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Journal

Environmental and Experimental Botany, 30(2)

ISSN

0098-8472

Authors

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Publication Date

1990

DOI

10.1016/0098-8472(90)90066-D

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EFFECTS OF OZONE AND SULFUR DIOXIDE ON TWO EPIPHYTIC ORCHIDS

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† Department of Biology, Oberlin College, Oberlin, OH 44074, U.S.A., ‡ Statewide Air Pollution Research Center, University of California, Riverside, CA 92521, U.S.A. and § Developmental and Cell Biology, University of California, Irvine, CA 92717, U.S.A.

(Received 24 July 1989; accepted in revised form 30 October 1989)

NYMAN L. P., BENZING D. H., TEMPLE P. J. and ARDITTI J. *Effects of ozone and sulfur dioxide on two epiphytic orchids*. ENVIRONMENTAL AND EXPERIMENTAL BOTANY **30**, 207–213, 1990.—Plants of *Encyclia tampensis* (*Epidendrum tampense*) and *Epidendrum rigidum* (Orchidaceae) exposed to 0.3, 0.6 and 1.2 ppm SO₂ or 0.15, 0.3 and 0.45 ppm O₃ for 6 hr as well as sequentially to 0.3 ppm O₃ (2 hr), 0.3 ppm O₃ plus 0.06 ppm SO₂ (2 hr), and 0.6 ppm SO₂ (2 hr) did not exhibit visible injuries. Exposures to pollutants were also without effect on stomatal conductance and Crassulacean acid metabolism (CAM, i.e. carbon fixation at night). The leaf resistance of the two orchids to these gases may be due to structural factors as well as to the generally lower sensitivity of CAM plants to pollutants.

INTRODUCTION

EVERGLADES National Park and adjacent areas at the southern tip of Florida are unique in the continental U.S. because of the large number of endemic epiphytic orchids and bromeliads. Rapid increases in urbanization and industrialization in south Florida have (1) destroyed habitats, (2) contributed to deteriorating air quality in the region, and (3) increased the threat to the south Florida biota. Prevailing east to west wind patterns, particularly during warmer months, carry industrial and automotive pollutants and other effluents from the densely populated coastal regions to the sensitive habitats in the Everglades National Park (ENP). In 1987 the monthly average O₃ levels in the park ranged from 15.2 to 45 ppb.⁽¹⁾ Between 1981 and 1984 SO₄²⁻ levels were 198, 177 and 157 eq ha⁻¹ yr⁻¹.⁽¹⁾ In 1987 the concentration was 114 eq/ha during the summer dropping to 54 eq/ha in the winter.^(1,2)

Epiphytic species of lichens and bryophytes are more susceptible to atmospheric pollutants than crustose or foliose forms, perhaps because of increased exposure to atmospheric deposition and relative lack of buffering capacity of the substrate.⁽¹⁶⁾ Spanish moss (*Tillandsia* spp.), an epiphytic bromeliad, has been used as a biomonitor of atmospheric deposition because of its capacity to absorb materials from the air.^(7,8,23) However, little is known regarding the susceptibility to air pollutants of epiphytic plants in general and orchids and bromeliads in particular. Some of these epiphytes are among the rarest plants in the U.S. and particularly vulnerable to air pollution. A number of these species are CAM plants which carry out gas exchange at night⁽¹¹⁾ and may or may not be susceptible to nocturnal pollution.

Populations of *Tillandsia balbesiana*, *T. paucifolia* and *T. utriculata* were monitored because these bromeliads characterize vegetation which is

severely affected by air quality problems. Germination and life table distributions indicated that *T. paucifolia*, the most closely examined species, was growing and reproducing normally. However, several populations located in the eastern region of ENP did exhibit up to threefold higher total sulfur (S) concentrations than others that were chosen because of their location 75–125 km west of major air pollution sources (Benzing, unpublished).

The objectives of this project were to characterize some responses to acute exposures of SO₂ and O₃ by two south Florida epiphytic orchids which fix carbon via CAM.

MATERIALS AND METHODS

Plant material

Two epiphytic orchids, *Encyclia tampensis* (*Epidendrum tampense*) and *Epidendrum rigidum* were collected in the Everglades National Park or in nearby swamp forests in January 1985. They were transported to the University of California, Irvine (UCI) and maintained there until July 1985 in a greenhouse with charcoal filtered air, a 25–30°C night temperature, natural light and 70–75% relative humidity. Several months before the experiments the plants were moved to the University of California, Riverside (UCR), where they were maintained in a similar greenhouse environment.

Exposure to sulfur dioxide and ozone

Plants were exposed to SO₂ or O₃ in nine continuously-stirred tank reactor (CSTR) exposure chambers 1.3 m in diameter and 1.36 m high, covered with 2 mil FEP Teflon film (Dupont Corp., Wilmington, DE). Chambers were supplied with greenhouse air at a rate of 1.2 air changes/min. All pollutant dispensing and sampling lines were made of 0.63 mm I.D. FEP Teflon and were calibrated for line loss efficiencies.

SO₂ was supplied to the chambers by metering anhydrous SO₂ into a stream of compressed air in a diluting manifold, thence into the chambers through valved flow meters. Concentrations of SO₂ were monitored with a pulsed fluorescent SO₂ analyzer (Model 43, Thermal Electric Corp., San Diego, CA). The SO₂ analyzer was calibrated using National Institute of Standards and

Technology (NIST) traceable permeation tubes. O₃ was generated from charcoal-filtered dry air by electrical spark discharge and was metered into the chambers through individual flow meters. Concentrations of O₃ inside chambers were monitored by a Dasibi O₃ analyzer (Dasibi Corp Model 1003 AH; Glendale, CA) calibrated monthly with a transfer standard certified by the California Air Resources Board.

Three plants of each species were exposed to 0.3, 0.6 and 1.2 ppm SO₂, or 0.15, 0.3 and 0.45 ppm O₃ for 6 hr on 4 consecutive days during the period of maximal stomatal conductance (2100–0800 hr). Five plants of each species were subjected to sequential expression of SO₂ and O₃ during the same night. Plants were first exposed to O₃ alone at 0.30 ppm for 2 hr (2000–2200 hr), then to O₃ at 0.30 ppm plus 0.6 ppm SO₂ for 2 hr (2200–0100 hr), and after that to 0.6 ppm SO₂ alone for 2 hr (0100–0300 hr). These concentrations were selected to represent the midpoint of O₃ or SO₂ levels used in previous exposures. All treatments (SO₂, O₃ and SO₂ plus O₃) were replicated four times.

Stomatal conductance

Stomatal conductance and transpiration were measured with a LI-COR Steady-State Porometer (Model LI-1600, Licor, Inc., Lincoln, NB) equipped with a narrow, 1 cm² aperture. Measurements of abaxial stomatal conductance were taken 2 weeks prior to the first exposure to determine baseline diurnal paths of conductance for the two orchids which are CAM species. Determinations were made of abaxial stomatal conductance and transpiration on five plants of each species at 3-hr intervals for 48 consecutive hr. During treatments with SO₂ or O₃, readings of abaxial stomatal conductance and transpiration were taken 1 hr before the start of exposures, midway through the 6-hr fumigation period, immediately after that and 12 hr after the exposure.

Malic acid determination

Tissue samples were taken with a 5 mm cork borer at 3-hr intervals and frozen immediately with dry ice. The tissues were ground, extracted with boiling water and titrated to pH 7.5 with 0.01 M NaOH.^(6,11,13,14)

FIG. 1. Nocturnal acidity in *Encyclia tampensis* and *Epidendrum rigidum*. (A) Diurnal rhythms. (B) Effects of O_3 and SO_2 singly and in combination.

Visible injury

Immediately following exposure, 12, 24, 48 hr and 2 and 12 weeks later, treated plants which were returned to the greenhouse were examined for signs of visible injury and metabolic dysfunction reflected in depressed nocturnal acidification (compared to controls). They were also examined by scanning electron microscopy (SEM) to observe possible occurrence of eroded cuticles or localized necrosis.

RESULTS

CAM

Epidendrum rigidum and *Encyclia tampensis* initiated CAM at approximately 2600 and 2200 hr, respectively (Fig. 1A). Deacidification was more rapid in *Encyclia tampensis* (Fig. 1A). Maximum titratable acidity was higher in specimens which remained in the greenhouse as opposed to control plants monitored in chambers flushed with ambient air (Fig. 1A vs Fig. 1B).

Fumigation with 0.15 ppm O_3 diminished

acidification in *Epidendrum rigidum* whereas treatments with 0.3 and 0.45 ppm enhanced it (Fig. 1B). O_3 at 0.15 ppm had little effect on *Encyclia tampensis* and exposure to 0.30 and 0.45 ppm promoted acid accumulation (Fig. 1B). Fumigation of *Epidendrum rigidum* with 0.3, 0.6 and 1.2 ppm SO_2 was accompanied by increased acidification especially at 0.3 ppm (Fig. 1B). Responses of *Encyclia tampensis* at 0.3 and 1.2 ppm were similar. Titratable acidity in leaves of *Epidendrum rigidum* was reduced by exposure to a combination of O_3 and SO_2 (Fig. 1B). Suppression of CAM was much less pronounced in *Encyclia tampensis*.

Stomatal conductance

Both *Encyclia tampensis* and *Epidendrum rigidum* exhibited maximal folial conductance at night (Table 1). Peak conductance was recorded at different times between 2100 and 0300 hr and shifted from the first to the second night of the study. Maximum stomatal conductances were 0.052 cm/sec for *E. tampensis* and 0.094 cm/sec for *E. rigidum*, about five to 10 times below those of

Table 1. Diurnal abaxial stomatal conductance (cm/sec) in *Encyclia tampensis* and *Epidendrum rigidum**

Measurement	Time (hr)	<i>Encyclia tampensis</i>	<i>Epidendrum rigidum</i>
1	0930	0.04 ± 0.009	0.03 ± 0.02
	1200	0.01 ± 0.0045	0.01 ± 0.01
	1500	0.02 ± 0.02	0.03 ± 0.01
	1800	0.02 ± 0.0071	0.02 ± 0.01
	2100	0.04 ± 0.02	0.02 ± 0.01
2	0000	0.05 ± 0.04	0.02 ± 0.01
	0600	0.02 ± 0.01	0.02 ± 0.01
	0800	0.05 ± 0.03	0.04 ± 0.04
	0900	0.01 ± 0.02	0.02 ± 0.02
	1200	0.02 ± 0.02	0.03 ± 0.01
	1500	0.02 ± 0.03	0.01 ± 0.03
	1800	0.002 ± 0.005	0.01 ± 0.01
	2100	0.05 ± 0.03	0.09 ± 0.04
3	0000	0.03 ± 0.01	0.02 ± 0.02
	0300	0.03 ± 0.01	0.020 ± 0.02
	0600	0.02 ± 0.02	0.036 ± 0.04
	0900	0.01 ± 0.01	0.030 ± 0.01

* Figures (mean ± standard deviation) represent measurements of five plants.

C₃ species, but within ranges recorded for other CAM plants.⁽²⁴⁾ Conductance values for both species were measured before, during, and after exposure to O₃, SO₂, and the two gases combined (Tables 1–3). Exposure to O₃ and/or SO₂ had no effect on stomatal conductance during or after fumigation.

Injury

There was no injury immediately following the fumigations nor did any necrosis, abnormal stem elongation or flower abortion occur in the months after treatment. Plants used in these experiments remained healthy in the greenhouse for approximately 18 months after the exposures. None of the fumigations caused any damage which could be seen with SEM.

DISCUSSION

The objectives of this study were to establish threshold values for injury or physiological effects. A factor which had to be taken into consideration

is that these species fix carbon via the Crassulacean acid metabolism (CAM) pathway.^(6,11) Plants exhibiting CAM are adapted to drought and have low gas exchange rates.^(15,24) Some are highly resistant to air pollutants.⁽²⁰⁾ Therefore, pollutant levels used in these experiments were higher than those that might be found in the environment (O₃: 0.15, 0.3 and 0.45 ppm vs 15–45 ppb at ENP for example).

SO₂ toxicity varies depending on exposure time, environmental conditions, the plant and its condition.^(18,25) Interveinal chlorosis is one of the most obvious symptoms.⁽¹⁹⁾ Leaf necrosis results from short exposures at high concentrations. Photosynthesis may be reduced by damage to the apparatus, competition between SO₂ and CO₂ for active sites on carboxylases or by effects on foliar conductance.⁽¹⁸⁾ Water use efficiency is often reduced while susceptibility to other stresses is increased. Chronic SO₂ exposure may increase leaf longevity and fertilize plants, thereby obscuring some adverse effects on metabolism.

Visible injury due to O₃ is often restricted to

Table 2. Stomatal conductance (cm/sec) of *Encyclia tampensis* exposed to O₃, SO₂ and a combination of the two between 2100 and 0300 hr*

Treatment (ppm)	Time (hr)			
	2000	0000	0300	1330
Control	0.015 (± 0.011)	0.01 $\pm$ 0.01	0.01 $\pm$ 0.00	0.01 $\pm$ 0.02
O ₃ 0.15		0.01 $\pm$ 0.01	0.01 $\pm$ 0.00	
0.30		0.00 $\pm$ 0.00	0.017 $\pm$ 0.00	
0.45		0.01 $\pm$ 0.007	0.01 $\pm$ 0.01	0.00 $\pm$ 0.00
SO ₂ 0.30		0.03 $\pm$ 0.03	0.02 $\pm$ 0.02	
0.60		0.01 $\pm$ 0.01	0.01 $\pm$ 0.00	
1.20		0.004 $\pm$ 0.005	0.02 $\pm$ 0.01	0.01 $\pm$ 0.01
O ₃ 0.30	0.033 (± 0.040)	0.01 $\pm$ 0.00	0.02 $\pm$ 0.01	0.01 $\pm$ 0.00
+ SO ₂ 0.60				

* Measurements were taken at 2000 (before exposures), 0000 (during), 0300 (after), and 1330 (next day) hr. Sequence of O₃ and SO₂ exposures is given in the text. The figures (mean $\pm$ standard deviation) represent three plants each from two replicate exposures.

Table 3. Stomatal conductance (cm/sec) of *Epidendrum rigidum* exposed to O₃, SO₂ and a combination of the two from 2100 to 0300 hr*

Treatment (ppm)	Time (hr)			
	2000	0000	0300	1330
Control	0.03 $\pm$ 0.02	0.02 $\pm$ 0.02	0.010 $\pm$ 0.01	0.03 $\pm$ 0.01
O ₃ 0.15		0.017 $\pm$ 0.00	0.01 $\pm$ 0.00	
0.30		0.01 $\pm$ 0.00	0.002 $\pm$ 0.002	
0.45		0.02 $\pm$ 0.00	0.01 $\pm$ 0.01	0.00 $\pm$ 0.00
SO ₂ 0.30		0.02 $\pm$ 0.03	0.01 $\pm$ 0.01	
0.60		0.01 $\pm$ 0.01	0.01 $\pm$ 0.01	
1.20		0.01 $\pm$ 0.01	0.01 $\pm$ 0.00	0.00 $\pm$ 0.00
O ₃ 0.30	0.04 $\pm$ 0.06	0.02 $\pm$ 0.02	0.003 $\pm$ 0.006	0.02 $\pm$ 0.02
+ SO ₂ 0.60				

* Measurements were taken at 2000 (before exposures), 0000 (during), 0300 (after), and 1330 (next day) hr. Figures (mean $\pm$ standard deviation) represent three plants each from two replicate exposures.

abaxial leaf surfaces and may include small blisters followed by cell collapse.⁽¹⁸⁾ Subsequent dehydration may produce silver or bronzed regions. O₃ can stimulate dark respiration with or without concomitant decreases in rates of reductive photosynthetic processes.⁽²⁵⁾ Effects on carbon balance and water use efficiency result from abnormal stomatal closure and damage to the photosynthetic mechanism. In addition, the gas may also inhibit nitrogen metabolism, promote leaf senescence and root development relative to shoot growth.⁽¹⁷⁾ Together SO₂ and O₃ often act synergistically and not always predictably.

Leaf structure^(21,22) and peculiarities of metabolism⁽⁴⁾ may have contributed to the insensitivity of these orchids to acute SO₂/SO₃ exposures. Maximum foliar conductances up to a full order of magnitude below those characteristic of more productive (and vulnerable) C₃ leaves probably protected mesophyll cells during the 6-hr exposures. Slow growth and metabolism probably also reduced vulnerability against permanent damage. Other life stages could be more vulnerable to toxic gases.

Both orchids are CAM plants, but they differ in the rate and degree of acidification (Fig. 1A). Deacidification in *Encyclia tampensis* is more rapid (from 1100 to 2200 hr) and acidification continues for a longer period (a total of 9 hr). In *Epidendrum rigidum* deacidification is slower (it requires 21 hr) and acidification proceeds for only 3 hr. This could be an indication that *Epidendrum rigidum* may fix carbon via both the CAM and C₃ pathways (I. P. Ting, University of California, Riverside, personal communication). Stress may cause such dual pathway plants to shift into CAM⁽¹⁵⁾ and this seems to be the case with *Epidendrum rigidum* (Fig. 1A). The stress caused by the pollutants (0.3 and 0.45 ppm O₃ and 0.3–1.2 ppm SO₂) brings about increased acidification (Fig. 1A). These observations which do not seem to have been reported before suggest that (1) the CAM characteristic may be stronger in some orchids than in others and (2) some orchids may shift into full or partial CAM only under stress.

Since they are CAM plants the leaves of both orchids should be most susceptible to injury by gases at night when their stomata are open. The roots of these species, like those of most epiphytic orchids, function not only as absorptive organs

but also fix carbon via CAM^(10,13) (for a review see Ref. 6). However no stomata are present in roots and gas exchange is regulated differently.^(12,26) Absence of damage suggests that both the roots and the leaves may be resistant to the treatments employed in these experiments. The velamen, a spongy layer of dead cells covering orchid roots (for a review see Ref. 21), may have provided protection. In well watered orchids (like the ones used in these experiments), the velamen may be fully or partially filled with water and could function as a protective barrier by trapping the gases. Even if a strong acid is formed when SO₂ dissolves in water-filled velamen cells, damage may be reduced because their walls are lignified and suberized. The effects of acid water in the velamen on mineral uptake by the roots cannot be estimated at present.

Little is known about seed or seedling biology of either species although fungal involvement is probably required for germination and early growth. Nor are there any reports regarding the effects of acidified precipitation on the mycorrhizal fungi of orchids. Low pH can retard or inhibit asymbiotic seed germination of orchids *in vitro*.^(3,5) The same may be true for symbiotic germination of nature.

Flowers may be a stage in orchid life cycle which would be vulnerable to SO₂ and O₃. Like damaged orchid flowers in general,⁽⁴⁾ flowers of *Encyclia tampensis* and *Epidendrum rigidum* injured by these gases can be expected to produce wound or stress ethylene which will shorten their life span. The shorter life span may in turn reduce exposure to pollinators and limit seed production as a consequence. In the long run this can deplete or eliminate populations.^(7,9)

Encyclia tampensis, *Epidendrum rigidum* and presumably the rarer epiphytic Florida orchids lack ecological resilience because their growth is slow. Therefore even minor reductions in fecundity, vigor or modest increases in mortality could have major effects on population structure and ultimately species survival. Numerous other threats to Florida epiphytes, especially falling water tables and fires, make a strong case for additional studies involving more realistic conditions to determine the threat which deteriorating air quality represents to a type of vegetation that includes some of the rarest plant species in the United States.

Acknowledgements—Supported in part by a grant from

the National Park Service to D.H.B. and J.A. We thank Dr J. P. Bennett and K. Stoltie for their assistance. J.A. and L.P.N. thank Dr S. M. Krassner (Acting Chairman of the Department at the time) for providing initial funding.

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