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The Upper Limit of Crop Yield

This classical problem may be analyzed as one of the photosynthetic efficiency of plants in arrays.

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I wish in this article to consider the principles which determine the upper limit of yield by the world's crop plants. This is a not uninteresting matter, determining as it does the upper limit of world population. A great deal has been found out in years gone by about how to grow crops effectively. We know about the mineral requirements of plants; we begin to understand in detail their water requirements. We know how to abolish pests and diseases, at least in principle. We know how to determine the optimum temperature conditions for a crop and how to match plant and climate by breeding. Let us therefore consider only crops grown under conditions in which optimal temperatures prevail, and in which the levels of mineral nutrition, water, and pest control are nonlimiting.

Under these conditions, it is generally agreed, the limiting factor in the productivity of plants is the photosynthetic efficiency with which the plant converts light energy to energy stored in plant material. Experimental determination of the efficiency with which plants convert and store solar energy is a simple enough matter. We plant some seeds, or other plant material, on a measured area of land. We determine at the end of the growing season how much dry weight of plant material—stems, leaves, roots, flowers, and so on—has been produced on our measured area of land. During the growing season, too, an integrating light meter of some kind has been used to measure the flux of visible light (light in the 4000- to 7000-angstrom, the portion of the spectrum that is absorbed by the photosynthetic equipment of plants) incident upon our measured area of land. We now determine the ratio of the number of calories captured in plant material (a number obtainable through combustion of the plant material back to CO_2) to the number of calories of visible-light flux received by our planted area. A substantial number of experiments of this kind have been carried out over the years in a variety of countries. Let us first summarize the facts of photosynthetic efficiency and then wrestle with the principles.

The facts are these.

1) In a great many experiments photosynthetic efficiencies of crop production of between 2 and 2.5 percent have been obtained (*1, 2*). This level of efficiency is in fact achieved in rice production in Japan, as well as in wheat production in Denmark (*1*).

2) Most agriculture the world over is carried on at a photosynthetic efficiency lower than 2.5 percent, but we know why. The efficiency is lower because of deficiencies in mineral nutrients and water, because of pests, or because of unsuitable temperatures.

3) There are, however, undoubted instances of efficiencies higher than 2.5 percent—for example, those cited by Blackman and Black (*3*) and by Wassink (*4*). Efficiencies as high as 5 percent or so have been recorded for a portion of the growing season.

Efficiency of Photosynthesis

Let us ask what the physical facts are that determine the efficiency of photosynthesis. Can we deduce from these facts what the maximum productivity of a crop might be expected to be?

The facts are quite simple. The efficiency of capture and storage of light by plants is determined by three principal factors. The first is the quantum efficiency of photosynthesis. In the photosynthetic reaction

$$CO_2 + H_2O + n \text{ quanta} \xrightarrow{\text{plant}} (CH_2O\text{—more plant}) + O_2$$

in general, n is of the order of 10. There is something inherent in the machinery of photosynthesis which requires that approximately 10 quanta be used for the reduction of one CO_2 molecule, at least at higher light intensities. Ten moles of quanta (10 einsteins) in the middle of the wavelength range usefully absorbed by chlorophyll supply about 520 kilogram calories. The reduction of 1 mole of CO_2 to the level of plant material captures and stores only 105 kilogram calories. The efficiency of the basic photosynthetic act is, therefore, $105/520 = 20$ percent. On this basis alone we expect a maximum photosynthetic efficiency of 20 percent. This is, of course, much higher than the efficiency actually observed in the field.

The second factor in the determination of photosynthetic efficiency concerns the contrasting ways in which photosynthetic rate and light absorption by plant systems change with increasing light intensity. We illuminate a leaf, chloroplast, or algal cell. As we increase the light intensity, the rate of

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photosynthesis increases over a substantial range. At some sufficiently high intensity, however, the photosynthetic rate becomes independent of the light intensity; it becomes light-saturated. For a typical leaf, light saturation occurs at a light intensity of 1/10 to 2/10 that of full sunlight. This is exemplified by the curve of Fig. 1, taken from the work of Gaastra with the leaf of the sugar beet (*5*).

The amount of light absorbed by the leaf changes with increasing light intensity in quite a different way. A constant fraction of the incident light is absorbed by leaves or chloroplasts, independent of intensity. The amount of light absorbed by a leaf therefore increases linearly with intensity. Typical sun leaves absorb on the order of 80 percent of the incident light; typical shade leaves, on the order of 60 or 70 percent.

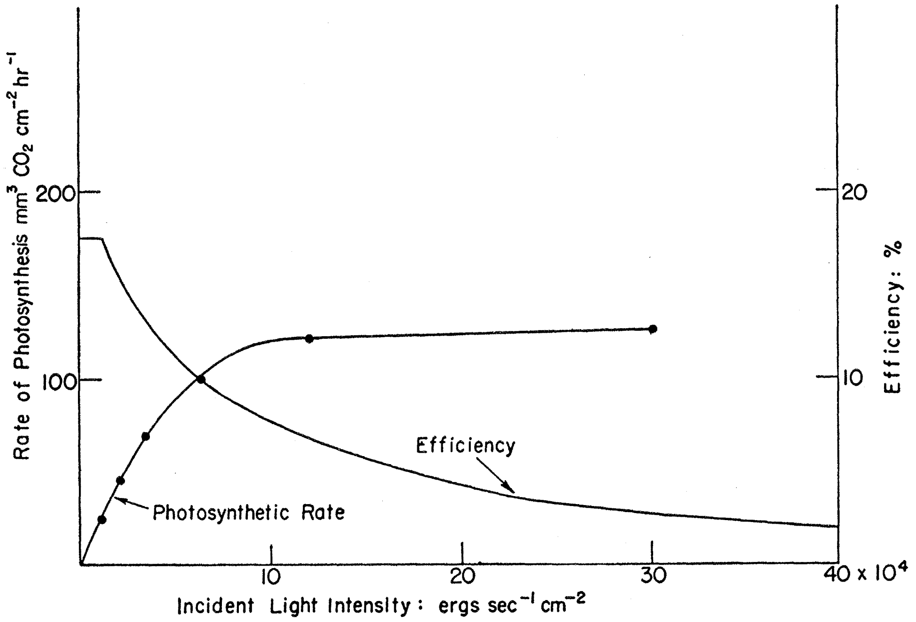

Fig. 1. Rate of photosynthesis in sugar beet leaf as a function of the energy of incident visible light (4000 to 7000A), together with efficiency of utilization of incident light in photosynthesis. [After Gaastra (*5*)]

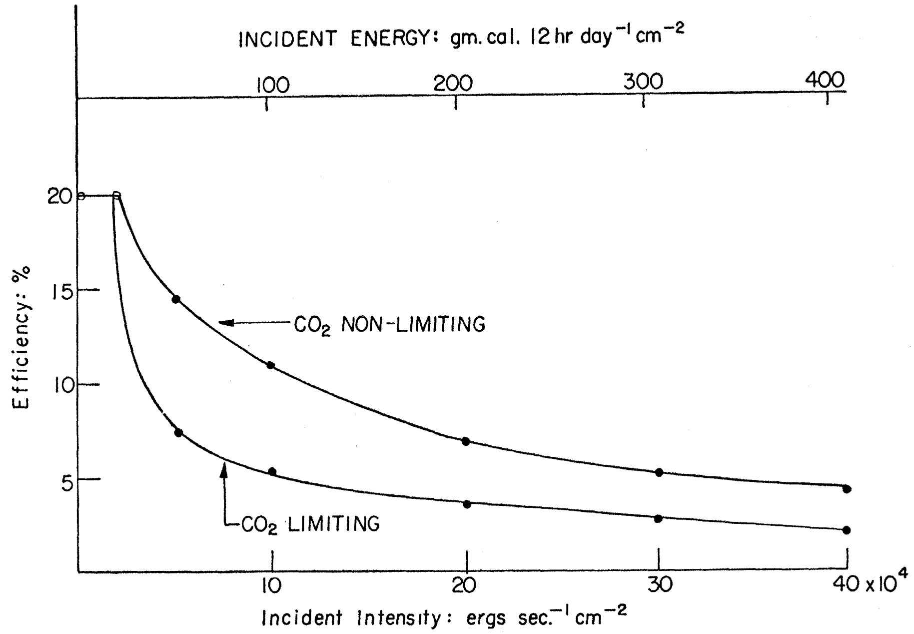

Fig. 2. Expected efficiency of utilization of the energy of incident visible light in photosynthesis as a function of the intensity, as calculated from Bush's relationship (*6*) for an infinite stand of plants (no border effects) of depth great enough to absorb all light energy, on the assumption that the efficiency of photosynthesis at intensities below saturation is 20 percent. In the derivation of the upper curve, nonlimiting CO_2 concentrations at all light intensities are assumed. The lower curve is derived on the arbitrary assumptions that limitation by the CO_2 concentration of air does not occur at light intensities of less than 1/20 the intensity of full sunlight but cuts photosynthetic rate in half at intensities greater than 1/8 the intensity of full sunlight.

Let us now consider the photosynthetic efficiency of a single leaf in full sunlight. The leaf absorbs 80 percent of the light incident upon it. One-fifth of the light so absorbed is used with an efficiency of 20 percent. The over-all efficiency of our leaf should then be not more than

$$(0.20 \times 0.20)/0.8 = 0.05$$

or 5 percent. A leaf exposed to full sunlight cannot, then, be expected to be highly efficient in utilizing light energy for photosynthesis.

In a real plant or a real array of plants, of course, light transmitted by the top layer of leaves is incident upon lower leaves, and so on. In general, as light passes through an assemblage of leaves it is absorbed according to Lambert's law, and light intensity falls off exponentially with path length through the absorbing assemblage. A crop ordinarily produces enough layers of leaves so that the final light intensity which emerges at the soil level is below the compensation intensity—that is, the intensity transmitted to the soil level is ordinarily less than that required to permit a leaf to carry on photosynthesis at a rate higher than its respiratory rate. In many kinds of crops, light travels, on the average, through three, four, and occasionally as many as six or seven layers of leaves, and 95 percent or more of the incident light is absorbed by the leaf assemblage. Since the lower leaves in a plant assemblage are exposed to intensities lower than the intensity of full sunlight, they are more efficient photosynthetically than the uppermost leaves, and the photosynthetic efficiency of the assemblage as a whole would, of course, be expected to be higher than that of the upper leaf alone.

These considerations are, however, unnecessarily crude, since the model can be readily refined. Each leaf is itself an assemblage of chloroplasts. These chloroplasts shade one another just as leaves do. It is evident from the curve of Fig. 1 that a leaf's photosynthetic rate increases linearly with increasing light intensity only over a narrow range, and that, above the upper limit of this range, the slope of the curve of photosynthetic rate vs. light intensity decreases steadily with increasing light intensity, even at intensities far below the final saturation level. Only at quite low intensities does the photosynthetic efficiency of the leaf approach the 20 percent expected on the basis of the quantum requirement of photosynthesis. At these low light intensities the topmost chloroplasts of the leaf are less than light-saturated. At intensities above about 1/20 of full sunlight (in the example of Fig. 1), the uppermost chloroplasts become light-saturated, and although the photosynthetic rate continues to increase with increasing light intensity, because of the increasing participation of lower-lying chloroplasts, still the uppermost chloroplasts are wastefully absorbing light at intensities higher than their saturation level.

Waste of Light Energy

Let us then consider a field of crop, a field covered by leaves, as an assemblage of chloroplasts, an assemblage of sufficient depth to absorb essentially all of the visible-light energy incident upon it. Let us further assume, as in Fig. 1, that the individual chloroplast becomes light-saturated at an intensity 1/20 that of full sunlight, but that absorption of light by chloroplasts follows Beer's law, a characteristic fraction of the incident light being absorbed by the chloroplast. What now will be the relation at any arbitrary incident-light intensity between the amount of light absorbed by the assemblage and the amount usefully absorbed and used in the conduct of photosynthesis? This matter has been considered by Vannevar Bush (*6*), who has shown that the pertinent relationship is

$$\frac{E_{\text{used}}}{E_{\text{incident}}} = \frac{I_{\text{sat'n}}}{I_{\text{incident}}} \ln \left(\frac{I_{\text{incident}}}{I_{\text{sat'n}}} + 1 \right)$$

where $E_{\text{used}}/E_{\text{incident}}$ represents the fraction of total incident-light energy used for photosynthesis, $I_{\text{sat'n}}$ represents the intensity at which the photosynthetic elements become light-saturated, and I_{incident} represents the intensity of light incident upon the uppermost layer of the assemblage.

Bush's relationship enables us to calculate that in an assemblage of chloroplasts each saturated at an intensity 1/20 that of full sunlight, of depth sufficient to remove substantially all of the incident light, and illuminated by the intensity of full sunlight, 20 percent of the total light energy is usefully absorbed, 80 percent is wastefully absorbed. The 20 percent of light energy usefully absorbed will then be used, as we have seen, with a quantum efficiency of 20 percent to yield an over-all effectiveness of 4 percent. Fuller consideration of this matter is given in Fig. 2, which summarizes the expected over-all efficiencies for utilization of light by photosynthesis for varying incident-light intensities, as calculated from Bush's relationship, on the assumption that light at intensities below the saturation intensity is used with an efficiency of 20 percent. The expected over-all efficiencies vary from 20 percent at low intensity to 4 percent at the intensity of full sunlight. The curve of Fig. 2 may serve to impress us with the fact that the major factor in determining photosynthetic efficiencies at intensities above the light-saturation intensity is nonfruitful absorption of light by light-saturated chloroplasts, and that this effect is one which increases with the intensity of incident light.

An efficiency of light utilization of 4 percent in full sunlight, as predicted in Fig. 2, has been frequently achieved with plants cultured in the presence of air enriched with CO_2 above the 0.03 percent (by volume) that is characteristic of ordinary air (*7, 8*). The rate of photosynthesis is in general, however, limited at higher light intensities by CO_2 concentration and may in fact, in several species, be increased by a factor of approximately 2 by increasing the CO_2 concentration to the saturation value of about 0.1 percent (by volume) (*7, 9*, and others). It is also true, however, as summarized by Rabinowitch (*10*), that the photosynthetic rate in many land plants at very low light intensities is not severely limited by the CO_2 concentration of air. This is evident from the photosynthetic-efficiency curve of Fig. 1. Concentrating our attention, however, on the higher light intensities characteristic of crop production, we may conclude that the photosynthetic efficiencies expected on the basis of the analysis given here will be cut approximately in half by the limitation imposed by CO_2 concentration, and that we may therefore expect over-all photosynthetic efficiencies of about 2 percent at the intensity of full sunlight, of about 3.5 percent at an intensity half that of full sunlight, of about 5 percent at an intensity one-fourth that of full sunlight, and of about 7.5 percent at an intensity one-eighth that of full sunlight. These relationships are indicated in Fig. 2.

That the photosynthetic efficiency of higher plants varies with the intensity of the incident light, and in a fashion generally in agreement with the prediction of Fig. 2, has been indicated by numerous experiments. Thus, Went (*11*) obtained an efficiency of light utilization of approximately 10 percent with tomatoes grown in light of an intensity approximately one-tenth that of full sunlight, while Gaastra has reported efficiencies with sugar beets of 12 to 19 percent under similarly low, or even lower, intensities. The work of Thomas and Hill (*12*) has shown that the photosynthetic efficiency of alfalfa plots increases from approximately 2 percent at the intensity of full sunlight to 3.7 to 4 percent at intensities from one-third to one-half the intensity of full sunlight. The photosynthetic efficiencies of sugar cane at varying intensities reported by Burr (*13*) increase with decreasing intensity and are in numerical agreement with the expectations of Fig. 2.

It should be remembered that increase in efficiency of photosynthesis with decrease in intensity of incident light involves a decrease in absolute yield of plant material. The higher the intensity of the light incident on our crop, the greater the expected yield, as indicated in Fig. 3.

It seems clear, therefore, that the photosynthetic efficiency of plant stands is determined, other matters being optimal, by the following factors: (i) at low light intensities, by the quantum efficiency of photosynthesis (CO_2 concentration is nonlimiting or not greatly limiting at very low intensities); (ii) at higher intensities, by the quantum efficiency of photosynthesis, and in addition, by the wastage of light energy inherent in the low light-saturation level of the chloroplasts; CO_2 concentration also becomes limiting at higher light intensities.

Clearly, then, a principal factor which depresses photosynthetic efficiency below the quantum efficiency at high light intensities is the low light-saturation level of the chloroplasts. Why is it that in leaves and chloroplasts light saturation occurs at intensities so far below the intensity of full sunlight? We know that this behavior is built into the structure of the chloroplast and is due to the fact that chloroplasts con-

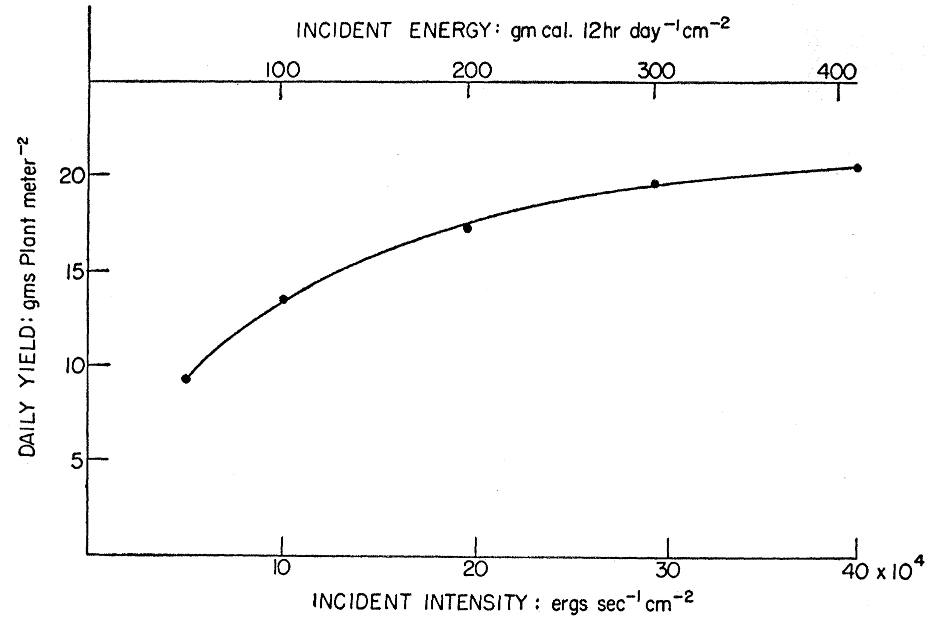

Fig. 3. Expected daily yield of plant material as a function of light intensity or of daily incident light energy. This curve is derived from the lower curve of Fig. 2.

tain a vast excess of chlorophyll molecules over the reducing centers which convert CO_2 to plant material. Emerson and Arnold (*14*) were the first to show, by flashing-light experiments, that the chloroplasts contain something over 2000 chlorophyll molecules per center capable of chemically reducing CO_2 and evolving oxygen. This arrangement has been found in the chloroplasts of all species as yet investigated. Why should this be so?

Analysis

My first suggestion in analyzing the problem is that plants are inefficient at high intensities because they are arranged to be efficient at low intensities. Photosynthesis is a process in which the energy of several quanta must be absorbed and transmitted to and concentrated in a single central spot, and this with some degree of simultaneity. Suppose, to put it crudely, that to achieve this result ten chlorophyll molecules are wired to each reducing center. Whenever the ten chlorophyll molecules simultaneously absorb their quanta, the reducing center can proceed with the chemistry of photosynthesis. This arrangement would work well at high light intensities, when the probability of simultaneous absorption of 10 quanta by the ten chlorophyll molecules is high. At low intensities, however, this arrangement will be poor indeed, since only rarely will 10 quanta be absorbed with the required degree of simultaneity by the photosynthetic unit. To make a chloroplast highly efficient at very low intensities, a better arrangement would be to have an infinite number of chlorophyll molecules wired to a single reducing center. The 10 required quanta could then be absorbed anywhere in the vast collecting panel and their energies could then be transmitted to the reducing center and instantly used in the process of photosynthesis. This arrangement, although it would operate well at infinitely low intensities, would operate very poorly indeed at any intensity sufficiently great to provide more than 10 quanta per unit of enzymatic turnover time per photosynthetic unit. I suspect, therefore, that plants in the course of evolution have sought a compromise between these two extremes: they have sought a compromise between a photosynthetic unit efficient at high intensity and one efficient at low intensity—namely, a compromise which maximizes yield over all of the light intensities to which chloroplasts are subject.

Although this analysis is only a qualitative one, and even though we know that CO_2 is not directly reduced by the light energy absorbed by chlorophyll molecules, it does have a certain over-all virtue. Photosynthesis is, in any case, a multiquantum process. Arrangements must be made in the chloroplast to compromise between the requirements for effectiveness at high intensity and the requirements for effectiveness at low intensity. It is logical to suspect that the compromise may be the one that results in maximum yield.

Conclusions

I conclude, then, that the upper limit of crop yield, as determined by the factors that regulate photosynthetic efficiency, is already being approached today in those regions with the highest level of agricultural practice—in parts of Japan, of Western Europe, and of the United States. This upper limit of crop yield corresponds to conservation in plant material of the order of 2 to 5 percent of the energy of the incident visible light, the exact figure depending upon the average intensity of the incident light. I conclude, too, that analysis of the principles which determine the upper limit of crop yield gives us greater insight into what might be done to alter and raise this upper limit. We have seen that plant efficiencies are in general limited, under high light intensities, by the CO_2 concentration of air. Might it be possible to breed plants for leaves in which there would be increased conductivity of CO_2, in order to lessen diffusion resistance to CO_2, or to shorten diffusion paths?

Most important is another consideration. We have seen that the low level of light intensity at which chloroplasts become light-saturated is the major factor leading to low photosynthetic efficiency at high light intensity. We have further seen that it is quite possible, and even probable, that the light-saturation level of the chloroplasts has been established by natural selection at a level which maximizes yield over all the intensities to which plants are subject. But this limitation is for chloroplasts of a rather simple model—chloroplasts in which a specific and optimal number of chlorophyll molecules are wired together to individual reducing centers to constitute individual photosynthetic units. Might we not imagine a new kind of chloroplast—a chloroplast which I will call a modulating chloroplast, which contains more than one reducing center per 2000 chlorophyll molecules? In our modulating chloroplast the ratio between chlorophyll molecules and functional reducing centers would be set by light intensity.

At low intensities the majority of the reducing centers would be shunted out of the circuit, leaving large light-collecting panels consisting of many chlorophyll molecules, to collect light for each functional reducing center, thus assuring simultaneous reception of the energy of 10 quanta by each center at frequent intervals. As light intensity increases, our modulating chloroplast would gradually shunt into operation a larger number of reducing centers, so that at infinitely high light intensity, for example, as many as one reducing center per ten chlorophyll molecules might become active. Such a modulating chloroplast should be able to operate at an efficiency equal to the quantum efficiency of photosynthesis over all light intensities from zero to that of full sunlight. Might it not be possible to breed plants for such an improved and more sophisticated type of chloroplast structure? It seems today a difficult problem. Perhaps it is an insoluble one. But it is certainly a goal worthy of consideration. The fruits would be large indeed (*15*).

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Stratospheric Residence Time of Strontium-90

An overall average residence time of 0.7 ± 0.1 year was observed during the period 1958 through 1960.

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Widely different values have been reported in the past for the stratospheric residence time of strontium-90. Libby (*1*) first pointed out the long residence of Sr^{90} in the stratosphere and estimated the mean stratospheric storage time to be 5 to 10 years. Machta and List (*2*) estimated the mean removal rate to be about 20 percent per year but later pointed out the possibility that the actual removal rate might be much greater (*3*). Kulp (*4*) proposed a value of 3 years for the residence time, and Storebö (*5*) reported that the residence time in the stratosphere should not be much more than 1 year, while Feely (*6*), in 1960, estimated the residence half-time to be less than 1 year, equivalent to a mean residence time of less than 18 months.

Martell and Drevinsky (*7, 8*), on the other hand, have reported that the concept of a well-mixed stratosphere and a mean stratospheric storage time appear largely inapplicable to the interpretation of stratospheric fallout. They proposed three stratospheric residence times, instead of one: (i) a few months or more for Soviet test debris in the polar stratosphere; (ii) 1 to 3 years for debris in the lower equatorial stratosphere; and (iii) 5 to 10 years for the debris at higher levels near the equator. Libby (*9*) has expressed a similar view.

Kuroda, Hodges, and Fry (*10*) have reported, however, that their data suggested an overall rate for transfer of Sr^{90} from the stratosphere which is roughly equivalent to an "apparent" mean stratospheric storage time of approximately 1 year or even less.

Since the measurements of the Sr^{90} concentrations in the entire series of rainfalls that occurred at Fayetteville, Arkansas, during the period 1958 through 1960 have been completed in our laboratory, it has now become possible to make an estimate of the overall average annual rate of transfer of Sr^{90} from the stratosphere without making many assumptions, such as previous workers had made, concerning the quantities and the origins of Sr^{90} injected into the stratosphere since the testing of nuclear weapons began. The test-suspension period provided an ideal opportunity to carry out this investigation. Fortunately, the stratospheric inventory of Sr^{90} was not much affected by the two small atom-bomb explosions set off by the French during this period (*11*).

The overall average residence time of Sr^{90} in the stratosphere, 0.7 ± 0.1 year (a value which corresponds to a residence half-time of 0.5 ± 0.1 year) as determined from the data on Sr^{90} concentration at Fayetteville from 1958 through 1960, is similar to the value given by Martell and Drevinsky (*7, 8*) for debris from Soviet tests (Fig. 1).

Concentration in Rain

Monthly average concentrations of Sr^{90} in rain ($\bar{C}$) were calculated from the equation

$$\bar{C} = \Sigma F / \Sigma R \tag{1}$$

where ΣF is the total amount of Sr^{90} (in 10^{-12} curies per square meter) transported by rain during the period of a month and ΣR is the total rainfall (in millimeters) during the same period. The values for $\bar{C}$ are shown in Table 1.

The data show that there is a marked seasonal variation of the Sr^{90} concentration in rain and that the concentration follows a cyclic pattern, with a maximum in the spring and a minimum in the fall, indicating that the rate of

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