plant cell redox power after ozone exposure. *Plant Biology*, 11 (Suppl. 1), 35–42.
- Dumont J, Spicher F, Montpied P, Dizengremel P, Jolivet Y, Le Thiec D (2013). Effects of ozone on stomatal responses to environmental parameters (blue light, red light, CO₂ and vapour pressure deficit) in three *Populus deltoides* × *Populus nigra* genotypes. *Environmental Pollution*, 173, 85–96.
- Edwards IP, Zak DR (2011). Fungal community composition and function after long-term exposure of northern forests to elevated atmospheric CO₂ and tropospheric O₃. *Global Change Biology*, 17, 2184–2195.
- Eltayeb AE, Kawano N, Badawi GH, Kaminaka H, Sanekata T, Morishima I, Shibahara T, Inanaga S, Tanaka K (2006). Enhanced tolerance to ozone and drought stresses in transgenic tobacco overexpressing dehydroascorbate reductase in cytosol. *Physiologia Plantarum*, 127, 57–65.
- Ernst D, Jürgensen M, Bahnweg G, Heller W, Müller-Starck G (2012). Common links of molecular biology with biochemistry and physiology in plants under ozone and pathogen attack. In: Matyssek R, Schnyder H, Oßwald W, Ernst D, Munch CJ, Pretzsch H eds. *Growth and Defence in Plants: Resource Allocation at Multiple Scales*. Springer, Berlin. 29–51.
- Fedina IS, Popova AV (1996). Photosynthesis, photorespiration and proline accumulation in water-stressed pea leaves. *Photosynthetica*, 32, 213–220.
- Feng YW, Shimizu H (2005). Effects of ozone and/or water stress on the growth of *Abies veitchii* seedlings. *Phyton-Annales Rei Botanicae*, 45, 591–594.
- Feng ZZ, Sun JS, Wan WX, Hu EZ, Calatayud V (2014). Evidence of widespread ozone-induced visible injury on plants in Beijing, China. *Environmental Pollution*, 193, 296–301.
- Feng ZZ, Kobayashi K (2009). Assessing the impacts of current and future concentrations of surface ozone on crop yield with meta-analysis. *Atmospheric Environment*, 43, 1510–1519.
- Flexas J, Bota J, Escalona JM, Sampol B, Medrano H (2002). Effects of drought on photosynthesis in grapevines under field conditions: An evaluation of stomatal and mesophyll limitations. *Functional Plant Biology*, 29, 461–471.
- Fontaine V, Cabane M, Dizengremel P (2003). Regulation of phosphoenolpyruvate carboxylase in *Pinus halepensis* needles submitted to ozone and water stress. *Physiologia Plantarum*, 117, 445–452.
- Foyer CH, Noctor G (2000). Oxygen processing in photosynthesis: Regulation and signalling. *New Phytologist*, 146, 359–388.
- Fu JM, Huang BR (2001). Involvement of antioxidants and lipid peroxidation in the adaptation of two cool-season grasses to localized drought stress. *Environmental and Experimental Botany*, 45, 105–114.
- Gerant D, Podor M, Grieu P, Afif D, Cornu S, Morabito D, Banvoy J, Robin C, Dizengremel P (1996). Carbon metabolism enzyme activities and carbon partitioning in *Pinus halepensis* Mill. exposed to mild drought and ozone. *Journal of Plant Physiology*, 148, 142–147.
- Grulke NE, Johnson R, Esperanza A, Jones D, Nguyen T, Posch S, Tausz M (2003a). Canopy transpiration of Jeffrey pine in mesic and xeric microsites: O₃ uptake and injury response. *Trees*, 17, 292–298.
- Grulke NE, Johnson R, Monschein S, Nikolova P, Tausz M (2003b). Variation in morphological and biochemical O₃ injury attributes of mature Jeffrey pine within canopies and between microsites. *Tree Physiology*, 23, 923–929.
- Grulke NE, Preisler HK, Rose C, Kirsch J, Balduman L (2002). O₃ uptake and drought stress effects on carbon acquisition of ponderosa pine in natural stands. *New Phytologist*, 154, 621–631.
- Grünhage L, Jäger HJ (2003). From critical levels to critical loads for ozone: A discussion of a new experimental and modelling approach for establishing flux-response relationships for agricultural crops and native plant species. *Environmental Pollution*, 125, 99–110.
- Guidi L, Nali C, Lorenzini G, Filippi F, Soldatini GF (2001). Effect of chronic ozone fumigation on the photosynthetic process of poplar clones showing different sensitivity. *Environmental Pollution*, 113, 245–254.
- Gupta P, Duplessis S, White H, Karnosky DF, Martin F, Podila GK (2005). Gene expression patterns of trembling aspen trees following long-term exposure to interacting elevated CO₂ and tropospheric O₃. *New Phytologist*, 167, 129–142.
- Haberer K, Herbinger K, Alexou M, Rennenberg H, Tausz M

- (2008). Effects of drought and canopy ozone exposure on antioxidants in fine roots of mature European beech (*Fagus sylvatica*). *Tree Physiology*, 28, 713–719.
- Hao YT, Lin M, Xue L, Wang ZY, Lin JT, Liang ZY, Sun BC, Tian MT (2014). Effects of ozone stress and drought stress on photosynthesis characteristics of *Syzygium hainanense* and *Alstonia scholaris* seedlings. *Journal of Anhui Agricultural University*, 41, 193–197. (in Chinese with English abstract) [郝云亭, 林敏, 薛立, 王志云, 林婧庭, 梁梓毅, 孙冰超, 田茂涛 (2014). 臭氧与干旱胁迫对海南蒲桃和盆架子幼苗光合生理的影响. 安徽农业大学学报, 41, 193–197.]
- Hatch M, Slack C, Bull T (1969). Light-induced changes in the content of some enzymes of the C₄-dicarboxylic acid pathway of photosynthesis and its effect on other characteristics of photosynthesis. *Phytochemistry*, 8, 697–706.
- Heath RL (1994). Alterations of plant metabolism by ozone exposure. In: Alscher RG, Wellburn AR eds. *Plant Responses to the Gaseous Environment: Molecular, Metabolic and Physiological aspects*. Springer Netherlands, Dordrecht. 121–145.
- Heath RL (2008). Modification of the biochemical pathways of plants induced by ozone: What are the varied routes to change? *Environmental Pollution*, 155, 453–463.
- Heath RL, Taylor GE (1997). Physiological processes and plant responses to ozone exposure. In: Sandermann H, Wellburn AR, Heath RL eds. *Forest Decline and Ozone: A Comparison of Controlled Chamber and Field Experiments*. Springer, Berlin. 317–368.
- Heber U, Kaiser W, Luwe M, Kindermann G, Veljovic-Javonovic S, Yin Z, Pfanz H, Slovik S (1995). Air pollution, photosynthesis and forest decline: Interactions and consequences. In: Schulze E-D, Caldwell MM eds. *Eco-physiology of Photosynthesis*. Springer, Berlin. 279–296.
- Herbinger K, Tausz M, Wonisch A, Soja G, Sorger A, Grill D (2002). Complex interactive effects of drought and ozone stress on the antioxidant defence systems of two wheat cultivars. *Plant Physiology and Biochemistry*, 40, 691–696.
- Herbinger K, Then C, Low M, Haberer K, Alexous M, Koch N, Remele K, Heerdt C, Grill D, Rennenberg H, Haberer KH, Matyssek R, Tausz M, Wieser G (2005). Tree age dependence and within-canopy variation of leaf gas exchange and antioxidative defence in *Fagus sylvatica* under experimental free-air ozone exposure. *Environmental Pollution*, 137, 476–482.
- Hoshika Y, Carriero G, Feng ZZ, Zhang YL, Paoletti E (2014). Determinants of stomatal sluggishness in ozone-exposed deciduous tree species. *Science of the Total Environment*, 481, 453–458.
- Hoshika Y, Omasa K, Paoletti E (2013). Both ozone exposure and soil water stress are able to induce stomatal sluggishness. *Environmental and Experimental Botany*, 88, 19–23.
- Hoshika Y, Watanabe M, Inada N, Koike T (2012). Ozone-induced stomatal sluggishness develops progressively in Siebold's beech (*Fagus crenata*). *Environmental Pollution*, 166, 152–156.
- Huang BR, Fu JM (2000). Photosynthesis, respiration, and carbon allocation of two cool-season perennial grasses in response to surface soil drying. *Plant and Soil*, 227(1–2), 17–26.
- Huseynova IM, Aliyeva DR, Aliyev JA (2014). Subcellular localization and responses of superoxide dismutase isoforms in local wheat varieties subjected to continuous soil drought. *Plant Physiology and Biochemistry*, 81, 54–60.
- ICP Vegetation (2011). Ozone pollution: A hidden threat to food security. Programme Coordination Centre for the ICP Vegetation. In: Mills G, Harmens H eds. *Programme Coordination Centre for the ICP Vegetation*. NERC/Centre for Ecology and Hydrology, Bangor, UK. 116.
- Inclan R, Gimeno BS, Dizengremel P, Sanchez M (2005). Compensation processes of Aleppo pine (*Pinus halepensis* Mill.) to ozone exposure and drought stress. *Environmental Pollution*, 137, 517–524.
- IPCC (Intergovernmental Panel on Climate Change) (2013). *Climate Change 2013: The Physical Science Basis. Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK and New York, USA. 1552.
- Iyer NJ, Tang Y, Mahalingam R (2013). Physiological, biochemical and molecular responses to a combination of drought and ozone in *Medicago truncatula*. *Plant, Cell & Environment*, 36, 706–720.
- Karlsson PE, Medin EL, Wickstrom H, Sellden G, Wallin G, Ottosson S, Skarby L (1995). Ozone and drought stress—Interactive effects on the growth and physiology of Norway spruce (*Picea abies* (L) Karst). *Water, Air, & Soil Pollution*, 85, 1325–1330.
- Karlsson PE, Pleijel H, Karlsson GP, Medin EL, Skarby L (2000). Simulations of stomatal conductance and ozone uptake to Norway spruce saplings in open-top chambers. *Environmental Pollution*, 109, 443–451.
- Karnosky DF, Pregitzer KS, Zak DR, Kubiske ME, Hendrey GR, Weinstein D, Nosal M, Percy KE (2005). Scaling ozone responses of forest trees to the ecosystem level in a changing climate. *Plant, Cell & Environment*, 28, 965–981.
- Karnosky DF, Werner H, Holopainen T, Percy K, Oksanen T, Oksanen E, Heerdt C, Fabian P, Nagy J, Heilman W, Cox R, Nelson N, Matyssek R (2007). Free-air exposure systems to scale up ozone research to mature trees. *Plant Biology*, 9, 181–190.
- Kaya MD, Okcu G, Atak M, Cikili Y, Kolsarici O (2006). Seed

- treatments to overcome salt and drought stress during germination in sunflower (*Helianthus annuus* L.). *European Journal of Agronomy*, 24, 291–295.
- Khan S, Soja G (2003). Yield responses of wheat to ozone exposure as modified by drought-induced differences in ozone uptake. *Water, Air, & Soil Pollution*, 147, 299–315.
- Kivimäenpää M, Sutinen S, Karlsson PE, Sellden G (2003). Cell structural changes in the needles of Norway spruce exposed to long-term ozone and drought. *Annals of Botany*, 92, 779–793.
- Kivimäenpää M, Sutinen S, Medin EL, Karlsson PE, Sellden G (2001). Diurnal changes in microscopic structures of mesophyll cells of Norway spruce, *Picea abies* (L.) Karst., and the effects of ozone and drought. *Annals of Botany*, 88, 119–130.
- Kou TJ, Chang HQ, Zhang LH, Xu XF, Guo DY, Zhou WL, Zhu JG, Miao YF (2009). Effects of ground-level O₃ pollution on the terrestrial ecosystem. *Ecology and Environmental Sciences*, 18, 704–710. (in Chinese with English abstract) [寇太记, 常会庆, 张联合, 徐晓峰, 郭大勇, 周文利, 朱建国, 苗艳芳 (2009). 近地层O₃污染对陆地生态系统的影响. *生态环境学报*, 18, 704–710.]
- Kronfuß G, Polle A, Tausz M, Havranek WM, Wieser G (1998). Effects of ozone and mild drought stress on gas exchange, antioxidants and chloroplast pigments in current-year needles of young Norway spruce [*Picea abies* (L.) Karst]. *Trees*, 12, 482–489.
- Kuehn AR, Grill S, Baumgarten M, Ankerst DP, Matyssek R (2015). Daily growth of European beech (*Fagus sylvatica* L.) on moist sites is affected by short-term drought rather than ozone uptake. *Trees*, 29, 1501–1519.
- Landolt W, Günthardt-Goerg M, Pfenninger I, Scheidegger C (1994). Ozone induced microscopical changes and quantitative carbohydrate contents of hybrid poplar (*Populus × euramericana*). *Trees*, 8, 183–190.
- Le Thiec D, Dixon M, Garrec JP (1994). The effects of slightly elevated ozone concentrations and mild drought stress on the physiology and growth of Norway Spruce, *Picea abies* (L.) Karst. and beech, *Fagus sylvatica* L., in open-top chambers. *New Phytologist*, 128, 671–678.
- Li L, Chen CH, Huang C, Huang HY, Zhang GF, Wang YJ, Chen MH, Wang HL, Chen YR, Streets DG, Fu JM (2011). Ozone sensitivity analysis with the MM5-CMAQ modeling system for Shanghai. *Journal of Environmental Sciences*, 23, 1150–1157.
- Li L, Manning WJ, Tong L, Wang XK (2015). Chronic drought stress reduced but not protected Shantung maple (*Acer truncatum* Bunge) from adverse effects of ozone (O₃) on growth and physiology in the suburb of Beijing, China. *Environmental Pollution*, 201, 34–41.
- Li QJ, Lu GC, Xue L, Tian MT, Lin M, Lin JT (2015). Effects of ozone and drought on fluorescence physiology of seedlings of three afforestation tree species in South China. *Journal of South China Agricultural University*, 36, 91–95. (in Chinese with English abstract) [李秋静, 卢广超, 薛立, 田茂涛, 林敏, 林婧庭 (2011). 臭氧与干旱胁迫对华南地区3种绿化树种. *华南农业大学学报*, 36, 91–95.]
- Löw M, Herbinger K, Nunn AJ, Haeberle KH, Leuchner M, Heerdt C, Werner H, Wipfler P, Pretzsch H, Tausz M, Matyssek R (2006). Extraordinary drought of 2003 overrules ozone impact on adult beech trees (*Fagus sylvatica*). *Trees*, 20, 539–548.
- Lutz C, Anegg S, Gerant D, Alaoui-Sosse B, Gerard J, Dizengremel P (2000). Beech trees exposed to high CO₂ and to simulated summer ozone levels: Effects on photosynthesis, chloroplast components and leaf enzyme activity. *Physiologia Plantarum*, 109, 252–259.
- Luwe MWF, Takahama U, Heber U (1993). Role of ascorbate in detoxifying ozone in the apoplast of spinach (*Spinacia oleracea* L.) leaves. *Plant Physiology*, 101, 969–976.
- Maier-Maercker U (1998). Image analysis of the stomatal cell walls of *Picea abies* (L.) Karst. in pure and ozone-enriched air. *Trees*, 12, 181–185.
- Manderscheid R, Jäger H-J, Schoeneberger M (1991). Dose-response relationships of ozone effects on foliar levels of antioxidants, soluble polyamines and peroxidase activity of *Pinus taeda* (L.): Assessment of the usefulness as early ozone indicators. *Angewandte Botanik*, 29, 188.
- Manes F, Donato E, Vitale M (2001). Physiological response of *Pinus halepensis* needles under ozone and water stress conditions. *Physiologia Plantarum*, 113, 249–257.
- Matyssek R, Innes JL (1999). Ozone—A risk factor for trees and forests in Europe? *Water, Air, & Soil Pollution*, 116, 199–226.
- Matyssek R, Kozovits AR, Schnitzler J-P, Pretzsch H, Dieler J, Wieser G (2014). Forest trees under air pollution as a factor of climate change. In: Tausz M, Grulke N eds. *Trees in a Changing Environment: Ecophysiology, Adaptation, and Future Survival*. Springer, Dordrecht, The Netherlands. 117–163.
- Matyssek R, Le Thiec D, Löw M, Dizengremel P, Nunn AJ, Häberle KH (2006). Interactions between drought and O₃ stress in forest trees. *Plant Biology*, 8, 11–17.
- Matyssek R, Sandermann H (2003). Impact of ozone on trees: An ecophysiological perspective. *Progress in Botany*, 64, 349–404.
- Matyssek R, Wieser G, Calfapietra C, de Vries W, Dizengremel P, Ernst D, Jolivet Y, Mikkelsen TN, Mohren GMJ, Le Thiec D, Tuovinen JP, Weatherall A, Paoletti E (2012). Forests under climate change and air pollution: Gaps in understanding and future directions for research. *Environmental Pollution*, 160, 57–65.
- Matyssek R, Wieser G, Ceulemans R, Rennenberg H, Pretzsch

- H, Haberer K, Loew M, Nunn AJ, Werner H, Wipfler P, Osswald W, Nikolova P, Hanke DE, Kraigher H, Tausz M, Bahnweg G, Kitao M, Dieler J, Sandermann H, Herbinger K, Grebenc T, Blumenroether M, Deckmyn G, Grams TEE, Heerdt C, Leuchner M, Fabian P, Haeberle KH (2010). Enhanced ozone strongly reduces carbon sink strength of adult beech (*Fagus sylvatica*)—Resume from the free-air fumigation study at Kranzberg Forest. *Environmental Pollution*, 158, 2527–2532.
- McLaughlin SB, Nosal M, Wullschlegel SD, Sun G (2007). Interactive effects of ozone and climate on tree growth and water use in a southern Appalachian forest in the USA. *New Phytologist*, 174, 109–124.
- Miller PR, McBride JR (1999). Oxidant air pollution impacts in the montane forests of southern California—A case study of the San Bernardino Mountains—Introduction. In: Miller PR, McBride JR eds. *Oxidant Air Pollution Impacts in the Montane Forests of Southern California*. Springer, New York.
- Mills G, Hayes F, Simpson D, Emberson L, Norris D, Harmens H, Buker P (2011). Evidence of widespread effects of ozone on crops and (semi-) natural vegetation in Europe (1990–2006) in relation to AOT40- and flux-based risk maps. *Global Change Biology*, 17, 592–613.
- Ministry of Water Resources, China (2006–2010). *Bulletin of Flood and Drought Disasters in China*. (in Chinese) [中国水利部 (2006–2010). 中国水旱灾害公报.] <http://www.mwr.gov.cn/zwzc/hygb/zgshzhgb/>. Cited: 2016-6.
- Mittler R, Zilinskas BA (1994). Regulation of pea cytosolic ascorbate peroxidase and other antioxidant enzymes during the progression of drought stress and following recovery from drought. *Plant Journal*, 5, 397–405.
- Monakhova OF, Chernyadèv II (2002). Protective role of kartolin-4 in wheat plants exposed to soil draught. *Applied Biochemistry and Microbiology*, 38, 373–380.
- Morgan PB, Ainsworth EA, Long SP (2003). How does elevated ozone impact soybean? A meta-analysis of photosynthesis, growth and yield. *Plant, Cell & Environment*, 26, 1317–1328.
- Nali C, Paoletti E, Marabottini R, Della Rocca G, Lorenzini G, Paolacci AR, Ciaffi M, Badiani M (2004). Ecophysiological and biochemical, strategies of response to ozone in Mediterranean evergreen broadleaf species. *Atmospheric Environment*, 38, 2247–2257.
- National Bureau of Statistics of China (2007–2012). China Statistical Yearbook. China Statistics Press, Beijing. (in Chinese) [国家统计局 (2007–2012). 中国统计年鉴. 中国统计出版社, 北京.]
- Nikolova PS, Andersen CP, Blaschke H, Matyssek R, Haeberle K-H (2010). Belowground effects of enhanced tropospheric ozone and drought in a beech/spruce forest (*Fagus sylvatica* L./*Picea abies* (L.) Karst.). *Environmental Pollution*, 158, 1071–1078.
- Noctor G, Foyer CH (1998). Ascorbate and glutathione: Keeping active oxygen under control. *Annual Review of Plant Physiology and Plant Molecular Biology*, 49, 249–279.
- Nonami H (1998). Plant water relations and control of cell elongation at low water potentials. *Journal of Plant Research*, 111, 373–382.
- Oksanen E (2003). Responses of selected birch (*Betula pendula* Roth) clones to ozone change over time. *Plant, Cell & Environment*, 26, 875–886.
- Pääkkönen E, Seppänen S, Holopainen T, Kokko H, Kärenlampi S, Kärenlampi L, Kangasjärvi J (1998). Induction of genes for the stress proteins PR-10 and PAL in relation to growth, visible injuries and stomatal conductance in birch (*Betula pendula*) clones exposed to ozone and/or drought. *New Phytologist*, 138, 295–305.
- Pandey D, Goswami C, Kumar B, Jain S (2001). Hormonal regulation of photosynthetic enzymes in cotton under water stress. *Photosynthetica*, 38, 403–407.
- Panek JA (2004). Ozone uptake, water loss and carbon exchange dynamics in annually drought-stressed *Pinus ponderosa* forests: Measured trends and parameters for uptake modeling. *Tree Physiology*, 24, 277–290.
- Panek JA, Goldstein AH (2001). Response of stomatal conductance to drought in ponderosa pine: Implications for carbon and ozone uptake. *Tree Physiology*, 21, 337–344.
- Panek JA, Kurpius MR, Goldstein AH (2002). An evaluation of ozone exposure metrics for a seasonally drought-stressed ponderosa pine ecosystem. *Environmental Pollution*, 117, 93–100.
- Paoletti E (2006). Impact of ozone on Mediterranean forests: A review. *Environmental Pollution*, 144, 463–474.
- Paoletti E, Grulke NE (2010). Ozone exposure and stomatal sluggishness in different plant physiognomic classes. *Environmental Pollution*, 158, 2664–2671.
- Parry MAJ, Andralojc PJ, Khan S, Lea PJ, Keys AJ (2002). Rubisco activity: Effects of drought stress. *Annals of Botany*, 89, 833–839.
- Pasqualini S, Batini P, Ederli L, Porceddu A, Piccioni C, de Marchis F, Antonielli M (2001). Effects of short-term ozone fumigation on tobacco plants: Response of the scavenging system and expression of the glutathione reductase. *Plant, Cell & Environment*, 24, 245–252.
- Pearson M, Mansfield T (1993). Interacting effects of ozone and water stress on the stomatal resistance of beech (*Fagus sylvatica* L.). *New Phytologist*, 123, 351–358.
- Pell EJ, Sinn JP, Eckardt N, Johansen CV, Winner WE, Mooney HA (1993). Response of radish to multiple stresses. 2. Influence of season and genotype on plant response to ozone and soil-moisture deficit. *New Phytologist*, 123, 153–163.
- Pelloux J, Jolivet Y, Fontaine V, Banvoy J, Dizengremel P

- (2001). Changes in Rubisco and Rubisco activase gene expression and polypeptide content in *Pinus halepensis* M. subjected to ozone and drought. *Plant, Cell & Environment*, 24, 123–131.
- Pignocchi C, Fletcher JM, Wilkinson JE, Barnes JD, Foyer CH (2003). The function of ascorbate oxidase in tobacco. *Plant Physiology*, 132, 1631–1641.
- Pirker KF, Reichenauer TG, Pascual EC, Kiefer S, Soja G, Goodman BA (2003). Steady state levels of free radicals in tomato fruit exposed to drought and ozone stress in a field experiment. *Plant Physiology and Biochemistry*, 41, 921–927.
- Pollastrini M, Desotgiu R, Camin F, Ziller L, Gerosa G, Marzuoli R, Bussotti F (2014). Severe drought events increase the sensitivity to ozone on poplar clones. *Environmental and Experimental Botany*, 100, 94–104.
- Pollastrini M, Desotgiu R, Camin F, Ziller L, Marzuoli R, Gerosa G, Bussotti F (2013). Intra-annual pattern of photosynthesis, growth and stable isotope partitioning in a poplar clone subjected to ozone and water stress. *Water, Air, & Soil Pollution*, 224, 1761.
- Pollastrini M, Desotgiu R, Cascio C, Bussotti F, Cherubini P, Saurer M, Gerosa G, Marzuoli R (2010). Growth and physiological responses to ozone and mild drought stress of tree species with different ecological requirements. *Trees*, 24, 695–704.
- Potters G, de Gara L, Asard H, Horemans N (2002). Ascorbate and glutathione: Guardians of the cell cycle, partners in crime? *Plant Physiology and Biochemistry*, 40, 537–548.
- Pretzsch H, Dieler J (2011). The dependency of the size-growth relationship of Norway spruce (*Picea abies* (L.) Karst.) and European beech (*Fagus sylvatica* L.) in forest stands on long-term site conditions, drought events, and ozone stress. *Trees-Structure and Function*, 25, 355–369.
- Qiu HJ, Cao MM, Hao JQ, Wang YL, Wang YM (2013). Analysis the relationship between drought frequency and scale of China in 1950–2010. *Scientia Geographica Sinica*, 33, 576–580. (in Chinese) [邱海军, 曹明明, 郝俊卿, 王雁林, 王彦民 (2013). 1950~2010年中国干旱灾情频率-规模关系分析. *地理科学*, 33, 576–580.]
- Quartacci MF, Navari-Izzo F (1992). Water-stress and free-radical mediated changes in sunflower seedlings. *Journal of Plant Physiology*, 139, 621–625.
- Rana G, Katerji N, Mastrorilli M (2012). Method for automatic determination of soybean actual evapotranspiration under open top chambers (OTC) subjected to effects of water stress and air ozone concentration. *Environmental Monitoring and Assessment*, 184, 6377–6394.
- Rao MV, Koch JR, Davis KR (2000). Ozone: A tool for probing programmed cell death in plants. *Plant Molecular Biology*, 44, 345–358.
- Renaut J, Bohler S, Hausman J-F, Hoffmann L, Sergeant K, Ahsan N, Jolivet Y, Dizengremel P (2009). The impact of atmospheric composition on plants: A case study of ozone and poplar. *Mass Spectrometry Reviews*, 28, 495–516.
- Retzlaff WA, Arthur MA, Grulke NE, Weinstein DA, Gollands B (2000). Use of a single-tree simulation model to predict effects of ozone and drought on growth of a white fir tree. *Tree Physiology*, 20, 195–202.
- Ribas A, Penuelas J, Elvira S, Gimeno BS (2005). Contrasting effects of ozone under different water supplies in two Mediterranean tree species. *Atmospheric Environment*, 39, 685–693.
- Sadras VO, Milroy SP (1996). Soil-water thresholds for the responses of leaf expansion and gas exchange: A review. *Field Crops Research*, 47, 253–266.
- Sandermann H (1996). Ozone and plant health. *Annual Review of Phytopathology*, 34, 347–366.
- Sanmartin M, Drogoudi PD, Lyons T, Pateraki I, Barnes J, Kanellis AK (2003). Over-expression of ascorbate oxidase in the apoplast of transgenic tobacco results in altered ascorbate and glutathione redox states and increased sensitivity to ozone. *Planta*, 216, 918–928.
- Schubert SD, Suarez MJ, Pegen PJ, Koster RD, Bacmeister JT (2004). On the cause of the 1930s Dust Bowl. *Science*, 303, 1855–1859.
- Schuppler U, He PH, John PCL, Munns R (1998). Effect of water stress on cell division and cell-division-cycle 2-like cell-cycle kinase activity in wheat leaves. *Plant Physiology*, 117, 667–678.
- Sergeant K, Spiess N, Renaut J, Wilhelm E, Hausman JF (2011). One dry summer: A leaf proteome study on the response of oak to drought exposure. *Journal of Proteomics*, 74, 1385–1395.
- Sharma PN, Malik CP (1993). Photosynthetic responses of groundnut to moisture stress. *Photosynthetica*, 29, 157–160.
- Shimizu H, Feng YW (2007). Ozone and/or water stresses could have influenced the *Betula ermanii* Cham. forest decline observed at Oku-Nikko, Japan. *Environmental Monitoring and Assessment*, 128, 109–119.
- Showman RE (1991). A comparison of ozone injury to vegetation during moist and drought years. *Journal of the Air & Waste Management Association*, 41, 63–64.
- Šircelj H, Tausz M, Grill D, Batic F (2005). Biochemical responses in leaves of two apple tree cultivars subjected to progressing drought. *Journal of Plant Physiology*, 162, 1308–1318.
- Sitch S, Cox PM, Collins WJ, Huntingford C (2007). Indirect radiative forcing of climate change through ozone effects on the land-carbon sink. *Nature*, 448, 791–794.
- Skärby L, Ro-Poulsen H, Wellburn FAM, Sheppard LJ (1998). Impacts of ozone on forests: A European perspective. *New Phytologist*, 139, 109–122.

- Sofa A, Tuzio AC, Dichio B, Xiloyannis C (2005). Influence of water deficit and rewatering on the components of the ascorbate-glutathione cycle in four interspecific *Prunus* hybrids. *Plant Science*, 169, 403–412.
- Sun MX, Zu CL, Xu JN (2004). Advances research on the impact of drought on plant: A review. *Journal of Anhui Agricultural Sciences*, 32, 365–367, 384. (in Chinese) [孙梅霞, 祖朝龙, 徐经年 (2004). 干旱对植物影响的研究进展. *安徽农业科学*, 32, 365–367, 384.]
- Talbi S, Romero-Puertas MC, Hernandez A, Terron L, Ferchichi A, Sandalio LM (2015). Drought tolerance in a Saharian plant *Oudneya africana*: Role of antioxidant defences. *Environmental and Experimental Botany*, 111, 114–126.
- Tanaka Y, Sano T, Tamaoki M, Nakajima N, Kondo N, Hasezawa S (2005). Ethylene inhibits abscisic acid-induced stomatal closure in *Arabidopsis*. *Plant Physiology*, 138, 2337–2343.
- Tezara W, Mitchell V, Driscoll S, Lawlor D (1999). Water stress inhibits plant photosynthesis by decreasing coupling factor and ATP. *Nature*, 401, 914–917.
- Tian HQ, Xu XF, Song X (2007). Drought impacts on terrestrial ecosystem productivity. *Journal of Plant Ecology (Chinese Version)*, 31, 231–241. (in Chinese with English abstract) [田汉勤, 徐小锋, 宋霞 (2007). 干旱对陆地生态系统生产力的影响. *植物生态学报*, 31, 231–241.]
- Tietz S, Wild A (1991). Investigations on the phosphoenolpyruvate carboxylase activity of spruce needles relative to the occurrence of novel forest decline. *Journal of Plant Physiology*, 137, 327–331.
- Torsethaugen G, Pell EJ, Asmann SM (1999). Ozone inhibits guard cell K^+ channels implicated in stomatal opening. *Proceedings of the National Academy of Sciences of the United States of America*, 96, 13577–13582.
- Vitale M, Salvatori E, Loreto F, Fares S, Manes F (2008). Physiological responses of *Quercus ilex* leaves to water stress and acute ozone exposure under controlled conditions. *Water, Air, & Soil Pollution*, 189, 113–125.
- Wagg S, Mills G, Hayes F, Wilkinson S, Cooper D, Davies WJ (2012). Reduced soil water availability did not protect two competing grassland species from the negative effects of increasing background ozone. *Environmental Pollution*, 165, 91–99.
- Wallin G, Karlsson PE, Sellden G, Ottosson S, Medin EL, Pleijel H, Skarby L (2002). Impact of four years exposure to different levels of ozone, phosphorus and drought on chlorophyll, mineral nutrients, and stem volume of Norway spruce, *Picea abies*. *Physiologia Plantarum*, 114, 192–206.
- Wang XL, Chen QC (1974). Plants as “atmospheric pollution monitoring alarm”. *The Plant Journal*, (4), 29–31. (in Chinese) [王勋陵, 陈庆诚 (1974). 利用植物作为大气污染“监测警报器”. *植物学杂志*, (4), 29–31.]
- Watanabe M, Yonekura T, Honda Y, Yoshidome M, Nakaji T, Izuta T (2005). Effects of ozone and soil water stress, singly and in combination, on leaf antioxidative systems of *Fagus crenata* seedlings. *Journal of Agricultural Meteorology*, 60, 1105–1108.
- Wellburn FAM, Lau KK, Milling PMK, Wellburn AR (1996). Drought and air pollution affect nitrogen cycling and free radical scavenging in *Pinus halepensis* (Mill). *Journal of Experimental Botany*, 47, 1361–1367.
- Wen Z, Wang L, Wang XK, Li L, Cui J (2014). Combined effects of O_3 and drought on leaf stomata of *Acer truncatum*. *Chinese Journal of Ecology*, 33, 560–566. (in Chinese with English abstract) [文志, 王丽, 王效科, 李丽, 崔健 (2014). O_3 和干旱胁迫对元宝枫叶片气孔特征的复合影响. *生态学杂志*, 33, 560–566.]
- Wilkinson S, Davies WJ (2009). Ozone suppresses soil drying- and abscisic acid (ABA)-induced stomatal closure via an ethylene-dependent mechanism. *Plant, Cell & Environment*, 32, 949–959.
- Wilkinson S, Davies WJ (2010). Drought, ozone, ABA and ethylene: New insights from cell to plant to community. *Plant, Cell & Environment*, 33, 510–525.
- Wittig VE, Ainsworth EA, Long SP (2007). To what extent do current and projected increases in surface ozone affect photosynthesis and stomatal conductance of trees? A meta-analytic review of the last 3 decades of experiments. *Plant, Cell & Environment*, 30, 1150–1162.
- Wittig VE, Ainsworth EA, Naidu SL, Karnosky DF, Long SP (2009). Quantifying the impact of current and future tropospheric ozone on tree biomass, growth, physiology and biochemistry: A quantitative meta-analysis. *Global Change Biology*, 15, 396–424.
- Xu H, Biswas DK, Li WD, Chen SB, Zhang L, Jiang GM, Li YG (2007). Photosynthesis and yield responses of ozone-polluted winter wheat to drought. *Photosynthetica*, 45, 582–588.
- Xu H, Yang JC, Chen SB, Jiang GB, Li KY (2007). Review of plant responses to ozone pollution. *Journal of Plant Ecology (Chinese Version)*, 31, 1205–1213. (in Chinese with English abstract) [许宏, 杨景成, 陈圣宾, 蒋高明, 李永庚 (2007). 植物的臭氧污染胁迫效应研究进展. *植物生态学报*, 31, 1205–1213.]
- Yang F, Miao LF, Xu Xiao, Li CY (2007). Progress in research of plant responses to drought stress. *Chinese Journal of Applied and Environmental Biology*, 13, 586–591. (in Chinese with English abstract) [杨帆, 苗灵凤, 胥晓, 李春阳 (2007). 植物对干旱胁迫的响应研究进展. *应用与环境生物学报*, 13, 586–591.]

- Yao YQ, Liu XP, Li ZZ, Ma XF, Rennenberg H, Wang X, Li HC (2013). Drought-induced H_2O_2 accumulation in subsidiary cells is involved in regulatory signaling of stomatal closure in maize leaves. *Planta*, 238, 217–227.
- Ye LH, Bao HY, Wang ZY, Lie GW, Chen HY, Zhang XP, Chen X, Ke H, Tian XQ, Tan JD (2014). Effects of ozone and drought on biomass allocation of four seedlings in South China. *Advanced Materials Research*, 864–867, 2478–2484.
- Yonekura THY, Oksanen E, Yoshidome M, Watanabe M, Funada R KT, Izuta T (2001b). The influences of ozone and soil water stress, singly and in combination, on leaf gas exchange rates, leaf ultrastructural characteristics and annual ring width of *Fagus crenata* seedlings. *Journal of Japan Society for Atmospheric Environment*, 36, 333–351.
- Yonekura T, Dokiya Y, Fukami M, Izuta T (2001a). Effects of ozone and/or soil water stress on growth and photosynthesis of *Fagus crenata* seedlings. *Water, Air, & Soil Pollution*, 130, 965–970.
- Yonekura T, Yoshidome M, Watanabe M, Honda Y, Ogiwara I, Izuta T (2004). Carry-over effects of ozone and water stress on leaf phenological characteristics and bud frost hardiness of *Fagus crenata* seedlings. *Trees*, 18, 581–588.
- Zhang JX, Kirkham MB (1994). Drought-stress-induced changes in activities of superoxide-dismutase, catalase, and peroxidase in wheat species. *Plant & Cell Physiology*, 35, 785–791.
- Zhang JX, Kirkham MB (1996). Enzymatic responses of the ascorbate-glutathione cycle to drought in sorghum and sunflower plants. *Plant Science*, 113, 139–147.
- Zhao MS, Running SW (2010). Drought-induced reduction in global terrestrial net primary production from 2000 through 2009. *Science*, 329, 940–943.

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