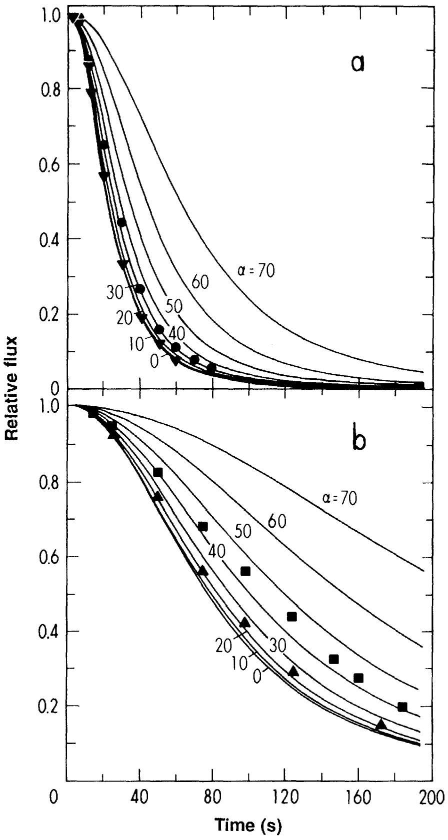

Fig. 5. Flux ratios $F_\theta/F_{\theta=\alpha}$, where F_θ is the value measured at zenith angle θ and $F_{\theta=\alpha}$ is the value at nearest approach, are shown for minimum zenith angles, α, of 0°, 10°, 20°, 30°, 40°, 50°, 60°, and 70°. (**a**) Data points for satellites A (▼) and B (●) are plotted for 260-km altitude. (**b**) Similarly, data points for satellites C (▲) and D (■) are for 800-km altitude.

December 1987 and Cosmos 1932 in March 1988. These satellites are in nearly circular orbits 260 km above the earth (*8, 10*). Their purpose is to locate large surface vessels and concentrations of smaller ships through active illumination by radar energy. The Soviet Union is the only nation that utilizes moderated nuclear reactors for power on satellites. In January 1989 the Soviets announced that at least two advanced-type reactors were placed in higher orbits in the preceding 2 years (*11*). These satellites are the most efficient, long-lived, and powerful ever put in orbit. These are most likely satellites C and D.

The UCR Telescope has the capability of detecting an A-type satellite reactor passing overhead at a distance of 2500 km with 5 σ significance. The longer observation time of reactors in the higher orbits partially counters the inverse square decrease in intensity. For locations other than overhead, the telescope's off-axis area factor and flatter time profile decrease the maximum satellite observation distance. The atmospheric attenuation difference between overhead and large zenith angles plays a minimal role with the balloon at 35-km altitude.

From Table 1 it can be seen that reactors in space may cause significant problems by increasing backgrounds, particularly for gamma-ray bursts. While precautions may be taken to program detectors to ignore these events, particularly for balloon observations, it may be more difficult to eliminate these events with satellite experiments.

REFERENCES AND NOTES

1. M. M. Waldrop, *Science* **242**, 1119 (1988).
2. C. Knox, *Sci. News* **134**, 340 (1988).
3. J. Primack, *et al., Science and Global Security*, in press.
4. T. J. O'Neill, W. E. Sweeney, O. T. Turner, A. D. Zych, R. S. White, *IEEE Trans. Nuc. Sci.* **NS-35**, 511 (1987).
5. J. Simone, T. O'Neill, O. T. Turner, A. D. Zych, *ibid.* **NS-32**, 124 (1985).
6. R. Vandenbosch and J. Huizenga, *Nuclear Fission* (Academic Press, New York, 1973), p. 360.
7. S. Aftergood, *Space Policy* **5**, 25 (1989).
8. *Aviat. Week Space Technol.* **123**, 18 (19 August 1985).
9. T. D. Thompson, *TRW Space Log 1957–1987* (TRW Space & Technology Group, El Segundo, CA, 1988).
10. N. Johnson, *The Soviet Year in Space 1987* (Teledyne Brown Engineering, Denver, CO, 1988), pp. 69–75.
11. W. J. Broad, *New York Times*, 15 January 1989, p. A1.
12. We thank NASA for valuable support from grant NGR-05-008-022 and the National Scientific Balloon Facility for their field, balloon launch, and recovery operations support.

26 January 1989; accepted 13 March 1989

Hydrogen Sulfide on Io: Evidence from Telescopic and Laboratory Infrared Spectra

DOUGLAS B. NASH AND ROBERT R. HOWELL

Evidence is reported for hydrogen sulfide (H_2S) on Io's surface. An infrared band at 3.915 (± 0.015) micrometers in several ground-based spectra of Io can be accounted for by reflectance from H_2S frost deposited on or cocondensed with sulfur dioxide (SO_2) frost. Temporal variation in the occurrence and intensity of the band suggests that condensed H_2S on Io's surface is transient, implying a similar variation of H_2S abundance in Io's atmosphere. The band was observed in full-disk measurements of Io at several orbital longitudes, including once at 24° (~0.5 hour after Io's reappearance after an eclipse)—but not after another reappearance at 22°—and once at 95° (on Io's leading hemisphere). These results suggest that condensed H_2S is sparse and variable but can be widespread on Io's surface. When present, it would not only produce the infrared band but would brighten Io's typical surface at ultraviolet and visible wavelengths.

PLANETARY SCIENTISTS HAVE LONG suspected that H_2S is present on Io. Recently published infrared (IR) spectra (*1*) may contain positive evidence for H_2S. Early visible-wavelength spectroscopic studies of Io suggested that elemental sulfur was a major surface constituent (*2, 3*) and a principal component in the Io torus (*4*). Because Io is immersed in Jupiter's radiation belts, it was thought that proton bombardment of the sulfur-rich surface could form transient H_2S on Io and a tenuous but transient atmosphere (*5, 6*). The possibility of photodissociation of endogenic H_2S on Io by solar ultraviolet (UV) radiation was suggested (*7, 8*). Ground-based IR spectroscopic searches for atmospheric components including H_2S were negative (*9*) but were followed by Voyager's 1979 discovery of active volcanism (*10*) and the detection of ~0.2 cm-atm of SO_2 gas near Loki and the setting of an upper limit of ~0.07 cm-atm of H_2S gas in Io's atmosphere near the sunlight terminator (*11*).

Other ground-based observations had revealed distinct bands in Io's reflectance spectra near 4 μm (*12, 13*) that identified solid SO_2 on Io's surface (*6, 14*). Laboratory studies suggested that H_2S or SO_2 could be adsorbed on Io's surface (*15*). Variation in the depth and shape of Io's 4-μm band over several years of observations (*12, 16*) was later shown to be due to differences in the spatial distribution of SO_2 on Io rather than temporal variation in the SO_2 concentration (*17*). Searches for temporal variation in the SO_2 band strength at constant orbital longitude were negative (*1, 18*).

Apparent temporal variability in Io's spectrum was discovered by Howell *et al.* (*1*), who obtained several spectra showing a new band near 3.915 (± 0.015) μm (*19*). The band was moderately strong in Io spectra on several occasions but was usually absent or weak. Because these spectra showed discrepancies compared to most others and because

---

D. B. Nash, Jet Propulsion Laboratory, California Institute of Technology, Pasadena, CA 91109, and San Juan Capistrano Research Institute, San Juan Capistrano, CA 92675.
R. R. Howell, Department of Physics and Astronomy, University of Wyoming, Laramie, WY 82071.

of concern about possible instrumental artifacts associated with the new spectrometer used for the observations, the spectra with the strong, 3.915-μm band were considered "anomalous" (*1*).

We have studied these and other spectra to determine the origin of the 3.915-μm band. The band is not present in laboratory reflectance spectra of SO_2 frost (*20*). The transient character of the band suggested that it was due to a volatile component on Io that was condensable under Io conditions but more volatile than SO_2. Because of our prior interest in H_2S (*5, 15*) and its high volatility compared to SO_2, these two species became our targets of interest. We proceeded from an unpublished IR spectrum of H_2S frost (*21*), which showed a band at about the correct wavelength but without the shape seen in the anomalous Io spectra. We conducted laboratory experiments with various combinations of H_2S and SO_2 frosts to simulate Io surface conditions. Because SO_2 frost is a major surface component on Io (*20*), we prepared deposits of layered and intimate mixtures of condensed SO_2 and H_2S and measured their IR reflectance spectra (*22*).

We found that a thin H_2S frost layer with a thickness of ≈0.1 mm has a strong, symmetric band with a minimum at 3.90 (± 0.01) μm (Fig. 1a, spectrum 1); we identify this as a fundamental stretching-mode band (*23*). When the frost is about 1 mm thick, the 3.90-μm band is saturated, developing a broad flat-bottomed minimum (Fig. 1a, spectrum 2).

A thin layer of H_2S frost on top of a thick substrate of SO_2 frost produces a spectrum [Fig. 1b, spectrum (B)] (*24*) that is a good match to the observed anomalous Io spectra, which contain a similarly shaped band at 3.915 (± 0.015) μm (Fig. 2) (*24*). One of the two Io spectra in Fig. 2 that prominently show the 3.915-μm feature was observed when Io was at an orbital longitude near 24°, about 35 min after Io emerged from Jupiter's shadow. A companion spectrum taken ~8 min later near Io longitude 25° did not show the 3.915-μm feature. One explanation is that the material on Io's surface causing the absorption feature was deposited during the preceding eclipse period when Io's surface was cooler and subsequently evaporated after Io emerged from the eclipse.

Judging from the rapid rate of change of the Io spectrum during the 8-min interval between posteclipse observations and from the laboratory sequence on frost evaporation shown in Fig. 1b, one could conclude that before the time of observation of the spectrum taken at longitude 24° on 2 August 1983 a considerable amount of H_2S must have been present on the surface (and a much stronger 3.915-μm absorption band present in Io's spectrum). However, during the observation on 2 August 1983, as Io came out of eclipse, an ancillary measurement by Howell *et al.* of the relative spectral brightness variation with time at 3.5 and 4.07 μm showed no significant depression of the brightness at 3.5 μm prior to obtaining the spectrum at 24° longitude. This result implies that if atmospheric or plume-derived H_2S was condensed on the surface during the preceding eclipse period, it was not optically thick at 3.95 μm [producing a deep, saturated band as in spectrum (A) of Fig. 1b]. At the emergence of Io into sunlight, the optical effect of this condensed H_2S on the full-disk spectrum did not change much until about ~40 min after the eclipse ended. The fact that on two other occasions (5 September and 21 September 1984) there was little or no 3.915-μm absorption during observations at longitude 22° (~15 min after eclipse) and 32° (~62 min after eclipse) suggests that the presence of the 3.915-μm band on 2 August 1983 represented not only a transient but an irregular (and infrequent) occurrence of H_2S frost on the surface. This frost, which is bright white in UV and visible wavelengths (*25*), would have produced a classic post-eclipse brightening event on Io that should have been detectable from Earth if suitable observations for it had been made then.

A second Io spectrum in the suite presented by Howell *et al.* (*1*) shows a similarly strong, 3.915-μm band; this spectrum was taken at longitude 95° on Io's leading hemisphere (Fig. 2, spectrum F). Spectra taken at other times near that longitude (*12, 16*) do not show such a distinct 3.915-μm band. Two other spectra (E and H) in the suite of Howell *et al.* (*1*) (Fig. 3) show a distinct but weak absorption band at 3.915 μm, which is consistent with the presence of a small amount of H_2S frost on Io's surface at those two times (17 June 1985 and 29 June 1983) and longitudes (70° and 306°, respectively). A survey of all available spectra shows no distinct sign of a 3.915-μm band in full-disk spectra for Io hemispheres viewed in the orbital longitude range increasing from 120° to 300°.

If a transient deposit of H_2S caused the 3.915-μm feature on Io's leading hemisphere surface during daytime conditions (that is, at orbital longitude near 90°), it must be related to unusual thermal or atmospheric activity. One possibility is that it could be related to the type of high-temperature, short-lived thermal outbursts observed on three occasions (*26*), on Io's leading hemisphere (near orbital longitudes 68°, 79°, and 83°). Because H_2S is much more volatile than SO_2, the occurrence of optically detectable H_2S frost on Io during non-eclipse conditions suggests two possible conditions: (i) the H_2S must, at least on occasion, be extremely abundant in Io's atmosphere to provide a saturation vapor pressure sufficient to condense surface frost in subsolar equatorial regions, where the surface temperatures are on the order of 120 to 140 K (*27*); or (ii) H_2S is being deposited from the atmosphere or plumes in colder, high-latitude, polar regions (*28*), where the surface density of atmospheric H_2S required to condense surface frost is correspondingly less. If this apparent leading-hemisphere transient H_2S event is related to the thermal

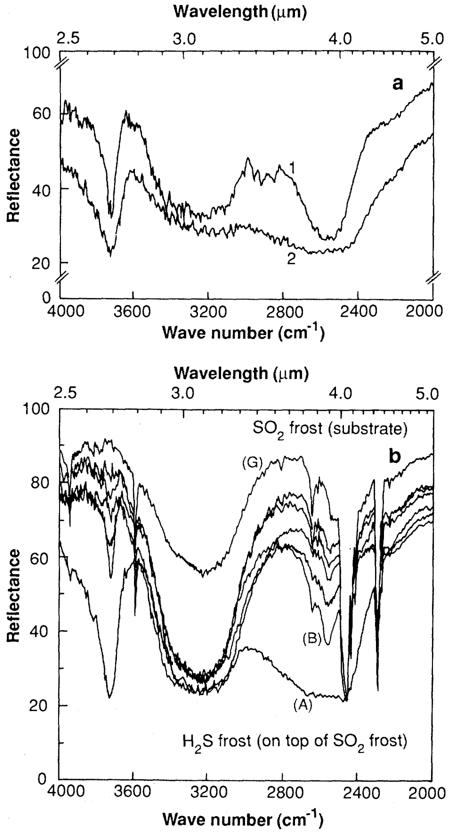

Fig. 1. Laboratory reflectance spectra of H_2S and SO_2 frosts, both containing contaminant H_2O (the broad feature centered near 3.1 μm). Spectral resolution was 4 cm^{-1} for all spectra. Spectral intensities are relative to KBr powder (packed). (**a**) H_2S frost on a stainless steel platen cooled to 77 K by liquid N_2; sample 1, ~0.1 mm thick; sample 2, ~1.0 mm thick; the vapor pressures over the frosts during the spectral measurements were ~2000 μm (0.003 atm) for sample 1 and ~1 psi (0.07 atm) for sample 2. (**b**) Sequence of spectra (A through G) taken during a period of 5 min as a layer of H_2S frost 1 mm thick evaporated from on top of a substrate of SO_2 frost about 2 mm thick; during this period a vacuum pump exhausted the chamber at a dynamic pressure of ~10 μm (10^{-5} atm). The cold-finger platen was maintained at 77 K during the sequence. In both (a) and (b) the optical path length through the vapor phase in the vacuum chamber was 25 cm. The SO_2 frost shows distinct bands at 2.53, 2.79, 3.56, 3.77, 4.07, 4.11, 4.14, and 4.36 μm.

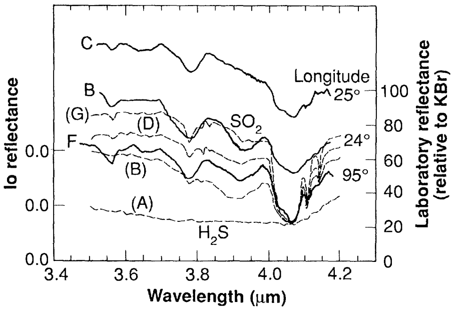

Fig. 2. Solid lines show full-disk (hemispherical) spectra of Io at three orbital longitudes; these are the so-called anomalous spectra of Howell *et al.* (*1*), which contain three principal bands due to SO_2 at 3.55, 3.77, and 4.07 μm. Spectral resolution of the Io spectra was 17 cm^{-1} for spectra B and C and 11 cm^{-1} for spectrum F. Resolution of the laboratory spectra was 4 cm^{-1}. Dashed lines show equivalent wavelength segments of the laboratory spectra of superimposed frost layers from Fig. 1b measured during the transition from the thick H_2S frost layer (bottom dashed curve) to the thick SO_2 frost substrate (top dashed curve). Laboratory spectra are scaled and arbitrarily plotted to bracket Io spectrum F. Letter designators for the laboratory spectra are the same as in Fig. 1b, and for the Io spectra are the same as in Howell *et al.* (*1*). Io spectra are offset vertically for clarity; laboratory spectra are not. Intensity scales for the two sets of data are not the same.

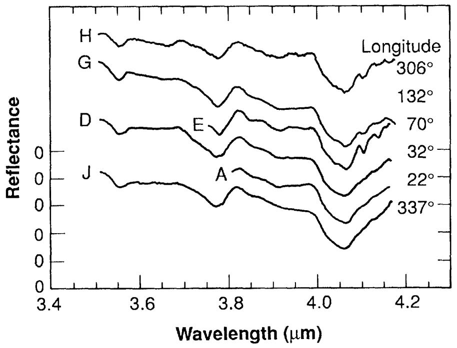

Fig. 3. Typical Io IR reflectance spectra at various orbital longitudes obtained by Howell *et al.* (*1*); the letter designators for each spectrum are the same as in (*1*).

outbursts, then they may have occurred at high-latitude source locations, although low-latitude sources are not ruled out.

The possibility that H_2S might occur at Io's poles was first suggested by Kuiper (*7*), who pointed out that sulfur deposits formed by UV decomposition of H_2S gas exhalations might account for the dark polar caps that were discovered by Minton (*29*). Fresh H_2S frost is a white to colorless material, but laboratory studies by Lebofsky and Fegley (*25*) showed that H_2S frost darkens when irradiated by UV light; its spectrum develops a sulfur-like absorption edge at ~0.45 μm and a symmetric absorption band at 0.59 μm. Nelson and Hapke (*8*) pointed out that photodissociated H_2S could result in deposits of S_2, which at cold temperatures are dark in color. Recent work by Steudel *et al.* (*30*) shows that UV radiation tends to darken sulfur allotropes. Matson *et al.* (*28*) are exploring an explanation for the dark surface units of Io's polar cap and a way to resolve certain anomalous atmospheric and ionospheric observations based on the idea of H_2S in Io's atmosphere.

On several runs with H_2S frost deposited on SO_2 frost, we found that the deepest band minimum in the 4-μm region occurred at 3.85 μm, with no distinct minimum at 3.90 μm. As pointed out to us (*31*), one possible explanation of this difference in the laboratory spectra of H_2S might be a difference between interstitial (or solid solution) H_2S in SO_2 and aggregated (crystalline) H_2S. One of the Io spectra in the suite of Howell *et al.* (*1*) (spectrum E at longitude 70° on 10 June 1985) (Fig. 3) shows a weak 3.85-μm feature in addition to a weak 3.92-μm feature [in addition to the 3.98-μm SO_2 gas band mentioned in (*1*)].

We found that laboratory spectra in which the H_2S band is a weak to moderate unsaturated feature do not qualitatively differ when the frost was made either by mixing and cocondensing approximately equal proportions of H_2S and SO_2 gas or by depositing H_2S frost on top of preexisting SO_2 frost and letting the composite deposit thin out by differential sublimation. In both cases pumping our vacuum chamber for about 5 min after the thick H_2S frost is in place resulted in a time sequence of spectra like that shown in Fig. 1b.

A survey of available Io spectra shows that the 3.915-μm band appears to be at least weakly present over a wide range of orbital longitudes, especially on the leading-inside hemisphere between orbital longitudes increasing from 300° to 120° (through the zero meridian). This "H_2S sector," interestingly, is approximately the same longitude sector once thought to be the source region of neutral sodium (Na) from Io's surface (*32*). Could there be a source connection between Na and H_2S? A surface material that could yield both species as a result of jovian hydrogen ion (proton) bombardment is sodium hydrosulfide (NaHS), a solid phase that on spectral grounds has been suggested as a component of Io's surface (*14, 15*).

We conclude that H_2S frost condensed on Io's surface can be responsible for the 3.915-μm absorption band discovered in several "anomalous" and even several relatively normal IR spectra of Io reported by Howell *et al.* (*1*). The transient nature and variability in strength of the 3.915-μm band implies that H_2S is sometimes present as a condensed volatile on Io's surface and likewise is a significant component of Io's atmosphere. The presence of H_2S frost on the surface would also cause temporal variations in the spectral brightness of Io's reflectance in the UV and visible regions. Other normal spectra (*12, 13, 18*) also show a hint of a band feature at 3.915 μm, suggesting that a small amount of condensed (or perhaps adsorbed or occluded) H_2S may be a more permanent feature on Io's surface than is indicated by the anomalous spectra of Howell *et al.* (*1*).

To our knowledge, H_2S has not been detected on any body in the solar system other than Earth. Its presence on Io has important geochemical, volcanic, atmospheric, and magnetospheric implications bearing on an improved understanding of processes active on Io.

Another diagnostic feature in the IR reflectance spectrum of laboratory H_2S frost [see Fig. 1 and data in (*21*) and (*23*)] is a strong absorption band near 2.7 μm (the $\nu_2 + \nu_3$ combination band). Future observers of Io should consider studying both the 2.7-μm region (not observable from the ground) and the 3.9-μm region of Io's spectrum for indications of surface deposits of H_2S.

REFERENCES AND NOTES

1. R. R. Howell *et al.*, *Icarus* **78**, 27 (1989).
2. W. Wamsteker, *Commun. Lunar Planet. Lab.* **9** (no. 167), 171 (1973); ———, R. L. Kroes, J. A. Fountain, *Icarus* **10**, 1 (1974).
3. F. P. Fanale, T. V. Johnson, D. L. Matson, *Science* **186**, 922 (1974).
4. I. Kupo, Y. Mekler, A. Eviatar, *Astrophys. J.* **205**, L51 (1976).
5. D. B. Nash and F. P. Fanale, *Icarus* **31**, 40 (1977).
6. B. W. Hapke, *Geophys. Res. Lett.* **6**, 799 (1979).
7. G. R. Kuiper, *Commun. Lunar Planet. Lab.* **10** (no. 187), 28 (1973).
8. R. M. Nelson and B. Hapke, *Icarus* **36**, 304 (1978).
9. U. Fink, H. Larson, T. N. Gautier III, *ibid.* **27**, 439 (1976).
10. L. A. Morabito, S. P. Synnott, P. N. Kupferman, S. A. Collins, *Science* **204**, 972 (1979).
11. J. Pearl *et al.*, *Nature* **280**, 757 (1979).
12. D. P. Cruikshank, T. J. Jones, C. B. Pilcher, *Astrophys. J.* **225**, L89 (1978).
13. J. B. Pollack *et al.*, *Icarus* **36**, 271 (1978); U. Fink, H. P. Larson, L. A. Lebofsky, L. S. Frierberg, H. Smith, *Bull. Am. Astron. Soc.* **10**, 580 (1978); D. P. Cruikshank, *Icarus* **41**, 240 (1980).
14. W. D. Smythe, R. M. Nelson, D. B. Nash, *Nature* **280**, 766 (1979); F. P. Fanale, R. H. Brown, D. Cruikshank, R. N. Clark, *ibid.*, p. 760.
15. D. B. Nash and R. M. Nelson, *ibid.*, p. 763.
16. R. Howell, unpublished data.
17. R. M. Nelson *et al.*, *Science* **210**, 784 (1980).
18. R. R. Howell, D. P. Cruikshank, F. P. Fanale, *Icarus* **57**, 83 (1984).
19. Judging from the depth of the band and the noise near the band minimum, we estimate the wavelength of the band minimum to be accurate to 0.015 μm.
20. D. B. Nash, M. Carr, J. Gradie, D. Hunten, C. Yoder, in *Satellites*, J. Burns and M. Matthews, Eds. (Univ. of Arizona Press, Tucson, 1986), pp. 629–688.
21. H. Kieffer, personal communication. The spectrum was produced in Kieffer's lab at the University of California, Los Angeles, by W. Smythe and L.

Pleskot in 1974. Their spectrum of H_2S frost shows a very broad band centered near 3.9 μm.

22. We did this at the Jet Propulsion Laboratory, using a liquid N_2–cooled stainless steel platen in a vacuum environmental chamber coupled to an IR spectrometer with KBr windows. Frosts were grown in two ways: (i) as individual frost layers with H_2S deposited either directly on the horizontal platen or on top of a previously deposited SO_2 frost substrate; and (ii) as a two-component frost formed by the cocondensation of a mixture of SO_2 and H_2S gases. We measured the spectra using a Fourier-transform IR spectrometer [D. Nash, *Appl. Opt.* **25**, 2427 (1986)] with a resolution of 4 cm^{-1}; we measured the IR biconical diffuse reflectance of the frost deposits as they sublime and change composition as a result of differential sublimation of the two volatile species. These fine-grained, highly porous frost deposits, which visually appear bright white, were grown to various bulk thicknesses up to ~2 mm.
23. Probably either ν_1 or ν_3 or a near coincidence of the two. J. R. Ferraro and U. Fink, *J. Chem. Phys.* **67**, 409 (1977); J. R. Ferraro, G. Sill, U. Fink, *Appl. Spectrosc.* **34**, 525 (1980).
24. The errors in spectra B, C, and F of Fig. 2 are approximately 5%. However, spectrum F is the average of four successive independent measurements (taken over a 37-min period), which show general agreement, and therefore features in it can be considered reliable. Spectrum B and spectrum C result from a single sequence of measurements stepping through the wavelength interval. Undetected problems, such as clouds or miscentering, could result in a dip in the spectrum at the wavelength region where this problem occurred. However, no such problems were noticed at the time, but they cannot be completely excluded. Additional discussion of observational and data reduction procedures can be found in (*1*).
25. L. A. Lebofsky and M. B. Fegley, *Icarus* **28**, 379 (1976).
26. F. C. Witteborn, J. D. Bregman, J. B. Pollack, *Science* **203**, 643 (1979); J. Goguen *et al.*, *Icarus* **76**, 465 (1988); T. V. Johnson *et al.*, *Science* **242**, 1280 (1988).
27. D. P. Simonelli and J. Veverka, *Icarus* **74**, 240 (1988); A. S. McEwen, T. Johnson, D. Matson, L. Soderblom, *ibid.* **75**, 450 (1988). At temperatures of 120 to 140 K, the equilibrium vapor pressure of H_2S is about 10^{-5} to 10^{-3} atm [R. Honig and H. Hook, *RCA Rev.* (September 1960), p. 360].
28. D. Matson, T. Johnson, A. McEwen, L. Soderblom, *Bull. Am. Astron. Soc.* **20**, 1125 (1988) (abstract).
29. R. B. Minton, *Commun. Lunar Planet. Lab.* **10** (no. 188), 35 (1973).
30. R. Steudel, G. Holdt, A. Young, *J. Geophys. Res.* **91**, 4971 (1986).
31. J. Pearl, personal communication; F. Salama, S. Sandford, L. Allamandola, D. Cruikshank, F. Witteborn, *Bull. Am. Astron. Soc.* **20**, 818 (1988).
32. R. W. Carlson, D. Matson, T. Johnson, J. Bergstralh, *Astrophys. J.* **223**, 1082 (1978); W. H. Smyth and M. Combi, *ibid.* **328**, 888 (1988).

33. We thank J. Pearl, D. Matson and F. Salama for helpful comments and suggestions and J. Pearl, S. Baloga, and J. Goguen for reviewing the manuscript. This work benefited from discussions that took place at the Io Clutch held in San Juan Capistrano on 18 to 19 August 1988, attended by D. Matson, J. Pearl, J. Lunine, T. Johnson, A. McEwen, J. Moses, F. Fanale, R. Gaskell, S. Baloga, and the authors. Portions of this research were carried out at the Jet Propulsion Laboratory under National Aeronautics and Space Administration (NASA) contract and at San Juan Capistrano Research Institute under NASA grant NAGW-1350, both sponsored by the NASA Planetary Geology and Geophysics Program. Additional support was provided to the University of Wyoming through grant NAGW-1276 supported by the NASA Planetary Astronomy Program. This is San Juan Capistrano Research Institute contribution no. 1.

29 November 1988; accepted 24 February 1989

Kappa B–Specific DNA Binding Proteins: Role in the Regulation of Human Interleukin-2 Gene Expression

BEATRICE HOYOS, DEAN W. BALLARD, ERNST BÖHNLEIN,
MIRIAM SIEKEVITZ, WARNER C. GREENE

Transcriptional activation of the human interleukin-2 (IL-2) gene, like induction of the IL-2 receptor α (IL-2Rα) gene and the type 1 human immunodeficiency virus (HIV-1), is shown to be modulated by a κB-like enhancer element. Mutation of a κB core sequence identified in the IL-2 promoter (−206 to −195) partially inhibits both mitogen- and HTLV-I Tax-mediated activation of this transcription unit and blocks the specific binding of two inducible cellular factors. These κB-specific proteins (80 to 90 and 50 to 55 kilodaltons) similarly interact with the functional κB enhancer present in the IL-2Rα promoter. These data suggest that these κB-specific proteins have a role in the coordinate regulation of this growth factor–growth factor receptor gene system that controls T cell proliferation.

THE GROWTH OF HUMAN T LYMPHOCYTES is regulated in part by antigen- or mitogen-induced expression of the cellular genes encoding IL-2 and the α subunit of the high-affinity IL-2 receptor (IL-2Rα, Tac, and p55) (*1*). Similarly, the long terminal repeat (LTR) of the type 1 human immunodeficiency virus (HIV-1) is stimulated by T cell mitogens (*2–4*), which contributes to the heightened state of HIV-1 replication that occurs in activated $CD4^+$ T lymphocytes but not in resting cells (*5*). The induced expression of both the HIV-1 LTR (*2–4*) and the IL-2Rα promoter (*6–8*) in Jurkat T cells by mitogens such as phytohemagglutinin (PHA), phorbol 12-myristic 13-acetate (PMA), or the human T cell lymphotropic virus type I (HTLV-I)–derived Tax protein may involve the action of related κB enhancer elements. These enhancer motifs directly interact with at least two inducible cellular proteins including NF-κB (51 kD) (*9*) and HIVEN86A (86 kD) (*6, 7, 10*).

We now describe our studies on the role of identical or related factors in the coordinate activation of the human IL-2 gene. Inspection of the 5′ flanking region of the IL-2 gene (*11, 12*) revealed a 12-bp promoter sequence located between nucleotides −206 and −195 (AGGGATTTCACC) that resembled the κB enhancer elements present in the IL-2Rα promoter (GGGGAATCTCCC) and the HIV-1 LTR ($^{A}_{G}$GGGACTTTCC). Although several functional domains have been defined in the IL-2 promoter (*13, 14*), regulatory effects mediated through this putative κB site have not been described.

To examine whether this IL-2 κB-like element functioned in IL-2 promoter induction, we used oligonucleotide-directed mutagenesis to alter selectively various nucleotides within the putative κB site of the wild-type IL-2 promoter (*13*). One clustered mutation, designated M1 (GGG→CTC at −205 to −203), was specifically selected because identical base substitutions in the κB elements of the IL-2Rα promoter and HIV-1 enhancer reduce mitogen- or *tax*-induced promoter activation as well as κB-specific protein binding activity (*2, 6–8*). The additional M4 and M5 mutations altered four and eight bases within this site, respectively, while the M6 mutation changed three bases located immediately 5′ of the κB-like element. The IL-2 M1, M4, M5, and M6 mutant promoters and wild-type counterpart (*14*) were subsequently linked to the chloramphenicol acetyltransferase (CAT) gene for comparative transient expression studies. These recombinant reporter plasmids, either alone or in combination with sense or antisense *tax* expression vectors (spFMT2LTR 82-2C and 82-4, respectively) (*15*), were introduced into Jurkat T cells, that were then stimulated with PHA or PMA (Fig. 1). In accord with our earlier studies (*15*), combinations of PHA plus PMA, Tax plus PHA, and Tax plus PMA increased CAT activity in cells transfected with pIL-2-CAT, whereas single agents were largely ineffective. In contrast, introduction of the M1, M4, and M5 mutations in IL-2 promoter inhibited the response obtained with each of these combinations of

---

B. Hoyos and M. Siekevitz, Mount Sinai Medical Center, Department of Microbiology, New York, NY 10029.
D. W. Ballard, E. Böhnlein, W. C. Greene, Howard Hughes Medical Institute, Departments of Medicine and Microbiology-Immunology, Duke University Medical Center, Durham, NC 27710.