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# THE ACCUMULATION OF ENERGY BY PLANTS.*

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A century ago the chief concern of civilization was the search for new sources of materials and for more effective ways of using them. During the past quarter century the realization has been growing that our energy resources are even more important and definitely limited. Our present social and economic status has been built largely through the use of the energy of coal, petroleum and gas. The ever threatening spectre of their exhaustion has turned the attention of many toward sunlight and plants—the original source of this geologically inherited capital. Plants will always be the primary food supply. Certain optimistic engineers have also proposed to solve the future fuel problem using plants as the gatherers of the sun's energy.

It has therefore seemed profitable to study this problem of the accumulation of energy by plants both for what information it may give as to our future energy resources, and for its interest as a picture of plant metabolism from the energy point of view. Why the energetics of *plant* metabolism have seemingly lagged so far behind those of *animal* metabolism will be more apparent if we digress for a moment and look into the history of our knowledge of animal and plant metabolism.

The study of the metabolism of animals has been in progress for two and a half centuries. It had its beginning apparently in the experiments of Hooke (1667) and Mayow (1674). The latter seems to have clearly recognized the necessity of something in the air, which we now call oxygen, both for the maintenance of combustion and of vital activity in animals. Mayow's work seems to have been overlooked in the development of the

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"phlogiston theory" during the succeeding century, and in 1774 Priestley rediscovered oxygen and its importance in the metabolism of animals.

With the writings of Lavoisier (1774–1789) came more precise proof that the gas exchanges involved in combustion and in respiration are essentially the same. Lavoisier built and used the first ice calorimeter and thereby attempted to show that the heat energy liberated in the animal body is derived from the oxidations taking place in metabolism.

Seventy years later, Regnault and Reiset (1849) advanced our knowledge of these processes with definite recognition of the so-called "respiration ratio," that is, the ratio of the volume of carbon dioxide released to volume of oxygen consumed. They showed quite definitely that the value of this ratio depends upon the food consumed. It is about unity when carbohydrates are consumed and less than unity when proteins and fats are used as food.

It was not until 1892, however, that a sufficiently accurate calorimeter was constructed by Rubner to show that in metabolism the energy income and outgo also constitutes a balance. Rubner introduced the "closed system" calorimeter in which experiments could be performed with animals for several days at a time. With his equipment it was possible to determine the potential energy of the food, the amount of oxygen consumed the amount of carbon dioxide liberated, the energy released and the potential energy still present in the body wastes. In this way he was able to secure results which established that fundamental law of metabolism, that energy is neither created nor destroyed within the animal body; that the energy liberated is equal to the potential energy of the food consumed; and that the conservation of energy is just as true within the animal body as it is in the environment.

However Rubner's determinations had an error of about one per cent, and this is too large for the complete establishment of a law. The more recent experiments of Atwater and Benedict conducted both with animals and men have finally removed the last doubt about the possibility of any other sources of energy. As a result of their work we know not only the precise metabolic energy values of a great variety of foods but we have exact determinations of the energy output under a great variety of environmental conditions, with the body at rest and in action, in health and in disease. Indeed these studies have been so enlightening that the metabolic rate has become an important method of diagnosis in medicine.

Finally, these studies of animal metabolism have established the fact that foods in addition to furnishing the material for the development and growth of the body, provide the energy to maintain bodily temperatures, for internal and external work, and for the synthesis of other substances found in the body.

The study of the metabolism of plants is a very different matter. Priestley (1774) showed that the "spoilt air" given off by animals would again support combustion and animal life if exposed to green plants in the light.

Ingenhous (1779) and De Saussure (1804) proved that plants absorb carbon dioxide and give off oxygen in sunlight and that these gas exchanges are reversed at night. De Saussure proved that the increase in dry weight of green plants occurs only when exposed to carbon dioxide. It remained for Dutrochet (1837) to show the connection between this process, which we now call photosynthesis, and the green tissues of plants and also that respiration in plants and animals is fundamentally the same.

A little later Leibig (1840) corrected the then prevalent notion that plants obtain all or a part of their carbon from the humus of the soil. But he seems to have had wholly erroneous notions of photosynthesis and respiration, and went so far as to deny that respiration comparable to that of animals occurs in plants. In spite of the excellent start toward a correct interpretation of photosynthesis and respiration, as late as 1860 the prevailing view seems to have been that plants merely exhibit two kinds of respiration, the one a diurnal and the other a nocturnal process.

All these early students of plants were denied an intelligent insight into the metabolism of plants because of their assumption from animal physiology that the food of a plant must come from the outside, a fallacy that is still being perpetuated by those who persist in speaking of "the plant food in the soil."

To Sachs (1865) belongs the honor of having first clearly stated the fundamentals of plant nutrition, and the connection between the chloroplasts and photosynthesis. Becquerel (1868) made the first attempt to determine the per cent of sunlight used by plants in photosynthesis on the basis of the plant materials produced per hectare and concluded that only about .4 of one per cent is utilized. The work of Sachs, Becquerel, and

Boussingault ushered in the modern period of our knowledge of plant metabolism.

The fact that in green plants exposed to the light photosynthesis, an energy consuming, or endothermic reaction, proceeds along with respiration, an exothermic process, complicates the study of metabolism of plants far beyond that of animals. There is seemingly no way by which the complementary gas exchanges involved in these two processes or the energy transformations can be simultaneously investigated. We can make short-time determinations of either process, and we can alternate light and darkness, and by modern methods of analysis obtain much information concerning both processes. At the same time it is clear that under these experimental conditions the relative amounts of carbohydrates and amino acids also change and with them the rate of respiration. At best we can make observations of but a few hours duration, and piece together the fragmentary determinations of energy income and outgo, and the relative rates of oxygen and carbon dioxide exchange. To complete the picture we should also be able to measure simultaneously the energy of sunlight.

It is just twenty years since Horace Brown (1905) presented to the Royal Society of London an energy budget of a green leaf.[1] This was the first attempt on an experimental basis to describe the metabolic processes of a plant organ in terms of energy income and outgo. Among other things he determined the proportion of light energy utilized by the leaf in photosynthesis, how much is absorbed, and how much passes to the environment. About the same time F. F. Blackman also published several papers that contributed to our information concerning the rates both of photosynthesis and respiration. The most notable recent contributions are those of Spohr who has corrected certain wrong impressions of the steps in these processes, and is gradually building a secure foundation for an understanding of the details of plant metabolism. But there is no probability that we shall have in the near future an experimental determination of the energy budget of a complete plant such as we have for a great variety of animals.

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[1]Brown, H. T. The Reception and Utilization of Energy by a Green Leaf. Nature, 71:522–526, 1905. See also for details Proceedings Roy. Soc. London, Series B, Vol. 76, which contains several papers by Brown, and one by F. F. Blackman.

The work of the animal physiologists, and the studies of non-green plants have shown that an energy budget can be calculated from the heat equivalents of food substances consumed and that the results so obtained are quite close to the results obtained by calorimetric experiments. Since there is no elimination of solid materials from plants, we have an advantage in that our calculations are not complicated by the energy content of these waste products.

As a result of measurements begun by Langley and continued by Abbott and his associates of the Smithsonian Institution we now have accurate determinations of the solar energy received at the earth's surface for a number of stations in the United States and these may be taken as the basis of our energy income.[2]

The chemical and physiological studies of crop plants at our Agricultural Experiment Stations have made available many data concerning dry weights, chemical composition, water requirements, and rates of respiration and growth. It ought therefore to be possible utilizing these figures to estimate the energy income, accumulation and outgo with sufficient accuracy to approximate a real energy budget for some of these plants.

Corn has been selected for this particular study because it probably represents the most efficient annual of temperature regions. It grows steadily throughout the season and forms a closed association sooner than any other of our crop plants. Moreover, there are available more data concerning corn than other crop plants.[3] Let us now examine the energy budget of a hypothetical acre of corn in the heart of the corn belt in north central Illinois where corn attains yields as great as anywhere, and not far from Madison, Wisconsin, one of the stations at which solar radiation has been studied. The growing season is from June 1 to September 8, one hundred days. The best yields have been with 10,000 plants to the acre. One hundred bushels, with a dry weight of 2160 kg. per acre, is the yield assumed

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[2]Kimball, H. H. Variations in the Total and Luminous Solar Radiation with Geographical Position in the United States. Monthly Weather Review, 47:769–793, November, 1919.

[3]Vivian, Alfred. First Principles of Soil Fertility, pp. 9–11. 1908.

Latshaw and Miller. Elemental Composition of the Corn Plant. Jour. Agr. Research, 27:845–859. 1924.

Briggs and Shantz. The Water Requirements of Plants. Bur. Plant Indus. Bull. 284 and 285. 1913.

Briggs and Shantz. Relative Water Requirements of Plants. Jour. Agric. Research, 3:1–63. 1914.

Kisselbach, T. A. Transpiration as a factor in Crop Production. Nebraska Agric. Exper. Sta. Tech. Bul. 6:1–214. 1915.

although it is not a maximum crop for the corn belt. How well an acre of corn covers the area is shown by the fact that during the latter half of the season nearly two acres of leaves are exposed to the light.

Table 1. Average Elemental Composition of the Corn Plant.

| | | | | |
|---|---|---|---|---|
| Corn Plant | Water 79.7% | | | |
| | Dry matter 20.3% | Organic matter 19.5% | Carbohydrates | 12.2 |
| | | | Fiber | 5.0 |
| | | | Fat | 0.5 |
| | | | Protein | 1.8 |
| | | | C | — 44.58 |
| | | | O | — 43.79 |
| | | | H | — 6.26 |
| | | | N | — 1.43 |
| | | | K | — 1.62 |
| | | | P | — .25 |
| | | | Ca | — .59 |
| | | | Mg | — .44 |
| | | | Fe | — .10 |
| | | | S | — .05 |
| | | | Cl | — .20 |
| | | Mineral Elements 0.8% | Na | — .15 |
| | | | Si | — .54 |

At maturity the average corn plant contains about 20 per cent of dry matter and about 80 per cent of water. (Table 1.) Of the dry matter, carbon makes up about 44.58 per cent. This is the most important figure for our calculations derived from the chemical analyses of the corn plants. We must also know the total amounts of mineral elements present which is 5.37 per cent from which we can derive the fact that 94.63 per cent of the plant's dry weight is organic matter. The dry weight of an average corn plant growing under these circumstances is 600 g., of which 216 g. makes up the grain 200 g. the stalk, 140 g. the leaves, and 44 g. the roots. The total weight of the 10,000 plants is 6000 kg. Subtracting from this the 322 kg. of mineral elements in the ash we have left 5678 kg. of organic matter, of which 2675 kg. is carbon.

Table 2. Glucose Equivalent of Accumulated Carbon.

| | | |
|---|---|---|
| Dry weight of ave. plant 600g | grain | 216 |
| | stalk | 200 |
| | leaves | 140 |
| | roots | 44 |
| Total dry wt. of 10,000 plants | | =6000 kg. |
| Total ash (5.37% of dry weight) | | = 322 kg. |
| Total organic matter of acre | | =5678 kg. |
| Total carbon accumulated (44.58%) | | =2675 kg. |
| Glucose equivalent of accumulated carbon | | =6687 kg. |

$C_6H_{12}O_6 : C_6 = 180 : 72$

To estimate the amount of photosynthesis we must determine the amount of carbon, because carbon enters the plant only by photosynthetic reduction of $CO_2$. The total carbon is 2675 Kilograms and the glucose equivalent of this carbon is 6687 kilograms. This is the amount of primary sugar equivalent to the carbon accumulated in the mature plant. (Table 2).

TABLE 3. GLUCOSE EQUIVALENT OF RESPIRATION.

| | |
|---|---|
| Estimated rate of $CO_2$ release = 1% of the dry wt per day | |
| Average dry weight for season (½ total wt.) | =3000 kg. |
| Average rate of $CO_2$ release (.01 × 3200) per day | = 30 kg. |
| Total $CO_2$ release during season | =3000 kg. |
| Carbon equivalent: C : $CO_2$ = 12 : 44 | = 818 kg. |
| Glucose equivalent $C_6H_{12}O_6$ : $C_6$ = 180 : 72 | =2045 kg. |

At maturity however, only a part of the carbon remains, for some has been lost as $CO_2$ in respiration (Table 3). The average rate of $CO_2$ loss is not far from one per cent of the dry weight per day. This would cause a daily loss of 30 kilograms of $CO_2$, and during the entire season a loss of 3000 kilograms. The glucose equivalent to this amount of carbon dioxide is 2045 kilograms.

Adding the amount of this lost glucose to the glucose equivalent of the carbon in the plant, gives the total glucose manufactured as 8732 kilograms. It requires energy equivalent to 3760 calories to produce one kilogram of glucose. Hence it required not far from 33 million calories to produce the entire photosynthetic product. (Table 4).

TABLE 4. ENERGY CONSUMED IN PHOTOSYNTHESIS.

| | |
|---|---|
| Glucose equivalent of accumulated carbon | 6687 kg. |
| Glucose equivalent of carbon oxidized | 2045 kg. |
| Total glucose manufactured | 8732 kg. |
| Energy required to produce 1 kg. glucose | 3760 Cal. |
| Total energy consumed in photosynthesis | 33 million Cal. |

We are now in a position to estimate the efficiency of the corn plant as a photosynthetic agent: (Table 5).

TABLE 5. EFFICIENCY OF PHOTOSYNTHESIS.

| | |
|---|---|
| Total energy available on acre during the growing season | 2043 million Cal. |
| Total energy used in photosynthesis | 33 million Cal. |
| Per cent of available energy used by the corn plant in photosynthesis, (efficiency of corn plant) | 1.6% |
| Of the total light spectrum measured, however, only about 20% is used in photosynthesis, hence the efficiency of the photosynthetic process is | 8% |

The total energy available according to the Smithsonian figures is 2043 million Calories. The energy utilized is 33 million, or 1.6 per cent. In photosynthesis however, only certain rays are effective, and these furnish about 20 per cent of the energy measured by the pyrheliometer.[4] Consequently the efficiency of photosynthesis in 100-bushel corn is 8 per cent.

Another source of energy loss to the plant is transpiration. From the water requirement studies of corn it is probable that in Illinois not far from 276 kilograms of water are evaporated during the growing season for every kilogram of its dry weight. (Table 6). The total weight of water lost in this way therefore is one and a half million kilograms. This is equal to 408,000 gallons or sufficient water to cover the acre to a depth of fifteen inches.

TABLE 6. ENERGY CONSUMED IN TRANSPIRATION.

Total dry weight of the aerial parts.................................5560 kg.
Estimated rate of water transpired per kg. of dry matter per season......276 kg.
Total water transpired by the acre..........................1.5 million kg.
Energy required to evaporate 1 kg. water at the average temperature of growing season.................................................593 Cal.
Total energy consumed in transpiration (593 × 1,534,560) = 910 million Cal.
Of the available energy (2043 million Cal.) transpiration consumed about 44.5%

The energy necessary to evaporate one kilogram of water at the average temperature of the growing season is 593 calories. Consequently 910 million Calories are expended in this way. This is equivalent to 44.5 per cent of the available energy.

TABLE 7. ENERGY RELEASED IN RESPIRATION.

Glucose consumed in respiration......................................2045 kg.
One kilogram of glucose releases....................................3760 Cal.
Total energy released in Respiration..........................7.7 million Cal.
Of the energy made potential in photosynthesis, Respiration releases....23.4%
Assuming that photosynthesis goes on 12 hours each day and respiration 24 hours each day, the average daily rate of photosynthesis is about 8 times the rate of respiration.

Respiration again releases a part of the energy rendered potential in photosynthesis. As we have seen 2045 kilograms of glucose are thus oxidized, and in consequence 7.7 million

[4]For the region of north central Illinois Professor Abbot estimates that the proportion of total energy contained among the rays utilized in photosynthesis is as follows:

| Wave-length limits | Air Mass 2 | Air Mass 3 |
|---|---|---|
| 670–635μ | 4.6% | 4.5% |
| 622–597μ | 3.4 | 3.1 |
| 587–565μ | 3.0 | 2.7 |
| 544–530μ | 1.9 | 1.7 |
| 495–420μ | 9.0 | 7.3 |
| Total.............. | 21.9% | 19.3% |

Calories are released within the plant. This energy raises the temperature of the plant and escapes to the environment, or it is used in synthesis of fats, proteins and other reduced organic substances.

The energy released in respiration amounts to 23.4 per cent—almost one-fourth of the energy absorbed in photosynthesis. This is far more than is needed to account for the endothermic reactions associated with food transformations within the plant.

Assuming that photosynthesis goes on 12 hours and respiration 24 hours each day, the average rate of photosynthesis must be about 8 times the rate of respiration.

TABLE 8. SUMMARY OF BUDGET.

| | | |
|---|---|---|
| Total energy available | | 2043 million Cal. |
| Used in photosynthesis | 33 million Cal. | |
| Used in transpiration | 910 million Cal. | |
| Total energy consumed | | 943 million Cal. |
| Energy not directly used by the plants | | 1100 million Cal. |
| Energy released by respiration | | 8 million Cal. |
| Of the available energy, 100-bushel-corn uses about | | 46% |
| The environment takes up about | | 54% |

We may now summarize the energy budget. The total income is 2043 million Calories. The expenditure for photosynthesis and transpiration is 943 million Calories. Respiration returns 8 million Calories. Therefore the plant uses about 46 per cent, and the environment takes up 54 per cent. As a result we are in a position to make a number of generalizations regarding the metabolism and growth of plants, both as to materials and energy.

1. An acre of 100-bushel corn uses during the growing season about 408,000 gallons of water or 15 acre-inches.

2. The evaporation of this water consumes about 45 per cent of the available light energy.

3. In photosynthesis the corn plant utilizes about 1.6 per cent of the energy available; its efficiency is about 8 per cent.

4. An acre of 100-bushel corn manufactures on the average 200 pounds of sugar a day.

5. Of the energy rendered potential in photosynthesis, 23.4 per cent is again released in respiration.

6. Of the sugar manufactured nearly one-fourth is oxidized in respiration.

7. Respiration releases several times as much energy as is needed to account for the reductions in the synthesis of fats, proteins and other compounds.

8. At maturity the grain contains about one-fourth of the total energy utilized in photosynthesis, or about .5 per cent of the energy available.

9. The average rate of photosynthesis is about eight times the rate of respiration.

10. Since the young corn seedling weighs .3 grams and the mature plant wighes 600 grams, on the basis of the compound interest law of growth the average daily increment in dry weight is 7.9 per cent.

Returning now to the questions proposed in the introduction to this paper regarding future food and fuel supplies. If corn is the most efficient of our temperate zone corn plants, and if 100-bushel corn can utilize only 1.6 per cent of the available energy, it must be apparent that the average crop plant falls far below this amount. It is evident also that we can never expect many of our other crop plants in temperate regions to equal this production, and we must agree that plants are very inefficient gatherers of energy.

The suggestion that our liquid fuels, petroleum and gasolene, may some day be replaced by alcohol made from plants is quite unreasonable. A little figuring will show that to substitute the energy of alcohol for the energy now being developed from gasolene would require all the corn now being grown in the United States.

The solution of our future fuel energy supplies lies rather in the discovery of the physics and chemistry of photosynthesis. We have in the past discovered the nature of many biological processes.

It is not so many years ago since it was thought that only plants and animals could synthesize organic compounds. Now we can make hundreds of them more efficiently than either plants or animals. There is no good reason to think that photosynthesis is impossible of explanation and imitation. Photosynthesis is a very inefficient process, but when we once know its photo-chemical basis we should be able to improve on it greatly and herein lies the best hope of future supplies of energy, almost unlimited and certainly inexhaustible.