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ART. XLIX.—*Respiration of Plants;* by W. P. WILSON, S.D.

THE process of breathing in animals and plants is essentially the same. In both the free oxygen from the air, or surrounding medium, is carried into the living tissues, where, after a series of chemical changes, carbonic acid, water and perhaps some minor compounds are evolved as excretory products.

The changes in the living cell, alike in animals and plants, determine the amount of oxygen taken up and the products given off. In both an increase of temperature is a direct effect of respiration.

In this process of respiration, for plants as well as animals, a certain amount of absolutely necessary force is secured for supplying the life-functions of the organism. If either the living animal- or plant-cell be deprived of oxygen for any considerable length of time the life activities cease, and, later, death ensues. This oxygen-respiration is then a constant need of the living cell, whether it be of plant or animal.

When plants possessing chlorophyll are exposed to the sunlight they carry on a process of assimilation, in which organic substance is produced from carbonic acid and water, and oxygen set free. The amount of carbonic acid decomposed and of oxygen given off, in this preparation of organic food for the plant, far exceeds, as a rule, the carbonic acid excreted and the oxygen taken up in respiration. Thus it happens that the process of respiration, in plants containing chlorophyll and exposed to the light, is a hidden one, and difficult of demonstration.

When plants are deprived of every trace of free oxygen by placing them in an atmosphere of nitrogen or of hydrogen, they still continue, so long as life exists, to excrete carbonic acid. The discovery of this fact, which has been observed for animals as well as plants, is not of recent date, although its signification was only recently understood. As early as 1798 Rollo* observed that barley, which had been wet for two days and then placed in a vacuum, excreted carbonic acid; and that at the end of twelve days, the amount equaled six times the volume of the barley.

Saussure† placed plants in an atmosphere of nitrogen to see if they would grow, and found that they excreted carbonic acid, which he remarks must have been produced at the expense of the substance of the plants.

At a still later date Bérard,‡ while experimenting on the preservation of fruits, placed green pears in a vacuum and observed for several days following an excretion of carbonic acid.

Broughton§ and also W. Pfeffer‖ have recorded the same phenomenon in plants deprived of free oxygen.

In 1875, Pflüger¶ obtained some very interesting results in animal respiration while experimenting on frogs. These animals, placed in an atmosphere of nitrogen, were found during the first five hours and a half to expire nearly the same amount of carbonic acid as if they had been placed in pure oxygen. In another of Pflüger's experiments, a frog continued to give off carbonic acid during eleven consecutive hours, and at the end of that time had apparently lost none of its normal powers. Pflüger showed that these chemical activities, which result in the expiration of carbonic acid in the absence of free oxygen, take place in the cells. He named the process *intramolecular respiration.*

In 1878 a critical résumé on the nature and signification of respiration in plants,** written by W. Pfeffer, brought together all the then known facts which could be made to bear on this subject. The similarity existing between animal and plant respiration was sharply noted, and the term *intramolecular respiration*, taken from Pflüger, was made to cover a like series of phenomena in plant life, viz: the chemical changes continu-

* Annales de Chimie, 1798, vol. xxv. p. 42.

† Recherches Chimiques, 1804, p. 201.

‡ Annal. de Chimie et de Physique, vol. xvi, 1821, p. 174.

§ Bot. Zeit. 1870, p. 647.

‖ Arbeit. d. Würzburger Instituts, 1871, Bd. I, p. 34.

¶ Archiv. für Physiologie, Bd. X. 1875, p. 313. Pflüger gives other references to investigators in animal physiology who had made similar experiments on frogs, dating back into the 18th century.

** Das Wesen und die Bedeutung der Athmung in der Pflanze, Landwirthschaftliche Jahrbücher, 1878, Bd. VII, p. 805.

ing to take place in the plant-cell after oxygen has been withdrawn, resulting always in the production of carbonic acid, and often in other more or less important products. In this article the author lays great stress on *intramolecular respiration* as being the *first cause* of the *oxygen* or *normal* respiration.

One of the next works of any special importance on plant respiration appeared in 1879.* Wortmann measured and compared the carbonic acid expired from germinating plants placed in common air, with that given off from an equal number of plants placed in a vacuum.

He states that for short periods of time (from one to three hours), the presence or absence of free oxygen makes absolutely no difference in the amount of excreted carbonic acid gas. On the basis of these results he proposed a new theory, viz: that all the carbonic acid produced in plant respiration has its origin in intramolecular decompositions; or, in other words, that the free oxygen of the air takes no direct part in the formation of the carbonic acid in respiration.

The following paragraphs consider briefly one phase of intramolecular respiration and give in very condensed abstract a series of experiments which will later be published in full.†

The main question, here discussed, is whether the carbonic acid excreted in plant-respiration *is or is not a partial product of direct oxidation from the free oxygen of the air.*

To decide this question, quantitative measurements were made of the expired carbonic acid from the same plants placed both in air and in hydrogen gas. The methods of experimentation used were the following: a constant current of air, previously freed from carbonic acid, was passed by means of an aspirator, first through a large number of germinating seeds, or other objects to be experimented upon, and then through long tubes filled with barium hydrate in which the carbonic acid given off by the seedlings was absorbed, essentially in accordance with Pettenkofer's method.‡ After a given time had elapsed, hydrogen, as an indifferent gas, was used to replace the air. This was quickly done by exhausting the air in the seed-vessel and tubes leading thereto, and then introducing hydrogen to take its place. A constant current of hydrogen was then passed over the seedlings, precisely as had been done previously with air.

The carbonic acid was determined for either half hourly or hourly intervals. This was easily accomplished by using two

* Wortmann, über die Beziehungen der intramolecularen zur normalen Athmung der Pflanze, in Arbeit d. Würzburg Instituts, 1880, Bd. II, p. 500.

† A much shorter abstract than the present appeared in German in "Flora," No. 6, 1882.

‡ Abhandlungen der Akademie d. Wissenschaften in München. Cl. II, Bd. IX, Abth. II, p. 229.

absorption tubes filled with barium hydrate, and so connected together by glass stopcocks that the current of air or gas, when passing through one tube, could be instantly turned through the other without interruption. Thus while the current passed through one tube, the other could be removed, emptied, refilled and replaced for the next half hour's determination.

In conducting an experiment, measurements were made first in air for several half hours, then the air was replaced by hydrogen, and after an equal number of half hours, for hydrogen was again substituted air, in which the third series of determinations took place. The last series in air was used to compare with the first, and it readily showed whether the seedlings had undergone any lasting change for want of oxygen. The temperature of the plants for any given experiment was not allowed to vary; also the current of air or gas was held constant for all the successive half hours.

A great advantage in the methods here adopted lay in subjecting the same seedlings, first to air, and then to hydrogen; thus the products of the respiration of the same plants under these two different conditions could be compared.*

A large number of seedlings were employed (from one to several hundred, according to size), thus ensuring the production of a comparatively large amount of carbonic acid in a short space of time, with which much more accurate measurements could be made than with small quantities. The amount of carbonic acid was determined by the volumetric method.

According to the investigations of Wortmann with seedlings of *Vicia Faba*, *Phaseolus multiflorus* and some others, the carbonic acid excreted in short spaces of time, one to three hours, was found to be the same whether oxygen was present or not.†

In the case of seedlings of *Vicia Faba*, with which Wortmann mostly experimented, I have found this to be substantially true; for all other germinating plants, flowers, or parts of plants there was an immediate decrease in the carbonic acid produced when oxygen was excluded. The first half hour's respiration in hydrogen often yielded but one third or even one-fourth the carbonic acid produced by the preceding half hour's respiration in air. After three or four consecutive half hours of intramolecular respiration, sometimes from the very first, a steady decrease in the carbonic acid was recorded for every following half hour. This was also found to be true for *Vicia Faba*. The following are the results obtained from

* Wortmann used two sets of plants, as nearly alike as selection would permit, one in vacuum compared with one in air.

† "Als ich jedoch die in ganz kurzen Zeiträumen—nach der ersten, zweiten und dritten Stunde—ausgeschiedenen Kohlensäuremengen mit einander verglich, so fand ich jedesmal. 'dass das in dieser Zeit durch intramoleculare Athmung ausgeschiedene Kohlensäurevolumen dem durch normale Athmung erzeugten gleich ist.'" Wortmann, l. c., p. 509.

Lupinus luteus.

I. Period.	Air.	1st half hour,	5·7 mgms.	CO_2.
		2d half hour,	6·6 "	"
II. Period.	Hydrogen.	3d half hour,	1·5 "	"
		4th half hour,	1·5 "	"
III. Period.	Air.	5th half hour,	3·9 "	"
		6th half hour,	5·7 "	"

The comparative decrease in the amount of expired carbonic acid in hydrogen is here greater than with many plants. The following fungus shows much less difference:

Cantharellus cibarius.

I. Period.	Air.	1 hour	=16·20 mgms.	CO_2.
II. Period.	Hydrogen.	½ hour=5·28; ½ hour=5·52	=10·80 "	"
III. Period.	Air.	1 hour	=16·20 "	"

It will be seen that with *Lupinus luteus* less carbonic acid was measured in the fifth than in the sixth half hour. This is partially based upon the fact that at the beginning of the fifth half hour the seed-vessels contained less carbonic acid than at the beginning of the sixth. With a constant current of air and a constant production of carbonic acid, it requires a little time after the air or gas has been changed before an equilibrium between the produced and the out-flowing gas establishes itself.

Among a large variety of germinating plants, branches with leaves, flowers, fruits and fungi, *Vicia Faba* has been the only plant which has given results differing from the above.

That the volume of carbonic acid expired in normal and in intramolecular respiration is the same, is, therefore, in accordance with the facts above stated, untrue. The theory which Wortmann founded upon this fallacy, viz: that the total volume of carbonic acid excreted in plant-respiration has its origin absolutely independent of the oxygen of the air, in intramolecular decompositions, falls also to the ground.

Moreover, if it had been found by experiment, that the volume of carbonic acid given off in intramolecular equaled that of normal respiration, Wortmann's theory would still fail.

This has been well shown by W. Pfeffer, in saying, substantially: if an equal amount of carbonic acid were formed in both intramolecular and normal respiration this would only prove that the same number of carbon affinities for oxygen had been satisfied in each case, would in no way indicate from whence the supply of oxygen came. And in case free oxygen was active in normal respiration, still in intramolecular, when free oxygen was absent, the full supply might yet be obtained through constant powerful attractive forces which could take oxygen from other combinations, and in this way give rise to secondary changes.*

Partial presence of Oxygen.—When seedlings of *Helianthus annuus* are placed in a current of common air for a given period of time, and then for the same length of time are exposed to a current of air made up of a mixture of one-fifth air and fourth-fifths hydrogen, a comparison of the excreted carbonic acid in both cases shows no difference whatever. Sufficient oxygen is present in the mixture to supply all demands made by the plants. When, however, the expired carbonic acid in the respiration of plants, placed first in air, and then in a mixture of $\frac{1}{20}$ air and $\frac{19}{20}$ hydrogen, is compared, one finds the amount much greater during respiration in air. Thus a trifle over one per cent of oxygen in the air is not sufficient to supply the demands for this gas made by such seedlings.

Influence of light on respiration.—The presence of light does not in any appreciable degree directly affect the amount of carbonic acid given off in the respiration of plants. I have experimented on Orobanche, Monotropa, Fungi and seedlings of several kinds. Neither in air nor in hydrogen gas, for plants placed in the light or in the dark, is there any difference in the excreted carbonic acid which can be measured.†

Tübingen, Würtemberg, April, 1882.