ability to judge the small tilts required by the testing procedure.

The angle of the test field which is judged left-pointing 50 percent of the time (and right-pointing 50 percent of the time) represents perceived straightness and was determined from psychometric plots of the observer's responses. Before adaptation, the mean angle for the ten observers deviated by only 3' from geometric straightness. After adaptation, all observers shifted their judgments of perceived straightness in the predicted directions for both sets of the test fields. In other words, after adaptation the test bars were tilted away from the adapting bars so that observers judged as straight an angle pointing in the direction of the adapting pattern (Fig. 1, B and C). The average shift of the angle representing perceived straightness summing the aftereffects on both halves of the field was 30.7' of arc, with a range from 10' to 64'. The orientations of the bars of the adapting patterns, either red tilted left and green tilted right, or vice versa, made no significant difference. After 24 hours an aftereffect was again measured, although it was not statistically significant.

Having demonstrated this aftereffect, we proceeded to determine its magnitude as a function of the angle between adapting and test bars. This function should indirectly reveal the breadth of tuning for edge orientation.

The experiments were carried out with the same procedures as before, except that the adapting patterns were simplified to those shown in Fig. 1C. Their tilts (off vertical) were 0, 5°, 10°, 15°, 20°, 25°, 30°, 40°, 50°, 60°, and 75°. Scanning was restricted to the central region of the pattern. Two observers (the authors) were run, once at each tilt with color pairs assigned randomly to direction of tilt. The results are shown in Fig. 2. The magnitude of the aftereffect peaks at an adapting tilt between 10° and 15° and approaches zero at a tilt of 40° (9). The shape of these curves is consonant with data on tilt aftereffects generated under comparable conditions with colorless adapting patterns (10, 11). It is also consistent with estimates of the breadth of tuning for orientation in the human visual system based upon masking experiments (11, 12).

Are the channels demonstrated by our results the same as those responsible for the McCollough effect? We

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suspect so, but the definitive answer must come from parallels established by further investigation of both phenomena.

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References and Notes

1. The older evidence consists of observations that the colored edge spectra produced by chromatic aberration of spectacle lenses and prisms gradually fade out. The earliest observation known to us was recorded by S. F. McFarland, *Trans. Amer. Ophthal. Soc.* **3**, 479 (1883); others include J. J. Gibson, *J. Exp. Psychol.* **16**, 2 (1933); I. Kohler, *Oester. Akad. Wiss. Phil. Hist. Kl.* **227**, 1 (1959); R. Held, paper read at Convention of Eastern Psychological Association, Philadelphia, April 1955; J. Hay, H. Pick, E. Rosser, *Science* **141**, 167 (1963); A. Hajos and M. Ritter, *Acta Psychol.* **24**, 81 (1965).
2. C. McCollough, *Science* **149**, 1115 (1965).
3. C. S. Harris and A. R. Gibson, *ibid.* **162**, 1506 (1968).
4. Lack of information about the tuning characteristics has led to controversy over the mechanism responsible for the effect. See L. S. Fidell, *Percept. Psychophys.* **8**, 235 (1970), and Harris and Gibson (3).
5. J. J. Gibson, *J. Exp. Psychol.* **20**, 553 (1937); R. Held, *Psychol. Beitr.* **6**, 439 (1962).
6. Models of this type date back at least to C. E. Osgood and A. W. Heyer, *Psychol. Rev.* **59**, 98 (1952), and are becoming increasingly prevalent as a result of the apparent analogy between the channels inferred from psychophysical observations and the selectively sensitive neural units revealed by electrophysiological study of the visual nervous system. See M. Coltheart [*Psychol. Rev.* **78**, 114 (1971)] and R. Over [*Psychol. Bull.* **75**, 225 (1970)] for reviews of these models and their logic.
7. See review by M. K. Malhotra, *Psychol. Forsch.* **30**, 1 (1966).
8. Because the color-specific channels may constitute only a fraction of the total number of orientation-specific channels, one might expect that if an adapting pattern differed from a test field in spectral composition, there would be a decrement from the size of the aftereffect obtained when both fields had the same spectral composition. But the decrement might be quite small, and consequently difficult to measure, relative to that produced by channels activated by the luminance to which all color-sensitive channels contribute. This conjecture may account for the results found in experiments on the classic figural aftereffect in which color has been used as an independent variable. See Malhotra (7).
9. Since the sign of the aftereffect magnitude depends upon the tilt of the adapting pattern, it is undefined for zero tilt. Consequently, those points are plotted both above and below the zero value of the ordinate, connected by a bar and tied to the curve with a dotted line.
10. S. S. Culbert, *J. Psychol.* **37**, 8 (1954).
11. T. H. Mayo, A. S. Gilinsky, A. Jachnowitz, *Proc. 76th Annu. Conv. Amer. Psychol. Ass.* **3**, 47 (1968).
12. F. W. Campbell and J. J. Kulikowski, *J. Physiol.* **187**, 437 (1966); R. W. Sekuler, *J. Exp. Psychol.* **70**, 401 (1965).
13. Support for the research was received under National Institute of Mental Health grant MH-07642. S.R.S. received support from Public Health Service training grant 5T01 GM 01064.

7 June 1971   ■

Carbon and Atmospheric Oxygen

Van Valen (1) maintains that the initial accumulation of free oxygen in our atmosphere cannot be satisfactorily explained by photosynthesis, apparently on the grounds that (i) the net photosynthetic production of oxygen today (rate of release by photosynthesis minus rate of consumption by oxidation of the biosphere and its fossils) is just sufficient to hold in check the oxygen sinks recognized by Holland (2) and others in volcanic gases, ferrous iron, and the like; and (ii) these sinks were more demanding in the past than now, whereas photosynthesis was presumably less productive. I will accept these two assumptions and attempt to show that Van Valen's conclusion does not necessarily follow from them.

As Van Valen points out, a large amount of organic carbon is stored in the sedimentary rocks and may be taken as corresponding to the aggregate net photosynthetic production of oxygen throughout geologic time. According to recent estimates the total mass of the sediments is 2×10^{24} grams or more (3) and their average carbon content is 0.4 percent (4), making 8×10^{21}

grams of carbon which corresponds, at a molar carbon-oxygen ratio of unity, to 2×10^{22} grams of oxygen (5). This agrees quite well with Holland's estimate (2) of the aggregate capacity of inorganic oxygen sinks throughout geologic time (1.8×10^{22} grams) and leaves a little bit (0.2×10^{22} grams) over for the atmosphere (which in fact contains only 0.1×10^{22} grams).

One possible view of atmospheric history is the following—for a considerable time after photosynthesis began carbon accumulated while the partial pressure of oxygen was held close to zero by the backlog of reducing agents derived from volcanic activity of the primitive earth. The eventual neutralization of these sinks required a net production of oxygen that exceeded the rate of continuing emanation of inorganic reducing agents; but as at that time the atmospheric oxygen concentration was too low to oxidize the biosphere appreciably and consequently the net production of oxygen was nearly equal to the rate of release by photosynthesis, it need not have been difficult to meet this requirement (6). Once the

sinks were neutralized, free oxygen began to accumulate and oxidation of the biosphere (and eventually its fossils) increased with the rising partial pressure of oxygen. The net rate of oxygen production was falling.

The net amount of oxygen produced by photosynthesis is represented by the carbon stored in the sediments. It appears (7) that an essentially constant mass of sediments has been turned over and over in the erosional cycle (whose connections with the metamorphic and magmatic cycles I am neglecting for the present purpose) for more than a billion years, perhaps since before photosynthesis began. As the partial pressure of oxygen rose, more and more of the fossil carbon exposed by erosion was oxidized, until the atmosphere reached a steady state with respect to oxygen, and the rate of oxidation of fossil carbon became almost equal to the rate of its incorporation from the biosphere into the sediments (8). That the sediments have been virtually in a steady state with respect to carbon since Precambrian times is suggested by the absence of any obvious age-correlated trend in the carbon distribution (9); and an ingenious argument by Broecker (10), based on carbon isotope ratios, points to the same conclusion. The present atmospheric concentration of oxygen may be held steady by the dependence of oxidation rates on the partial pressure of oxygen; moreover, fluctuations in photosynthetic activity should eventually be compensated by variations in the rate at which buried carbon is exposed to oxidation after passing through the sedimentary cycle (11).

My essential point is that the fossil carbon now stored in the sediments seems adequate to balance a reasonable estimate of the inorganic oxygen sinks. The data of geochemistry are seldom accurate enough to make mass balances that conclusively verify any particular hypothesis. The usefulness of such calculations lies rather in their ability to reveal order-of-magnitude discrepancies that will discredit a hypothesis until adequately explained. Thus, the present discussion does not prove that our oxygen supply was built up by photosynthesis; it merely shows that, on the evidence so far available, it might have been.

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References and Notes

1. L. Van Valen, *Science* **171**, 439 (1971).
2. H. D. Holland in *The Origin and Evolution of Atmospheres and Oceans*, P. J. Brancazio and A. G. W. Cameron, Eds. (Wiley, New York, 1964), pp. 86–101.
3. A. B. Ronov and A. A. Yaroshevsky, *Amer. Geophys. Union Monogr.* **13**, 37 (1969); R. M. Garrels and F. T. Mackenzie, *Evolution of Sedimentary Rocks: A Geochemical Approach* (Norton, New York, 1971).
4. A. B. Ronov, *Geochemistry* **5**, 510 (1958).
5. This estimate would be increased by taking into account the carbon in metamorphosed sediments.
6. H. D. Holland (2) has estimated the aggregate capacity of the sinks through geologic time at about 2×10^{22} grams of oxygen, corresponding to an average annual capacity of say 5×10^{12} grams. At present about 10^{17} grams of oxygen are released annually by photosynthesis [see W. S. Broecker, *Science* **168**, 1537 (1970)]. If the early volcanic emanations were ten times as voluminous as the average over geologic time and photosynthesis only one-tenth as productive as today, oxygen production would still outdistance the addition of inorganic reducing agents by a factor of 100.
7. R. M. Garrels and F. T. Mackenzie, *Science* **163**, 570 (1969); J. Gilluly, in preparation.
8. The continuing demands of inorganic sinks would seem to require a slight excess of burial over oxidation, but the difference between these is probably an order of magnitude less than either of them. The present rate of burial of carbon, based on a sedimentation rate of 10^{16} grams per year [C. B. Gregor, *Nature* **228**, 273 (1970)] of sediment with an average carbon content of 0.4 percent (4), is 4×10^{13} grams per year. The average rate of release of reducing agents by volcanoes throughout geologic time has been equivalent to about 5×10^{12} grams of oxygen per year (6).
9. See (4) above. Ronov has demonstrated significant-looking fluctuations in the carbon content of the sediments, but no unidirectional trend.
10. W. S. Broecker, *J. Geophys. Res.* **75**, 3553 (1970).
11. This mechanism would operate slowly: the half-life of the sedimentary pile seems to be several hundred million years (R. M. Garrels and Yuan Li, personal communications).
12. I thank R. M. Garrels for patiently guiding me onto the right track.

21 July 1971

Gregor modifies and makes more detailed one of several alternatives I suggested for the oxidation of the earth's atmosphere (1). As with the other alternatives, however, I still see difficulties.

The present net production of molecular oxygen by photosynthesis (that is, after plant respiration) is about (1 to 5) $\times 10^{17}$ grams per year (2). This suffices to oxidize an entire atmosphere of methane (5×10^{21} grams) in 10^4 or 10^5 years, which is negligible geologically. Other atmospheric compositions would give a shorter time. Lower values of net production of oxygen would of course give proportionally longer times. About 10^{22} grams of reduced carbon would be deposited during the same interval (3).

Furthermore, the rather high frequency of discovery of microfossils in suitable middle and early Precambrian sediments suggests that the biota was not many orders of magnitude less abundant than that today (4). The prevalence of forms morphologically similar to modern algae, and the occurrence in sediments of possible breakdown products of chlorophyll, suggest a major role for photosynthesis in the acquisition of energy by organisms. Gregor seems to accept this in his note number 6 (5).

Therefore, my original reason for questioning this alternative, that it "implies . . . that there would be an enormous volume of reduced carbon buried . . . in a geologically negligible time," still seems valid. It is not insuperable, as Gregor points out, but neither are the difficulties with other alternatives.

This alternative also implies that the greatest concentration of reduced carbon occurs in rocks formed when the atmosphere was becoming oxidized, and that the concentration progressively declines later, with cycles of declining amplitude, as the sediments formed at that time become recycled and diluted with sediments from sedimentary rocks formed in the reducing atmosphere and with sediments from "primary" igneous rocks. Gregor's argument indicates that this second prediction is not yet verified either, although the error of estimate may be as large as the expected decline during the Phanerozoic.

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References and Notes

1. Other alternatives also involve photosynthetic production of oxygen, however.
2. E. Rabinowitch and Govindjee, *Photosynthesis* (Wiley, New York, 1969); R. H. Whittaker, *Communities and Ecosystems* (Macmillan, London, 1970). The error may be larger than indicated.
3. Note that more carbon must be deposited than is present in the methane, so either there is another carbon source of major proportions or much of the carbon is oxidized by an unknown cause. Carbon dioxide, the source of carbon in photosynthesis and a possibly large component of the middle Precambrian atmosphere, is an obvious candidate. Such a partly oxidized atmosphere would give proportionally less burial of reduced carbon, but even 10^{21} grams, the amount required to compensate for the present atmospheric oxygen, is a lot.
4. Another alternative, advocated by some (personal communications), requires that the biota, or at least photosynthesis, be more abundant.
5. Although he does not say so, the carbon that Gregor discusses is all reduced, so his calculations need not be modified except for consideration of the large errors of estimate, which he later acknowledges.
6. I thank Dr. Gregor for permitting me to comment on an earlier version of his note. A Research Career Development Award from the National Institutes of Health partly supported this work.

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