and AH is at 60 cm. In core 50-E, the bottom sample from 126 to 128 cm was dated as 2650 ± 160 ybp and AH is at 30 cm. In core R4-30, the sample from 148 to 150 cm was dated as 910 ± 130 ybp and AH is at 50 cm. Average sedimentation rates between the bottom carbon-14 dated sediment, the agricultural horizon, and the surface sediment (dated A.D. 1985, the time of core collection) were adjusted according to the pollen concentration in each 2-cm interval to give the sedimentation rate for each interval. In the method, we assumed that pollen influx was uniform during periods of similar vegetation cover and species composition for both the pre-European period and the post-European period. Because pollen grains are Stokesian particles, hydrodynamically similar to fine sediment, their transport in water is also similar to fine sediment. The majority of the pollen enters the estuary from the atmosphere. Rates of sediment accumulation then correspond inversely to pollen concentration, and can be calculated for each interval (in this case 2 cm) of the core, with the equation $R_{0\text{-}2} = \bar{n}/n_{0\text{-}2}\bar{R}$, where $R_{0\text{-}2}$ is the sedimentation rate for 0-2 cm, $\bar{n}$ is the average number of pollen grains per dated interval, $\bar{R}$ is the average sedimentation rate (d/t) for the dated interval, d is the depth of a dated horizon in the core, and t is the time in years of the dated horizon. Once the sedimentation rates are calculated for each interval of a core, a chronology was established by dividing the depth of the interval by the sedimentation rate for that interval, giving the number of years represented.

11. G. M. MacDonald, R. P. Beukens, W. E. Kieser, *Ecology* 72, 1150 (1991).
12. G. S. Brush, E. A. Martin, R. S. DeFries, C. A. Rice, *Quat. Res.* **18**, 196 (1982).
13. R. A. Berner, *Colloq. Int. C.N.R.S.* 293, 35 (1980).
14. M. B. Goldhaber and I. R. Kaplan, in *The Sea, Vol. 5*, E. D. Goldberg, Ed. (Wiley, New York, 1962), pp. 569–655.
15. R. Raiswell, F. Buckley, R. A. Berner, T. F. Anderson, *J. Sediment. Petrol.* **58**, 812 (1988).
16. J. J. Middleburg, *Geochim. Cosmochim. Acta* **55**, 815 (1991).
17. M. D. Krom and R. A. Berner, *J. Sediment. Petrol.* **53**, 660 (1983).
18. A Carlo-Erba CNS Analyzer at the Maryland Geological Survey, Baltimore, Maryland, was used to analyze all samples. Replicates of every seventh sample were always within 0.1% and usually within 0.01%. Calibration standards used were estuarine sediment samples of known TOC, N, and S content provided by the Maryland Geological Survey. Organic C and organic N were calculated as the difference between dried and ashed sediment sample measurements of C and N.
19. E. L. Hennessee, P. J. Blakeslee, J. M. Hill, *J. Sediment. Petrol.* **56**, 674 (1986).
20. R. A. Berner, *Geochim. Cosmochim. Acta* **48**, 605 (1984).
21. C. J. Lord and T. M. Church, *ibid.* **47**, 1381 (1983).
22. J. F. Donoghue, *Quat. Res.* **34**, 33 (1990).
23. C. B. Officer, D. R. Lynch, G. H. Setlock, G. R. Helz, in *The Estuary as a Filter*, V. S. Kennedy, Ed. (Academic Press, New York, 1984), pp. 131–157.
24. J. M. Hill, J. P. Halka, R. D. Conkwright, K. Koczot, J. Park, *Continent. Shelf Res.*, in press.
25. H. G. Washington, *Water Res.* **18**, 653 (1984). The Shannon-Wiener index (H') is the most widely used diversity index in ecology. $H' = \Sigma(n_i/n)\ln(n_i/n)$, for $i = 1$ to s, where H' is the community diversity, n is the total number of organisms per sample, n_i is the number of individuals per taxon and s is the total number of species in a unit area (or volume).
26. J. M. Bosch and J. D. Hewlett, *J. Hydrol.* **55**, 3 (1982).

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Magma Generation on Mars: Amounts, Rates, and Comparisons with Earth, Moon, and Venus

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Total extrusive and intrusive magma generated on Mars over the last ~3.8 billion years is estimated at 654 × 10^6 cubic kilometers, or 0.17 cubic kilometers per year (km^3/yr), substantially less than rates for Earth (26 to 34 km^3/yr) and Venus (less than 20 km^3/yr) but much more than for the Moon (0.025 km^3/yr). When scaled to Earth's mass the martian rate is much smaller than that for Earth or Venus and slightly smaller than for the Moon.

EXPLORATION OF MARS IN THE LAST two decades has shown that volcanism was important in the evolution of this terrestrial planet (*1–4*). Images of its surface reveal a variety of volcanic landforms, including vast lava plains and shield volcanoes more than 500 km across. Strong Fe^{2+} absorptions in spectral reflectance measurements of the surface indicate that much of the surface has a mafic composition (*5*). Soil x-ray fluorescence spectra suggest that parent rocks were also probably basaltic (*6*). Photogeologic mapping (*7–9*) shows that volcanic units cover at least half of Mars' surface and that volcanism was important from the terminal stages of heavy bombardment and initial crustal formation through the formation of the geologically younger surfaces seen today.

Because volcanism appears to be dominant in the evolution of Mars, an assessment of the history of magma generation and comparison of that history with other terrestrial planets is warranted. Although deriving a complete history must await more data, such as in situ measurements of the full range of compositions on Mars, significant progress can be made with information currently available. Earlier studies (*10, 11*) made initial estimates of the volcanic materials erupted on Mars through time. Those studies were limited, however, in that the thicknesses of lava flows making up the martian plains were assumed to average 1 km; moreover, there was no attempt to determine the amounts of magma generated as intrusive materials but not erupted. We address both of these limitations in this report.

To determine the amounts of magma produced through time on Mars, we (i) mapped exposed volcanic materials to determine their areal extent; (ii) estimated their thicknesses using the techniques of De Hon (*12*) for lava plains and published topography for volcanic constructs and the Tharsis region; (iii) assigned ages to the mapped units (*7–9*) using impact crater distributions; (iv) determined volumes from (i) and (ii); (v) extrapolated volcanic volumes by age for areas covered by younger rocks, on the basis of the work of Tanaka *et al.* (*11*); and (vi) inferred the amounts of intrusive magmas on the basis of ratios of intrusive-to-extrusive materials on Earth (*13*). We then derived the rate of magma production on Mars and compared the results with rates estimated for Venus, Earth, and the Moon.

We used photographic mosaics of Mars (*14*) as bases for mapping exposed volcanic materials. Units and ages previously defined on small-scale maps (*7–9*) were reassessed and modified as appropriate. We took a conservative approach in that we excluded some smooth, featureless plains previously interpreted as volcanic deposits where we could not identify distinctive volcanic features. Consequently, we estimate that the total area of Mars surfaced with volcanic units is 66.2 × 10^6 km^2, or 46% of the surface, somewhat less than earlier estimates. Two methods were used to determine the volumes of exposed volcanic materials. For large volcanic constructs and the Tharsis Rise (the major volcanic province), volumes were derived directly from the topography (*14*). Topographic data were combined with paleostratigraphic reconstructions taken partly from Scott and Tanaka (*15*) in order to partition the volumes as a function of geologic age. Most (82.4% by area) exposed

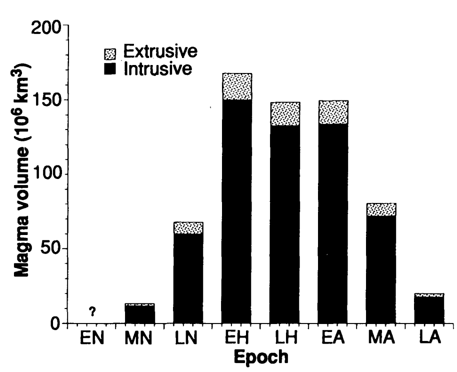

Fig. 1. Histogram of intrusive, extrusive, and total magma production for each martian epoch; EN, Early Noachian; MN, Middle Noachian; LN, Late Noachian; EH, Early Hesperian; LH, Late Hesperian; EA, Early Amazonian; MA, Middle Amazonian; LA, Late Amazonian.

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Table 1. Summary of martian magma volumes; all volumes are in 10^6 km^3. ext, extrusive; int, intrusive.

Epoch	Area of plains (10^6 km^2)	Exposed volume of plains	Thickness of plains (km)	Ext. volume of plains*	Volume from topography	Total ext. volume	Total magma volume at given ext:int ratios 5:1	8.5:1	12:1
Late Amazonian	1.06	0.29	0.27	0.33	1.78	2.11	13	20	27
Middle Amazonian	3.28	1.04	0.32	1.42	7.07	8.49	51	81	110
Early Amazonian	7.93	2.22	0.28	3.61	12.15	15.76	95	150	205
Late Hesperian	7.63	1.87	0.24	4.54	11.09	15.63	94	148	203
Early Hesperian	22.52	3.95	0.18	10.83	6.82	17.65	106	168	229
Late Noachian	9.31	1.28	0.14	4.31	3.46	7.77	47	74	101
Middle Noachian	2.85	0.47	0.17	1.39	0.00	1.39	8	13	18
Early Noachian	?	?	?	?	?	?	?	?	?
Total	54.57	11.12	0.20	26.43	42.37	68.80	413	654	894

*Includes exposed and buried volcanic materials.

volcanic materials occur as plains deposits and plateaus. In these areas, we estimated the thicknesses of volcanic units by examining partly buried impact craters or buried craters for which imprints of the rim are visible (*12*). By the use of crater depth-to-diameter ratios determined from observations of nonflooded craters, the thickness of overlying materials can be derived. This method may yield minimum values because the craters analyzed could rest on older volcanic materials that would be excluded in the estimates. On the other hand, if the craters were degraded at the time of lava flooding, use of their current diameters may lead to a high estimate of lava thickness.

Using the mapped areal extents and their derived thicknesses, we determined volumes of volcanic materials for each epoch of geologic time on Mars. We used the time scale of Scott and Carr (*16*) as modified by Tanaka (*17*), which includes eight epochs (Table 1 and Fig. 1). Assignment of ages in years will ultimately depend on radiometrically calibrated dates from samples of major martian units. Until then, ages are based on impact crater distributions for representative surfaces and extrapolations from cratered surfaces on the Moon for which radiometric dates have been obtained. However, gravity scaling of crater sizes from the Moon to Mars, proximity of Mars to the asteroid belt, and other complications induce uncertainties into the age extrapolations. We used the crater count calibrations of Tanaka *et al.* (*18*) to assign ages to each martian epoch.

Some older surface units, including volcanic rocks, are undoubtedly buried or partly buried by younger materials, such as sediments. Tanaka *et al.* (*11*) addressed this problem by establishing ratios for exposed to total materials for each epoch. We used these same ratios for our estimates of buried volcanic material.

Magma reaching the surface of a planet as volcanic eruptions represents only part of the total amount of magma generated. Crisp (*13*) compiled extensive information on rates of magma emplacement and volcanic output on Earth and estimated ratios of intrusive-to-extrusive magma. Estimates ranged from ~12:1 for continental (that is, thick crustal) areas to <5:1 for oceanic (thin crustal) environments; extremes were <16:1 for the Oslo, Norway, area and 1:1 to 2:1 for Fuego, Guatemala. Using these values as a guide, we have applied intrusive-to-extrusive ratios for Mars of 12:1 and 5:1 to bracket typical values on Earth. For an average ratio of 8.5:1, the total volume of magma is 654 × 10^6 km^3 (Table 1 and Fig. 2) since the formation of a stable crust 3.9 billion years ago (Ga). The compilation (Table 1 and Figs. 1 and 2) suggests that magma production peaked during the Early Hesperian, or ~3.3 Ga, when 168 × 10^6 km^3 of magma was generated. This large volume is represented by vast outpourings of plateau-forming lavas and inferred intrusions into underlying ancient impact-brecciated crust. However, because much of the early (Noachian) record has been heavily modified by erosion, volumes of volcanic materials and associated intrusive magmas may be underrepresented for the early history of Mars.

The average thickness of volcanic plains is now inferred to range from 170 m in Late Noachian to 320 m in Middle Amazonian. The overall average thickness, 200 m, is substantially less than the 1.0-km average estimated earlier (*10*). This revision significantly reduces the total volume of volcanic materials. The thickness is half that of typical mare basalts on the Moon (*22*). Average

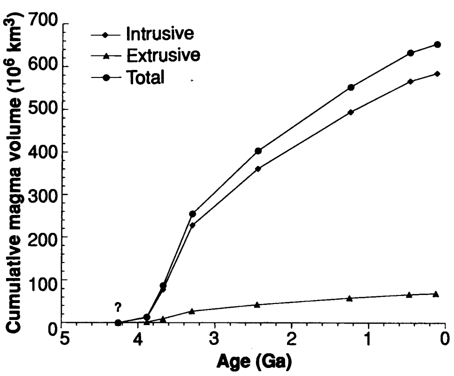

Fig. 2. Cumulative magma production on Mars as a function of time [ages from (*18*)].

Table 2. Planetary magma production. Rates for Venus are for the last ~1 billion years; for Earth, over the last 180 million years; for the Moon, over the last 3.85 billion years; and for Mars, over the last 3.9 billion years.

Planetary body	Mass compared to Earth	Total extrusives (10^6 km^3)	Extrusive production (km^3/yr)	Total magma production* (km^3/yr)	Scaled extrusive production† (km^3/yr)	Scaled total production‡ (km^3/yr)	Reference
Venus	0.815		≤2.0	≤19	≤0.082	≤0.78	(*20, 21*)
Earth	1.000		3.7 to 4.1	26 to 34	1.0	1.0	(*13*)
Moon	0.012	10	0.0024	0.025	0.052	0.069	(*22*)
Mars	0.107	68.8	0.018	0.17	0.042	0.052	

*Assumes intrusive to extrusive ratio of 8.5:1 for Venus, Moon and Mars. †Scaled to Earth mass and Earth extrusive production rates (~3.9 km^3/yr) over the last 180 million years (*13*). ‡Scaled to Earth mass and total magma production rates (~30 km^3/yr) over the last 180 million years (*13*).

thicknesses of volcanic deposits on Mars increase in younger eruptions. This trend could reflect changes in styles of eruption, changes in magma composition or viscosity, or other effects. In general, higher rates of eruption and magmas that are more mafic in composition produce longer, thinner flows. Thus, the relatively thin volcanic deposits in the Noachian and Early Hesperian epochs could reflect highly fluid lava flows that spread over large areas and initially ponded in low-lying regions within the heavily cratered terrain. From geochemical considerations, Burns and Fisher (*19*) suggested that ultramafic lava flows such as komatiites may be present on Mars. On Earth, komatiites are considered to have been extremely fluid and erupted rapidly at high temperatures, characteristics that are consistent with the thin lava flows suggested in early Mars' history.

Comparison of magma production on Mars with Earth and Venus (Table 2) shows that extrusive (volcanic) production rates appear to be a function of planetary mass; Mars has the lowest rate (0.018 km^3/yr). Differences in planetary interiors and styles of tectonism make selection of intrusive-to-extrusive ratios difficult. For simplicity of comparisons, the same 8.5:1 ratio derived from Earth and used for Mars was also applied to Venus.

Results for total magma production rates following accretion and formation of a stable crust (Table 2) also scale with planetary mass. However, even when scaled to Earth's mass and production rate, the magma production on Mars is significantly lower than for the other terrestrial planets. Compared to the Moon (normalized to Earth), lunar magma production appears anomously high, and rates for both extrusive and total magma production are greater than values for Mars, despite the much smaller size of the Moon. This comparison suggests that magma generation on the Moon may have been affected by processes or factors such as tidal stresses by Earth, similar to models applied to outer planet satellites that experience volcanism (*23*).

REFERENCES AND NOTES

1. M. H. Carr, *J. Geophys. Res.* **78**, 4049 (1973).
2. ——— *et al.*, *ibid.* **82**, 3985 (1977).
3. R. Greeley and P. D. Spudis, *Rev. Geophys. Space Phys.* **19**, 13 (1981).
4. P. Mouginis-Mark *et al.*, in *Mars*, H. H. Kieffer *et al.*, Eds. (Univ. of Arizona Press, Tucson, in press).
5. E. A. Guinness *et al.*, *J. Geophys. Res.* **92**, E575 (1987); R. B. Singer *et al.*, *ibid.* **84**, 8415 (1979); R. B. Singer and T. L. Roush, *Bull. Am. Astrophys. Soc.* **15**, 826 (1983); R. B. Singer, *Adv. Space Res.* **8**, 59 (1985); P. Pinet and S. Chevrel, *J. Geophys. Res.* **95**, 14435 (1990).
6. B. C. Clark *et al.*, *J. Geophys. Res.* **87**, 10059 (1982).
7. D. H. Scott and K. L. Tanaka, *U.S. Geol. Surv. Misc. Invest. Ser. Map I-1802-A* (1986).
8. R. Greeley and J. E. Guest, *U.S. Geol. Surv. Misc. Invest. Ser. Map I-1802-B* (1987).
9. K. L. Tanaka and D. H. Scott, *U.S. Geol. Surv. Misc. Invest. Ser. Map I-1802-C* (1987).
10. R. Greeley, *Science* **236**, 1653 (1987).
11. K. L. Tanaka *et al.*, *Proc. Lunar Planet. Sci. Conf.* **18**, 665 (1988).
12. R. A. De Hon, *Proc. Lunar Planet. Sci. Conf.* **10**, *Geochim. Cosmochim. Acta Suppl.* **11**, 2935 (1979).
13. J. A. Crisp, *J. Volcan. Geotherm. Res.* **20**, 177 (1984).
14. U.S. Geological Survey, *Atlas of Mars*, 1:2,000,000 controlled photomosaics; and 1:15,000,000 topographic maps are published as part of the *Miscellaneous Investigations Series*.
15. D. H. Scott and K. L. Tanaka, *Icarus* **45**, 304 (1981).
16. D. H. Scott and M. H. Carr, *U.S. Geol. Surv. Misc. Invest. Ser. Map I-1083* (1978).
17. K. L. Tanaka, *J. Geophys. Res.* **91**, E139 (1986).
18. ———, D. H. Scott, R. Greeley, in *Mars*, H. H. Kieffer *et al.*, Eds. (Univ. of Arizona Press, Tucson, in press).
19. R. G. Burns and D. S. Fisher, *J. Geophys. Res.* **95**, 14415 (1990).
20. R. E. Grimm and S. C. Solomon, *Geophys. Res. Lett.* **14**, 538 (1987).
21. J. W. Head *et al.*, *Science* **252**, 276 (1991).
22. J. W. Head and L. Wilson, *Geochim. Cosmochim. Acta*, in press.
23. P. M. Cassen, S. J. Peale, R. T. Reynolds, in *Satellites of Jupiter*, D. Morrison, Ed. (Univ. of Arizona Press, Tucson, 1982), pp. 93–128.

24. This study was supported by the Office of Planetary Geology, National Aeronautics and Space Administration. We thank E. Lo, L. Bolef, and the late T. Townsend for computer programming. J. McHone, J. Crisp, and an anonymous reviewer provided helpful reviews of the manuscript.

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Indole-3-Acetic Acid Biosynthesis in the Mutant Maize *orange pericarp*, a Tryptophan Auxotroph

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The maize mutant *orange pericarp* is a tryptophan auxotroph, which results from mutation of two unlinked loci of tryptophan synthase B. This mutant was used to test the hypothesis that tryptophan is the precursor to the plant hormone indole-3-acetic acid (IAA). Total IAA in aseptically grown mutant seedlings was 50 times greater than in normal seedlings. In mutant seedlings grown on media containing stable isotope-labeled precursors, IAA was more enriched than was tryptophan. No incorporation of label into IAA from tryptophan could be detected. These results establish that IAA can be produced de novo without tryptophan as an intermediate.

THE PLANT HORMONE AUXIN, OR INdole-3-acetic acid (IAA), has been studied for more than 100 years (*1*), yet it remains unclear how the principal endogenous auxin is synthesized. The amino acid tryptophan is considered to be a precursor to IAA in plants because of structural similarities and because it appears to be the precursor in bacteria (*2*) and in plant cells transformed by *Agrobacterium tumefaciens* (*3*). Efforts to characterize the intermediates and enzymes involved in IAA biosynthesis have established that plants are competent to synthesize IAA from tryptophan by several different pathways (*4*). Nevertheless, microbial contamination, cellular compartmentation, and possible multiple pools of precursors have combined to make the data ambiguous.

Relatively little tryptophan is converted to IAA in sterile plant material (*5*). In an auxin bioassay with *Avena* coleoptiles, there is no growth response to tryptophan under sterile conditions, although anthranilic acid is active (*6*). In *Lemna gibba*, D-tryptophan is not converted to IAA, and the rate of conversion from L-tryptophan is far lower than would be expected for a direct precursor (*7*).

We have done a biochemical analysis of mutant plants that are incapable of making tryptophan to determine whether tryptophan is a precursor to IAA. One of the problems with producing plant amino acid auxotrophs is gene redundancy. A conditional tryptophan auxotroph of *Arabidopsis thaliana*, with a mutation in the tryptophan synthase (E.C. 4.2.1.20) B subunit (*trpB*) gene, contains a second gene encoding *trpB* activity (*8*). The expression of this second, nonmutated, gene would limit the utility of this mutant for studies of auxin metabolism, because the requirements for hormone precursor are expected to be low relative to other uses for tryptophan. Maize also has two *trpB* genes (*9*). We describe here the analysis of IAA biosynthesis in a maize tryptophan auxotroph, *orange pericarp* (*orp*); this phenotype results from recessive mutations in both unlinked *trpB* loci (*10*).

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