RATE OF RESPIRATION AS RELATED TO AGE.*

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(Accepted for publication, June 21, 1926.)

It is usually stated in the literature that respiration is most rapid in the young and actively growing parts of a plant and decreases with age; and sometimes it is said that respiration conforms to the grand period of growth.

Considerable experimental evidence upholds the first statement. Bonnier and Mangin 1 studied the respiration of several different plants, among them Evonymus japonica. Leaves 1 year old respired more per volume of leaf than leaves produced the year of the experiment. Data for other plants were obtained (at different temperatures as far apart as 13 degrees but no corrections were made). M. A. Maige 2 found that most flowers produce more CO₂ per gm. of green weight in the bud stage than when open, but some respire most actively in the open stage. G. Maige 3 found that the intensity of respiration of floral organs decreased with age, except in the pistil, which often showed increased respiration as long as it continued to develop. Nicolas 4 found that of two samples of twigs the younger had a higher rate of respiration. Studying young and adult leaves he obtained the same results. Briggs, Kidd, and West 5 state that, "the evidence available (Helianthus) is that the respiration per unit dry-weight of the whole plant at constant temperature decreases with age."

* Paper from the Department of Botany of the University of Michigan, No. 250.
On the other hand A. Mayer,\(^6\) and also Rischawi\(^7\) claim to have demonstrated that the respiration follows the grand period of growth. These investigators enclosed seedling plants in a respiration chamber, and either by daily measurements of the O\(_2\) intake or of the CO\(_2\) given off arrived at the conclusion that there was a grand cycle of respiration conforming to the grand period of growth. In their experiments the normal photosynthetic activity of the plants was prevented and no account was taken of any changes in weight due to the metabolism of the plants. In other words, their results record the respiratory changes in a growing plant independent of any loss or increase in the weight of the plant during its growing period.

The purpose of the present investigation has been to determine carefully the relation between rate of respiration and age. To accomplish this an effort was made to determine the comparative rate of respiration in successive leaves of several plants. In the plants chosen new leaves continue to appear at the top of the plant until the panicles are formed. Before these are formed, however, some of the older leaves at the base have withered away. The successive leaves of these plants, therefore, constitute an age series. In corn the total leaves may number anywhere from 18 to 24, but at any one time there are usually not more than 8 to 12 leaves. In sorghum the total number of leaves developed is 25 to 30 with 8 to 15 active leaves present at one time. In oats and wheat there are only 4 to 6 leaves at any one time. The number of active leaves present appears to be related to age, varietal differences, and water supply. During a dry season the life cycle of a leaf is shorter than during a wet season.

In determining the rate of respiration, the active leaves of the plants were removed and the total CO\(_2\) given off by each leaf was simultaneously determined, by placing the leaves in a battery of Pettenkofer tubes. Inasmuch as the leaves of a plant were all removed at the same time, placed in their respective respiration chambers at the same time, and the CO\(_2\) given off was determined for the same interval, and further, since temperature and other external conditions were identical, it follows that any differences in the rate of respiration are due to differences in the leaves themselves.


The rate of respiration given is the amount of CO₂ given off per gm. of dry matter or per gm. of green weight for the duration of the experiment. Since there were variations in the duration of the experiments and also in the temperature conditions, the rates of respiration in one experiment cannot, except in a general way, be compared with the rates in another. In general, the duration of an experiment was from 18 to 22 hours.

All possible precautions were taken to insure that the air entering the respiration chambers was free from CO₂; care was also taken that all the CO₂ was absorbed by the barium hydroxide tubes. The barium hydroxide after having been standardized was kept in containers entirely free from CO₂.

To illustrate the procedure a typical experiment will be described. A corn plant with ten healthy leaves has been selected in the field. It is brought into the laboratory and the leaves are carefully removed and placed in separate bottles of 500 cc., capacity which are completely covered with black paper. The experiment is arranged as follows: First come 10 CaCl₂ towers filled with pieces of soda lime to absorb the CO₂ from the entering air; following each tower is a bottle containing a solution of BaOH, to indicate whether all the CO₂ has been absorbed; to these bottles are attached the respiration chambers, covered with black paper, which in turn are attached to the Pettenkofer tubes, containing 100 to 150 cc. of standardized BaOH (the amount depends on the size of the plant; with large plants more BaOH is used than with small plants); each tube is followed by a bottle containing a solution of BaOH, to insure that all CO₂ has been absorbed by the standardized BaOH; these bottles are connected by Y-tubes to a single aspirator, by means of which the air is drawn through the apparatus. The rate and size of the gas bubbles passing through each tube are regulated so as to be the same in all tubes. Before the experiment is started the respiration bottles are thoroughly freed of all CO₂ by running CO₂-free air through them. The experiment is then run for 22 hours. At that time the BaOH in each tube is titrated with N/10 oxalic acid.

1 cc. of N/10 oxalic acid is equivalent to 0.0022 gm. of CO₂, and from the difference between the original titrations of the standardized BaOH and the titrations at the end of the experiment the amount of CO₂ can readily be calculated.
The amount of CO₂ has been calculated both on the basis of dry and of green weight. The results are similar, and as it is more usual to employ dry weight than green weight, and as the respiration is undoubtedly more closely related to the dry material than to the water of the plant, only the data calculated for dry weight are given. As pointed out before, no two experiments were carried out under identical conditions, nor were the plants themselves identical; some of these experiments were performed during the summer of 1923, others during 1924. For this reason no average of the experiments can be obtained. A few of the experiments have been selected as illustrating the condition in these plants.

Corn (Zea Mays) was the original plant worked with and the results of a few of the experiments are given in Fig. 1. Curves A, B, and C represent plants of different ages with varying number of leaves. Curve A shows that there is a decrease in rate of respiration with age when the plant is very young, while B shows that as the plant ages...
and the number of leaves increases the rate of the older leaves increases above that of those slightly younger; and C (a plant with ten leaves) shows that the oldest leaves may actually respire more than do the youngest leaves on the plant. Curve D represents an experiment with the corn stem, which shows that there is a decrease in respiration with increase in age.

In Fig. 2 Curves A, B, and C represent respiration in *Sorghum vulgare*. All of these experiments show that at first there is a decrease in respiration as the leaves age, but that after a certain age has been reached there is a gradual increase in rate, which in some instances is nearly as great as that in the youngest leaves. Curve D represents leaves of sunflower (*Helianthus annuus*), and in this as well as in other experiments on sunflower there is a decrease from the first with no subsequent increase.

Fig. 3 represents results obtained with oats (*Avena sativa*). The two experiments were conducted at the same time. These experiments show that the respiration in the oldest leaves is much more rapid than in the youngest.
In Fig. 4 are results of two experiments with nearly mature wheat (*Triticum sativum*). These plants had five leaves but the two oldest ones were dying and so cannot be counted. Both experiments show that the oldest healthy leaves respired more vigorously than the youngest leaves of the plants.

The plants represented in Figs. 3 and 4 were nearly mature and the youngest leaves had already reached the age at which the respiration is at its lowest; all the curves but B of Fig. 4 show only increase in respiration with age rather than a decrease followed by an increase.

![Graph](image)

**Fig. 3.** Two oat plants nearly mature. The two experiments were conducted at the same time. These curves strikingly bring out individual differences.

**Fig. 4.** Two wheat plants, nearly mature; each plant had 5 leaves, but the two lowermost were practically dead. The two experiments were conducted at the same time. They also show individual differences.

It is quite apparent from the data given that when dry weight is taken as a criterion for judging the comparative rate of respiration in the various leaves of corn, sorghum, sunflower, oats, and wheat the respiration cycle does not correspond to the grand period of growth, nor is there a decrease in respiration with age except in the leaves of sunflower and corn stem. The reason other investigators have not noted this before is that not enough controlled experiments have been performed. In most instances a few leaves of one age were taken at one time at a certain temperature and a few leaves of a different age at another time, at a temperature different from the first, without any correction being applied. As far as the writers are aware no experiments have been performed in which a series of leaves or other plant
parts, differing in age, have been studied at the same time. It is obvious from the figures given in this paper that, if only two leaves had been taken, in practically all instances the older leaves would have respired less than the very youngest on the plant, but it is equally obvious that by taking very young leaves, middle aged, and old leaves at the same time, the old leaves are found to respire more rapidly than the middle aged ones, though usually less than the youngest.

The writers are not prepared to say that as protoplasm ages it respires less and that as it gets still older it begins to respire more actively. But it seems that when the amount of CO₂ given off is calculated on the basis of dry weight the rate of respiration increases to some extent after middle age. This is true of the leaves of corn, sorghum, oats, and wheat, but not of sunflower leaves and corn stems.

The amount of CO₂ given off per gm. of dry or of green weight is probably not a good criterion of respiration. That, however, is customary. As a cell increases in size and in age, the total amount of protoplasm probably remains the same while the dry material (cell wall, stored food, etc.) increases. The respiration is presumably connected with the protoplasm. Then if the amount of respiration of an old leaf is calculated on the basis of the total dry weight (cell wall, stored food, etc.) it is obvious that the rate per gm. of dry weight is going to be less than in the young leaves, though the rate per gm. of protoplasm may be the same. The writers have unpublished data to show that as leaves grow older there is an increase in the percentage of dry material up to a certain age, when there is sometimes a decrease. A method which would take into account only the amount of protoplasm would be much more accurate. Perhaps the CO₂ could be calculated on the basis of amino nitrogen or total nitrogen in a plant part.

**SUMMARY.**

In the present paper it is shown that as the leaves of corn, sorghum, wheat, and oats increase in age there is a decrease in rate of respiration; but that as the leaves become still older (past about middle age) the rate gradually increases.