



Stomatal response of swordfern to volcanogenic CO₂ and SO₂ from Kilauea volcano

Lawrence H. Tanner,¹ David L. Smith,¹ and Amanda Allan¹

Received 9 April 2007; revised 10 June 2007; accepted 9 July 2007; published 9 August 2007.

[1] The experimentally determined relationship between atmospheric $p\text{CO}_2$ and plant stomata has been used to interpret large but transient changes in atmospheric composition, such as may have resulted from the eruptions of flood basalt. However, this relationship has not been tested in the field, i.e. in the vicinity of active volcanoes, to examine the specific effects of volcanogenic emissions. Moreover, the interpretation of paleoatmospheric $p\text{CO}_2$ from fossil stomatal data assumes that the stomatal response resulted solely from variation in $p\text{CO}_2$ and ignores the potential effect of outgassed SO_2 . We hypothesize that volcanogenic SO_2 also has a significant effect on leaf stomata and test this hypothesis by measuring the stomatal index of the common swordfern (*Nephrolepis exaltata*) in the plumes of the actively outgassing vents of Kilauea volcano. We find that, compared to control locations, stomatal index is lowest at sample sites in the plume of Halema'uma'u Crater, where concentrations of both CO_2 and SO_2 are much higher than background. However, sites located directly in the plume of Pu'u O'o, where SO_2 levels are high, but CO_2 levels are not, also yield low values of stomatal index. We propose that shifts in the stomatal index of fossil leaves may record transient atmospheric increases in both SO_2 and CO_2 , such as may be caused by eruptions of flood basalts. Calculations of $p\text{CO}_2$ based on stomatal frequency are likely to be exaggerated. **Citation:** Tanner, L. H., D. L. Smith, and A. Allan (2007), Stomatal response of swordfern to volcanogenic CO_2 and SO_2 from Kilauea volcano, *Geophys. Res. Lett.*, 34, L15807, doi:10.1029/2007GL030320.

1. Introduction

[2] The demonstrated decrease in stomatal index (SI; the number of stomata relative to the number of epidermal cells) of C_3 plants grown at elevated $p\text{CO}_2$ is thought to be a phenotypic response that improves water-use efficiency [Beerling *et al.*, 1998]. Stomatal initiation occurs early during leaf growth and is set well before leaf maturity. Thus, SI is immune to short-term variation in $p\text{CO}_2$ [Royer, 2001]. Consequently, stomatal indices from fossil leaves are now considered a proxy for paleo- $p\text{CO}_2$ [see, e.g., Kürschner *et al.*, 2001; Royer, 2001; Royer *et al.*, 2001]. Particularly significant is the use of this relationship to interpret large but transient changes in atmospheric composition that may result from catastrophic geologic processes, such as the eruption of large flood basalt provinces. For example, the release of CO_2 from the outgassing of a large volume of

basaltic lava has been cited as triggering an interval of intense greenhouse warming that resulted in a mass extinction at the Triassic-Jurassic boundary (200 million years ago) [Yapp and Poths, 1996; McElwain *et al.*, 1999; McHone, 2003]. Similar transient increases in paleo- $p\text{CO}_2$ have been identified at other important paleontologic boundaries using fossil stomatal data, including the Permian-Triassic (250 million years ago) and the Cretaceous-Tertiary (65 million years ago) [Retallack, 2001; Beerling *et al.*, 2002].

[3] The use of stomatal indices from fossil plants to calculate paleoatmospheric composition relies on the assumption that the stomatal response resulted primarily from variation of atmospheric $p\text{CO}_2$. Notably, the key paleontological boundaries at which substantial transient decreases in stomatal indices are noted (the Permian-Triassic, Triassic-Jurassic, and Cretaceous-Tertiary) also correspond to massive eruptions of flood basalt (the Siberian Traps, Central Atlantic Magmatic Province, and Deccan Traps, respectively), each with potential volumes of several million cubic kilometers. Basaltic magmas, like those that comprise the provinces, are rich in elemental sulfur, which is emitted to the atmosphere as outgassed SO_2 during the eruptions. Therefore, in addition to CO_2 emissions, the possible environmental effects of large flood basalt eruptions may include the loading of the atmosphere with SO_2 . The volumes of SO_2 outgassed during large basaltic eruptions are comparable in magnitude to those of CO_2 [Thordarson *et al.*, 1996], but because the ambient concentrations of these gases in the atmosphere differ by more than five orders of magnitude, the net effect of outgassing is significantly greater for atmospheric SO_2 .

2. Location and Methods

[4] We examined the stomatal response to volcanogenic outgassing by measuring stomatal frequency of the common fern species swordfern (*Nephrolepis exaltata*) at various locations on Hawai'i. Sampling focused on sites on Kilauea, a basaltic shield volcano on the southeastern flank of Hawai'i. Most eruptions in recent decades have been confined to the summit and east rift zone, and the craters created by these eruptions serve as point sources of long-term CO_2 and SO_2 emissions. Measurements of emissions compiled by U.S. Geological Survey personnel between 1992 and 2001 utilizing correlation spectrometry show that SO_2 emissions from the Halema'uma'u crater (in the summit caldera) and the currently erupting (since 1983) Pu'u O'o vent have consistently averaged near 2000 t/d, with the bulk of these emissions emanating from the Pu'u O'o vent [Elias *et al.*, 1998; Elias and Sutton, 2002]. The summit, however, produces a large volume of CO_2 , c. 8500 t/d [Gerlach *et al.*, 2002], while CO_2 emissions from Pu'u O'o

¹Department of Biological Sciences, Le Moyne College, Syracuse, New York, USA.

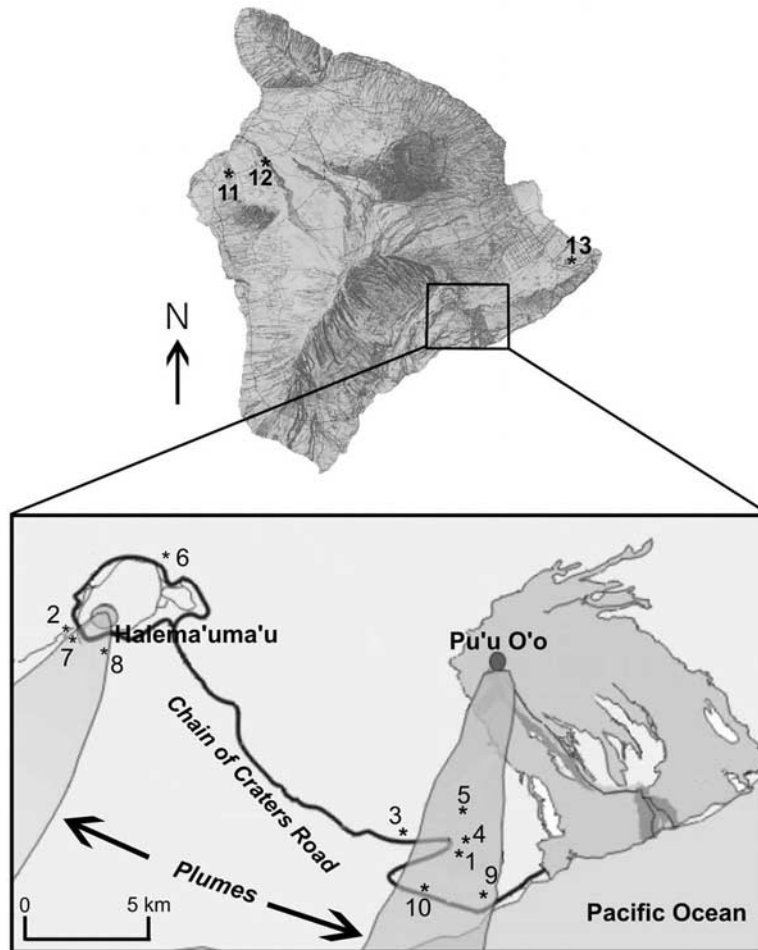


Figure 1. Location map of sample sites on Hawaii (adapted from *Elias and Sutton* [2002]). Sites 11–13 on inset map.

are low [*Gerlach et al.*, 1998]. North-northeast (c. 30° east of north mean direction) trade winds disperse these emissions in plumes strongly directed to the south-southwest (Figure 1). Consequently, areas downwind of the active vents are subjected to frequent and prolonged elevation of volcanogenic emissions. Immediately downwind of Halema'uma'u, CO₂ levels within the plume may exceed 1200 ppmv, and SO₂ levels approach 4 ppmv [*Gerlach et al.*, 2002]. By contrast, 1 km downwind of Pu'u O'o, CO₂ levels within the plume are less than 0.5 ppm, but maximum SO₂ levels exceed 3 ppmv [*McGee and Gerlach.*, 1998]. *Longo et al.* [2005] measured (by diffusion tube) SO₂ levels of c. 0.14 ppmv at a location within the Pu'u O'o plume at a location 8 km from the vent.

[5] The fern *Nephrolepis* was selected for study for its widespread occurrence on the island and for the large and easily distinguished stomata and epidermal cells. In January 2005, we collected samples of swordfern from ten sites within Volcanoes National Park and three additional sites at other locations on the island (Figure 1). The locations within the park (Table 1: sites 1–10) are varying distances (1 to 11 km) to the south to southwest of the outgassing vents. Specifically, sites 1, 4, 5, 9 and 10 all lie within the south-directed plume of Pu'u O'o, as mapped by *Elias and Sutton* [2002]; site 3 is just outside the core of this plume to the west. Sites 2, 7 and 8 are located within the plume of Halema'uma'u, approximately 1 km from the crater. Site 6

is located 3 km to the northeast (upwind) of Halema'uma'u. The additional locations (sites 11–13) were chosen as controls and are located 70 km to the northwest (Sites 11 and 12) and 35 km to the northeast (Site 13). At each site, multiple specimens were collected from plants with a consistent, predominantly well-irradiated position to minimize potential sun v. shade effects. Ten samples were prepared from the fronds of at least two separate plant specimens per sample location. For each sample, a minimum total of 200 cells (stomata and epidermal cells combined) were counted from digital images of the underside of the frond surface captured by transmitted light microscopy at a magnification of 200X. Therefore each sample site represents a minimum count total of 2000 cells. For each sample site, we calculated values of stomatal index (SI: calculated as 100 times the number of stomata divided by the number of epidermal cells plus stomata). Results are presented in Table 1.

3. Results

[6] Potential variables among the sample locations include CO₂ and SO₂ levels, precipitation, and elevation. Precipitation varies between those sample sites on the southeast side of the island (200–230 cm/yr) and those to the northwest (c. 130–150 cm/yr), but previous work [e.g.,

Table 1. Stomatal Data With Sample Location Information

Site	Location	SI	Standard Error	Elevation, m
1	N19°18′49.5″, W155°07′41.2″	22.3	1.8	398
2	N19°24′09.5″, W155°17′40.8″	19.2	1.3	1148
3	N19°18′50.8″, W155°09′01.2″	23.8	2.7	541
4	N19°18′54.0″, W155°07′37.1″	21.0	1.6	404
5	N19°19′21.7″, W155°07′28.2″	20.2	2.0	498
6	N19°25′56.4″, W155°15′41.6″	22.3	1.6	1196
7	N19°23′59.6″, W155°17′43.6″	20.3	1.9	1136
8	N19°23′47.9″, W155°17′11.5″	19.8	2.3	1154
9	N19°17′08.0″, W155°07′01.9″	20.3	1.3	98
10	N19°17′36.3″, W155°08′41.3″	21.5	2.6	148
11	N19°46′08.3″, W155°55′55.7″	25.8	1.8	643
12	N19°49′41.2″, W155°49′09.8″	24.1	2.3	681
13	N19°29′36.8″, W154°52′10.3″	25.3	1.8	135

Royer, 2001] has determined that water stress has little control on stomatal index. Sample site elevations range from 98 m above sea level to 1295 m above sea level. Contrasting trends in stomatal frequency v. altitude have been demonstrated for tropical and temperate species [Greenwood *et al.*, 2003; McElwain, 2004], but regression analysis of our data indicates that SI is independent of altitude ($R^2 = 0.09$, $p = 0.29$). Consequently, we consider differences in the concentration of airborne CO₂ and SO₂ the primary cause of variation of the stomatal index of swordfern on Hawaii.

[7] The data of McGee and Gerlach [1998], Gerlach *et al.* [1998, 2002], and Longo *et al.* [2005], described above, allow us to compare qualitatively the levels of CO₂ and SO₂ at the various sample sites with the measured SI. The lowest values of SI (19.2 to 20.3) occur at sites 2, 7 and 8, located proximal and downwind of Halema'uma'u. These sample sites are assumed to be subject to consistent exposure to CO₂ levels two to three times ambient (up to 1200 ppmv), and SO₂ levels elevated by up to three orders of magnitude (up to 4 ppmv). Site 6 (SI = 22.3) is proximal to Halema'uma'u, but located upwind. We note however, that this site is near fumaroles, and so elevated levels of both CO₂ and SO₂ are likely, but not quantified by extant data. Sites 1, 4, 5, 9 and 10 are downwind of Pu'u O'o and within the plume. At these sites, SO₂ levels are likely an order of magnitude lower than near the vent, i.e., in the range of 100 ppbv [Longo *et al.*, 2005], but still two orders greater than ambient. Given the low CO₂/SO₂ ratio (c. 0.2) in this plume [Gerlach *et al.*, 1998], $p\text{CO}_2$ at these sample sites is assumed near ambient. Values of SI for these sites range from 20.2 to 22.3. Site 3 (SI = 23.8) is west of Sites 1, 4 and 5, and to the west of the mapped plume boundary. McGee and Gerlach [1998] demonstrated that SO₂ levels decrease sharply transverse to the plume axis, by an order of magnitude within one kilometer, and so Site 3 levels are assumed significantly lower than at 1, 4 or 5. SI is significantly higher at those locations well upwind or distant from Kilauea; values at Sites 11, 12 and 13 are the highest measured, ranging from 24.1 to 25.8. The mean SI for these sample sites is 5.3 higher than the mean for sites downwind from Halema'uma'u, and 4.0 higher than the sites downwind from Pu'u O'o. Sites 11 and 12 are located to the northwest of Kilauea volcano and well-isolated from the volcanic plumes by the presence of the two high elevation

(>4000 m) shield volcanoes, Mauna Loa and Mauna Kea. The data of Longo *et al.* [2005] suggest SO₂ levels on this part of the island are typically less than 1.0 ppbv. We have no data on CO₂ for this area, but assume ambient levels. Site 13 is distant and upwind of the volcanic vents, and so in the absence of data, we assume near ambient levels of CO₂ and SO₂ for this site as well.

4. Discussion

[8] The difference in SI between the control sites (11, 12 and 13) and the sites downwind of Halema'uma'u (Sites 2, 7 and 8) is explainable by the well-known influence of elevated $p\text{CO}_2$. This, however, does not explain the effect of the Pu'u O'o plume (sites 1, 4, 5, 9 and 10), in which CO₂ levels are near ambient. We attribute the lower SI at these sites to the effects of volcanogenic SO₂. In contrast to the body of research documenting the relationship between atmospheric $p\text{CO}_2$ and stomatal index, there exist few data examining comparable effects of long-term exposure to SO₂. Fortunately, literature exists describing the anatomical and physiological changes resulting from the exposure of plants, particularly crop varieties, to airborne pollutants, including SO₂. For example, in *Phaseolus vulgaris*, long-term exposure to SO₂ caused reduced photosynthesis and/or transpiration, resulting in leaf senescence [Saxe, 1983]. Closure at elevated SO₂ possibly may be a consequence of the inhibition of photosynthesis by SO₂ as this leads to an increase in CO₂ levels in the substomatal cavity [Iqbal *et al.*, 1996]. Therefore, stomatal closure appears to be a protective response to elevated atmospheric levels of both SO₂ and CO₂.

[9] The relationship for SO₂ has not been examined experimentally, although one study of the effects of industrial pollution on the tree *Syzygium cumini* observed a decrease in both stomatal density and index that correlated with concentrations of SO₂ and NO₂ [Jacob, 2003]. Winner and Mooney [1985] studied the tolerance of various plant species to the SO₂ plume on Kilauea by placing potted plants at various distances from an active vent in the Kilauea Caldera and by establishing study plots of the existing vegetation at various distances downwind from one contemporaneously active crater (Pauahi Crater). SO₂ levels at their study sites varied from over 100 ppmv (proximal to a vent) to 0 ppmv. They found, as other studies

have, that species tolerance to leaf injury from the SO₂ is dependent on the tendency to close leaf stomata on exposure. Accordingly, we interpret our data to indicate that long-term exposure of swordfern to elevated SO₂ levels (i.e., in the range of 100 ppbv) in the Pu'u O'o plume triggers a phenotypic response of reduced stomatal frequency relative to the number of epidermal cells, thus minimizing the inhibiting effects of SO₂ on photosynthesis. This response appears to be triggered by levels of SO₂ that are more than an order of magnitude lower than the level of CO₂ that triggers a similar response. This is not surprising given the low ambient concentrations of SO₂ in the atmosphere, and the apparent sensitivity of leaf stomata to this gas. The lowest SI values, encountered in the Halema'uma'u plume, likely reflect a compounding effect of elevated levels of both CO₂ and SO₂.

[10] Basaltic magmas typically contain high levels of elemental sulfur. Values exceeding 2000 ppmv are measured from historic fissure eruptions, of which 80–85% may be released to the atmosphere as volatile emissions [Thordarson *et al.*, 2001], and historic eruptions, such as Laki, Iceland (1783), have demonstrated the potential for widespread atmospheric distribution of the emitted SO₂ [Thordarson *et al.*, 1996]. By analogy, the eruption of large igneous provinces, such as Deccan which were more than five orders of magnitude larger than the Laki flows, likely emitted well over 10¹⁸ g of sulfur as SO₂ [Self *et al.*, 2006]. Much SO₂ outgassed during effusive basalt eruptions is thought to remain in the troposphere, although a significant portion may be driven into the stratosphere by convection [Woods, 1993]. The environmental effects of large sulfur emissions during such prolonged flood basalt eruptions are not clear, but the formation of H₂SO₄ aerosols is known to increase atmospheric opacity and result in reduced short-wave radiant heating, causing global cooling [Sigurdsson, 1990]. In the troposphere, SO₂ washes out quickly and typically has a residence time of only weeks to months. In the stratosphere, however, the acid aerosols may reside much longer, for periods of several years or less, and so the effects of continuing eruptions may be cumulative. Importantly, large igneous provinces do not erupt continuously, but rather as a series of pulses of several thousand cubic kilometers, each lasting years to decades, separated by quiescent periods. Individual eruptive pulses likely loaded the atmosphere at a rate of approximately 200 ppbv a⁻¹, although the cumulative increase over the duration of an eruptive episode would depend largely on the effective partitioning of the released SO₂ between troposphere and stratosphere. The consequence of this loading, and the resultant atmospheric opacity would have been cooling episodes of as much as 6°C (by scaling to modern eruptions [Sigurdsson, 1990]) that lasted for the duration of the eruptive episodes. Additionally, these releases potentially would have raised average atmospheric SO₂ levels to several hundred ppbv and triggered a phenotypic stomatal response in plant species that grew during the eruptive episodes.

5. Conclusions

[11] This study demonstrates the local effects of volcanogenic gases on the stomatal frequency of a single plant

species. The compounded effects of SO₂ and CO₂ result in significant lowering of SI. Notably, these data also demonstrate that SO₂ alone causes a lowering of SI similar to that well documented for CO₂. Historic eruptions, for example Laki, Iceland in 1783, have demonstrated the potential for widespread atmospheric distribution of SO₂ outgassed by basaltic lava [Thordarson *et al.*, 1996]. The large flood basalt provinces that erupted at the paleontologic boundaries cited above have projected volumes five orders of magnitude greater than the Laki flows. By implication, these long-term eruptions may have produced a similar phenotypic response in plant species across large areas of the globe that is indistinguishable from that produced by elevated *p*CO₂. Therefore, calculations of *p*CO₂ change at these boundaries, and the invocation of associated catastrophic greenhouse warming as a mechanism for extinction, must be reassessed. Accordingly, it is also necessary to examine more closely the impact of volcanogenic SO₂ on the global environment and the potential role of SO₂ outgassing as a mechanism of extinction. Clearly, additional work is needed to quantify the effect of SO₂ on stomatal indices of plants extant at major paleontologic boundaries (e.g., *Ginkgo*), such as the Permo-Triassic, Triassic-Jurassic, and Cretaceous-Tertiary. Only then may it be possible to parse the relative environmental effects of SO₂ and CO₂ during these geologically important environmental events.

[12] **Acknowledgments.** Funding for the project was provided by the National Science Foundation Division of Integrative Organismal Biology (Award 0407166). We also thank the Department of Biology at University of Hawaii, Hilo, for use of microscopy facilities during conduct of this study, and JennyLee Osborn for assistance in collecting the data. Andrea Marzoli and an anonymous reviewer provided comments that substantially improved this manuscript.

References

- Beerling, D. J., J. C. McElwain, and C. P. Osborne (1998), Stomatal responses of the "living fossil" *Ginkgo biloba* L. to changes in atmospheric CO₂ concentrations, *J. Exp. Bot.*, **49**, 1603–1607.
- Beerling, D. J., B. H. Lomax, D. L. Royer, G. R. Upchurch, and L. R. Kump (2002), An atmospheric *p*CO₂ reconstruction across the Cretaceous-Tertiary boundary from leaf megafossils, *Proc. Nat. Acad. Sci.*, **99**, 7836–7840.
- Elias, T., and A. J. Sutton (2002), Sulfur dioxide emission rates from Kilauea volcano, Hawai'i, an update: 1998–2001, *U.S. Geol. Surv. Open File Rep.*, **02-460**.
- Elias, T., A. J. Sutton, J. B. Stokes, and T. J. Casadevall (1998), Sulfur dioxide emission rates of Kilauea volcano, Hawaii, 1979–1997, *U.S. Geol. Surv. Open File Rep.*, **98-462**.
- Gerlach, T. M., K. A. McGee, A. J. Sutton, and T. Elias (1998), Rates of volcanic CO₂ degassing from airborne determinations of SO₂ emission rates and plume CO₂/SO₂: Test study at Pu'u O'o cone, Kilauea volcano, Hawaii, *Geophys. Res. Lett.*, **25**, 2675–2678.
- Gerlach, T. M., K. A. McGee, T. Elias, A. J. Sutton, and M. P. Doukas (2002), Carbon dioxide emission rate of Kilauea volcano: Implications for primary magma and the summit reservoir, *J. Geophys. Res.*, **107**(B9), 2189, doi:10.1029/2001JB000407.
- Greenwood, D. R., M. J. Scarr, and D. C. Christophel (2003), Leaf stomatal frequency in the Australian tropical rainforest tree *Neolitsea dealbata* (Lauraceae) as a proxy measure of atmospheric *p*CO₂, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, **196**, 375–393.
- Jacob, M. (2003), The anatomical and physiological responses of *Szygium cumini* (L.) Skeels to coal with special reference to wood production, Ph.D. thesis, 237 pp., Jamia Hamdad Univ., New Delhi, India.
- Iqbal, M., M. Z. Abidin, M. Mahmooduzzar, M. Yunnus, and M. Agrawal (1996), Resistance mechanisms in plants against air pollution, in *Plant Response to Air Pollution*, edited by M. Yunnus and M. Iqbal, pp. 195–240, John Wiley, New York.
- Kürschner, W. M., F. Wagner, D. L. Dilcher, and H. Visscher (2001), Using fossil leaves for reconstruction of Cenozoic paleoatmospheric CO₂ concentration, in *Geological Perspectives of Global Climate Change*, *Stud.*

- Geol.*, vol. 47, edited by L. C. Gerhard, W. E. Harrison, and B. M. Hanson, pp. 155–176, Am. Assoc. Pet. Geol., Tulsa, Okla.
- Longo, B. M., A. Grunder, R. Chuan, and A. Rossignol (2005), SO₂ and fine aerosol dispersion from the Kilauea plume, Kau district, Hawaii, USA, *Geology*, 33, 217–220.
- McElwain, J. C. (2004), Climate-independent paleoaltimetry using stomatal density in fossil leaves as a proxy for CO₂ partial pressure, *Geology*, 32, 1017–1020.
- McElwain, J. C., D. J. Beerling, and F. I. Woodward (1999), Fossil plants and global warming at the Triassic-Jurassic boundary, *Science*, 285, 1386–1390.
- McGee, K. A., and T. M. Gerlach (1998), Airborne volcanic plume measurements using a FTIR spectrometer, Kilauea volcano, Hawaii, *Geophys. Res. Lett.*, 25, 615–618.
- McHone, J. G. (2003), Volatile emissions from central Atlantic magmatic province basalts: Mass assumptions and environmental consequences, in *The Central Atlantic Magmatic Province: Perspectives from the Rifted Fragments of Pangea*, *Geophys. Monogr. Ser.*, vol. 136, edited by W. E. Hames et al., pp. 241–254, AGU, Washington, D. C.
- Retallack, G. J. (2001), A 300-million-year record of atmospheric carbon dioxide from fossil plant cuticles, *Nature*, 411, 287–290.
- Royer, D. L. (2001), Stomatal density and stomatal index as indicators of paleoatmospheric CO₂ concentration, *Rev. Palaeobot. Palynol.*, 114, 1–28.
- Royer, D. L., R. A. Berner, and D. J. Beerling (2001), Phanerozoic atmospheric CO₂ change: Evaluating geochemical and paleobiological approaches, *Earth Sci. Rev.*, 54, 349–392.
- Saxe, H. (1983), Long-term effects of low levels of SO₂ on bean plants (*Phaseolus vulgaris*), *Physiol. Plants*, 57, 101–107.
- Self, S., M. Widdowson, T. Thordarson, and A. E. Jay (2006), Volatile fluxes during flood basalt eruptions and potential effects on the global environment: A Deccan perspective, *Earth Planet. Sci. Lett.*, 248, 517–531.
- Sigurdsson, H. (1990), Assessment of atmospheric impact of volcanic eruptions, in *Global Catastrophes in Earth History*, edited by V. L. Sharpton and P. D. Ward, *Spec. Pap. Geol. Soc. Am.*, 247, 99–110.
- Thordarson, T., S. Self, N. Oskarsson, and T. Hulsebosch (1996), Sulfur, chlorine, and fluorine degassing and atmospheric loading by the 1783–1784 AD Laki (Skaftár Fires) eruption in Iceland, *Bull. Volcanol.*, 58, 205–225.
- Thordarson, T., D. J. Miller, G. Larsen, S. Self, and H. Sigurdsson (2001), New estimates of sulfur degassing and atmospheric mass-loading by the 934 AD Eldgjá eruption, Iceland, *J. Volcanol. Geotherm. Res.*, 108, 33–54.
- Winner, W. E., and H. A. Mooney (1985), Ecology of SO₂ resistance, *Oecologia*, 66, 387–393.
- Woods, A. W. (1993), A model of the plumes above basaltic fissure eruptions, *Geophys. Res. Lett.*, 20, 1115–1118.
- Yapp, C. J., and H. Poths (1996), Carbon isotopes in continental weathering environments and variations in ancient atmospheric CO₂ pressure, *Earth Planet. Sci. Lett.*, 137, 71–82.

A. Allan, D. L. Smith, and L. H. Tanner, Department of Biological Sciences, Le Moyne College, 1419 Salt Springs Road, Syracuse, NY 13214, USA. (tannerlh@lemoyne.edu)