THE
BOTANICAL GAZETTE*FEBRUARY 1912*

THE LIBERATION OF HEAT IN RESPIRATION

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(WITH EIGHT FIGURES)

In September 1908, the BOTANICAL GAZETTE¹ published an account of some preliminary experiments, of a qualitative sort, in which I had used silvered Dewar flasks as respiration calorimeters. Continued experimenting with these flasks, and the reports of correspondents, have further confirmed their usefulness in physiological laboratories. They have also led me to doubt whether, after all, a study of the heat yield alone will lead one very far toward a solution of the problems presented by respiration.² In this paper, however, I propose to give the data of some of my experiments, continuing and extending the work previously reported, and after that to discuss the possible significance of the results.

The quantity of heat liberated by germinating peas

In the preliminary paper already referred to, my experiments were necessarily rough, in accuracy below the efficiency of the apparatus, which, however, was used under laboratory conditions and not under constant temperature. The necessity of working in a constant temperature is apparent, when any attempts to determine heat yields is being made, since the experiments continue through several days. Constant temperature rooms are generally hard to secure and hard to keep clear of fungus spores, bacteria, etc.

¹ BOT. GAZ. 46:205-220. 1908.² Plant World 12:193-198. 1909.

The Botanical Department of this University has been particularly fortunate in falling heir to two large chambers, the temperature of which has been remarkably constant during the months in which temperature records have been kept. These rooms are underground, built of concrete, and were used at one time as tanks in which fuel oil was stored. With a change in the means of heating our building, these tanks ceased to be used. The site of the experiment house, which was built in the summer of 1908, was so selected that these two tanks came under the floor of the greenhouse. The tanks were then cleaned of the residual fuel oil, and were ready for use as constant temperature chambers when the house over them was completed. Each is entered through a man-hole in the floor of the greenhouse, the descent being over an iron ladder. Walls, floor, roof, and ladder are of such material that they may be washed or hosed off with an antiseptic solution, which may then be quickly swabbed up. The air, never excessively dry, can easily be maintained at any degree of humidity that one chooses, by occasionally sprinkling the walls. The following table will indicate the temperatures in one of these tanks during a period of nearly five months, these temperatures being taken by a maximum-minimum thermometer of the United States Weather Bureau pattern.³ They are as follows:

Date	Time	Room	Maximum	Minimum	Differences
March 26....		16.4°C.			
March 28....	10:00 A.M.	16.25	17.22°	16.67°	0.55°
March 29....	9:30 A.M.	16.2	17.11	16.61	0.50
March 30....		16.2	17.11	16.61	0.50
March 31....			17.05	16.55	0.50
April 1....			17.22	16.55	0.67
April 2....			17.22	16.50	0.72
May 12....			18.89	17.78	1.11
May 13....			18.89	18.05	0.34
May 14....			18.61	18.05	0.56
May 15....			18.61	18.05	0.56
May 16....			18.83	18.05	0.78
May 17....			18.77	17.73	0.94
May 18....			19.07	17.91	1.06
August 13....	10:30 A.M.	20.5	20.55	17.78	

Inspection of this table shows that the lowest maximum was on March 31, a temperature of 17.05° C. The lowest minimum was

³ Bausch & Lomb Optical Co.'s Catalogue, no. 17,004.

two days later, April 2, a temperature of 16.50° C. The highest maximum came at some time during my absence in the summer vacation, a temperature of 20.55° C., which, however, differed from the temperature at the time I made and recorded the observation on August 13 by only 0.05° . The highest minimum was in mid May. Between the highest and lowest maxima there was a difference of 3.5° ; between the highest and lowest minima a difference of 1.55° ; and between highest maximum and lowest minimum a difference of 4.05° from late March to mid August, with an average daily range of 0.71° on 13 days in March, April, and May. It is needless to say that these chambers might be warmed, and presumably their temperatures would be very nearly as constant, but in this mild climate, in which there is little frost even at night in midwinter, and still less excessive heat in midsummer, artificial heat seems unnecessary, at least for experiments on the respiration of such germinating seeds as peas.

Having thus established the remarkable constancy in the temperature of these chambers, I may now pass to a consideration of the apparatus employed. I have used silvered Dewar flasks made by Burger of Berlin and imported "duty free." These Burger-Dewar flasks are stamped and numbered by the maker. Their efficiency is very uniform. Experience with the unsigned flasks of other makers quickly shows that they are not so uniformly efficient as they should be. For the sake of convenience and economy, not at first realizing my mistake, I have continued to use flasks of about 250 cc. capacity. But I am sure that flasks of not less than double this capacity would be more satisfactory because involving smaller physical errors.⁴ Most of the flasks are simply double-walled round-bottom flasks, like fig. 1, but I have had four made in which, as indicated by fig. 2, the interior drains through a tube opening at *a*. This opening is small, but it seems to be sufficient to carry off carbon dioxide as well as water. At the same time, it does not greatly reduce the efficiency as an insulator of a well-made flask, and does add materially to its convenient use, making it possible to

⁴ See OSTWALD-LUTHER, *Physikalisch-chemische Messungen* 2:189, 1902, where BERTHELOT's results are cited as indicating that it is not practicable to use calorimeters of less than half-liter capacity.

soak seeds in the flask, and then, when one is ready, to draw off the water without exposing or disturbing the other contents. The efficiency of silvered double-walled Dewar flasks used as insulators

FIG. 1

FIG. 2

is indicated by the following experiment. Four flasks, numbered 1, 3, 4, and 6, held in pairs in the wooden filter stands usual in chemical laboratories, were set on a table in my laboratory. Into each were introduced 140 cc. of hot, distilled water; a long thermometer reading to tenths of a degree was placed in each flask and held, with the bulb almost touching the bottom, by a tight plug of absorbent cotton placed in the neck. The successive

thermometer readings and other data follow:

FLASK	AUGUST 26, 1909				AUGUST 27, 1909	SEPTEMBER 1, 1909
	11:30 A.M.	1:45 P.M.	3:05	5:05	11:05 A.M.	2:15 P.M.
1.....	72.4°C.	67.05°	64.4°	60.8°	41.0°	21.4°
3.....	73.1	61.75	56.7	50.6	27.4	21.0
4.....	60.05	54.0	51.12	47.5	Hg col. separated	
6.....	63.4	57.6	54.74	51.0	20.5	20.75
Room.....	21.11	20.75	21.2	20.75	20.5	20.75

A similar experiment is recorded in the following table, in which drained flasks were used in constant temperature room A:

FLASK	APRIL 18, 1910		APRIL 19, 1910	
	11:04 A.M.	12:05 P.M.	12:20 P.M.	4:15
11-5.....	68.7°	65.6°	32.4°	30.2°
12-2.....	72.7	69.9	38.6	36.25
14-6.....	61.1 (broke)	46.9	17.8	17.8
8-8.....	51.15	49.9	30.7	28.9
Room.....	17.0	17.5	17.3	17.3

The graphic representation of these figures, as in the accompanying curves (figs. 3 and 4), indicates more plainly the different degrees of efficiency as insulators possessed by different flasks, even of the same manufacture. The record of flask 14 with thermometer 6, in fig. 4, shows very strikingly the part played by the vacuum as an insulator between the two silvered walls of these

FIG. 3.—Graphic representations of temperatures in silvered Dewar flasks and in the laboratory.

double-walled flasks, for I cracked this just after pouring in the warm water. Although I kept the water in the inner flask, the vacuum surrounding it was destroyed. The temperature fell to approximately that of the room, almost as rapidly as in a single-walled unsilvered vessel. For obvious reasons, the rate of fall in temperature is most rapid when there is the greatest difference in the temperatures within and without the flask. This fact is impor-

FIG. 4.—Graphic representations of temperatures in silvered Dewar flasks and in the constant temperature room

tant in connection with respiration experiments in which heat production is being studied; for evidently the flasks, as well as the organisms within them, will lose heat most rapidly through the air when the air is decidedly cooler than they are, whether because the air is actually cold, or because the heat liberated by the organisms in the flask accumulates. The total heat liberated, therefore, must be the sum of the heat lost through radiation, etc., plus that retained by the flask. By placing the flasks in a constant temperature, the rate, and therefore the amount, of heat-loss can be determined for each flask and each degree of difference in temperature.

Another factor to be reckoned before we can attempt even approximately to determine heat yields is the heat equivalent of each combination of apparatus. This work has revealed to me, as I never suspected before, the limitations of the ordinary thermometer as an instrument of precision. In the following determinations, as will be seen below, I have used the same thermometers and the same cotton plugs in the same flasks throughout the series of experiments, thus determining the heat equivalents of each calorimeter, consisting of thermometer, Dewar flask, and plug. Indeed, I kept the flasks in the same places on the wooden filter stands and even on the same spot on my table. These latter precautions are, however, strainings at gnats, for the camel of unavoidable error to be swallowed is very large, owing to the small size of the flasks.

The method followed to ascertain the heat equivalent of each set of apparatus was fundamentally as follows, although I modified one detail or another in the series of determinations which I attempted. Into a flask, the temperature within which is known and recorded, 200 cc. (100 cc. if the flask already contains 100 cc.) of warm distilled water, at a known temperature, are *quickly* poured; the temperature within the flask is again recorded, as soon as it has again become fairly stable. The fall in the temperature of the water poured into the flask indicates that the flask and the inclosed air, thermometer, and cotton plug, have taken up warmth from the water. If all the water could be delivered into the flask at the temperature recorded, the fall in temperature would indicate only the amount of heat taken from the water by the apparatus. But this ideal condition I have found practically unattainable.

Working with only 200 cc. of water, at the most, I have never been able to pour this water from the flask in which it was heated into the Dewar flask so quickly that no heat was lost. I used a thin-walled round flask for heating the measured quantity of water; I cut the neck of the flask to a length of 2 cm.; while being heated the flask was held by a small wooden test tube holder of the usual form; the thermometer for determining the temperature of the water remained with its bulb under water in the flask while it was heated; and I took pains not to let the flask touch anything after taking it from the flame, until it was emptied. By holding the flask with the wooden holder while the water in it was warming, I warmed the holder, and as wood is a non-conductor, I felt that I was taking the least possible heat from the water myself in pouring it. In these and in other ways, therefore, I have taken such pains as I could to reduce the inevitable error to its lowest terms; but the error in calorimetry is stated by LUTHER-OSTWALD to be about 1 per cent under the most favorable conditions, and with larger volumes of liquid than I have so far been able to use. A typical series of figures follows, with the averages of a considerable number of determinations for four calorimeters.

April 2, 1910	No. 11-5	No. 12-2	No. 14-6	No. 8-8
Temperature, empty	27.6°	29.2°	29.1°	28.7°
Add 200 cc.	45.0	42.0*	42.0	40.
Becomes	43.2	40.75	40.5	38.55
Loss	1.8	1.25	1.5	1.45
Calories lost	360.0	247.0	300.0	290.0
Gain temperature	15.6	11.55	11.4	9.85
Calories per degree	23.07	21.4	26.3	29.4

* Measured 197 cc.

The averages for four calorimeters follow:

No. 11-5, 15 determinations average	24.7	calories per °C.
No. 12-2, 15	"	"
No. 14-6, 10	"	"
No. 8-8, 13	"	"

The average of these four calorimeters is 25.6 calories per Centigrade degree. This means that the average calorimeter, consisting of a silvered Dewar flask of 250 cc. capacity made by Burger of Berlin, a long thermometer graduated to tenths of a degree, and a cotton plug suitable to close the neck of the flask, required a quan-

tity of heat represented by about 25 calories to warm its interior 1° C. Thus, if the temperature in one of these calorimeters goes up 10° C., about 250 calories had been taken by the apparatus itself. This is known as the "heat equivalent" of the apparatus, and is a quantity which must always be added or subtracted in determining the amounts of heat liberated or taken up by a given organism, process, or reaction.

In addition to the heat lost by radiation, etc., from the insulating calorimeter, and the heat absorbed by the whole apparatus (flask, thermometer, and plug) and the air contained by it, the material within the flask will also absorb heat. It is necessary, therefore, to determine the heat equivalents of the material worked with, whether these materials are seeds or solutions. The solutions may contain nutritious substances in which such organisms as bacteria, yeasts, or fungi are living. In any case, the heat equivalents of all the substances or materials involved in the experiment must be ascertained. Thus, on one day I weighed out six lots of air-dry peas of 75 gr. each, putting these in crystallizing dishes, which I covered with glass lids and kept for 24 hours at a temperature of about 18° C. Six Dewar flasks with thermometers and plugs, and containing some distilled water, were also placed under the same condition. After 24 hours I drained (but did not dry) the flasks, and put one lot of peas in each, reading the temperature of each. I assumed that the peas had in this time taken on a uniform temperature before being put into the flasks. The slight differences in temperature, therefore, were presumably due to slight differences in the temperatures of the flasks and to slight differences in the amounts of heat due to friction in pouring the air-dry peas into the flasks. Then I poured 100 cc. of warm distilled water at a known temperature into each flask and, when the temperature had become stable, recorded it. The data are as follow:

Flask	Therm.	Temp.	100 cc. aq.	Becomes	Loss
1.....	1	19.7°	57.0°	45.3°	1170 cal.
2.....	2	19.2	55.5	43.5	1200
3.....	3	19.3	56.0	44.2	1180
4.....	4	19.5	54.0	43.0	1100
5.....	5	19.8	52.0	41.2	1080
6.....	6	19.8	49.5	40.4	910

From these figures and from the previous determinations of the average number of calories required to raise each set of apparatus one degree in temperature, I calculated the number of calories required to raise 75 gr. of air-dry peas 1° . These figures and the average follow:

To raise 1° requires:

1=45.70	calories less average no. calories required to raise $1-1^{\circ}-11.62=34.08c$
2=49.38	" " " " " " " " " $2-1^{\circ}-13.25=36.13c$
3=47.78	" " " " " " " " " $3-1^{\circ}-12.81=34.97c$
4=46.80	" " " " " " " " " $4-1^{\circ}-13.49=33.31c$
5=50.46	" " " " " " " " " $5-1^{\circ}-11.67=38.79c$
6=44.17	" " " " " " " " " $6-1^{\circ}-10.54=33.73c$

Total		211.01c
Average to raise 75 gr. air-dry peas 1°		35.16c
" " " 1 gr. " " 1°		0.4688c

From this it appears that it takes 0.468 of a calory to raise one gram of air-dry peas 1° in temperature. A repetition of the experiment with the same apparatus and under similar conditions gave an average of 0.457 of a calory per gram of air-dry peas.

The same experiment was repeated on a later date with this modification; 6 lots of air-dry peas weighing 75 gr. each were put in the same 6 Dewar flasks and washed in a concentrated aqueous solution of mercuric bichloride. After rinsing twice with boiled distilled water, the peas were covered with 100 cc. of boiled distilled water in each flask, thermometers and cotton plugs were inserted as usual, and the whole allowed to stand for 24 hours in the laboratory. The temperatures in the flasks and in the room at the hours stated were as follow:

FLASK	MARCH 10, 1909			
	12:00 M.		2:00 P.M.	
1.....	16.0°	Room 18°	16.55°	Room 20.5°
2.....	16.0		16.50	
3.....	16.0		16.70	
4.....	16.8		17.20	
5.....	17.5		18.10	
6.....	17.5		18.05	

The next day the temperatures were recorded as below, and 100 cc. of warm distilled water at the temperatures reported were poured into each flask. Flask 5 exploded at this stage. The following figures indicate the heat equivalents of the five remaining lots of peas, and these yield an average of 1.41 calory per degree for 75 gr. of peas weighed air-dry and soaked for 24 hours in 100 cc. of boiled distilled water. This figure would be the sum of the heat equivalent of pea substance weighed air-dry and water, if no change had taken place in the substance of the peas during this interval of 24 hours in water; but assuming, for the moment at least, the correctness of the figure 1.41 calory per degree, one must realize that in this time germination had begun, and that the materials in the peas had begun to undergo changes, not only from absorption and the solution or dilution of the soluble substances in the peas, but from digestion and other metabolic processes. The figure 1.41 calory per degree, therefore, may be correct or approximately so, for peas which had been for 24 hours under conditions favorable to germination, and hence were not necessarily identical in composition with air-dry peas of the same variety.

MARCH 11, 1909, 9:30 A.M.; ROOM 15.75°

1.....	18.7°	100 cc. aq. 64.3°	Becomes 39.12°	Loss 2518 cal.
2.....	18.4	56.4	35.9	2050
3.....	18.4	60.2	37.8	2240
4.....	19.4	58.5	37.6	2090
5.....	19.3	Exploded		
6.....	19.4	56.0	35.7	2030

To raise 75 gr. peas soaked 24 hrs. *in situ* 1° requires:

1-123.11	calories less average for flask 1 and therm.	1-11.62=101.49 cal.
2-116.42-13.25	" " " " " 2 " " 2	=103.17 "
3-114.87-12.81	" " " " " 3 " " 3	=102.06 "
4-114.83-13.49	" " " " " 4 " " 4	=101.34 "
6-123.78-10.54	" " " " " 6 " " 6	=113.24 "
Average for 75 gr. peas soaked per degree		=106.26 "
" " 1 " " " " "		= 1.41 "

I think we are now ready to proceed to ascertain the heats liberated by peas from the beginning of germination until it has progressed for several days. An experiment was set up as follows:

March 26, 11:30 A.M.; room temperature 16.4° C. Five lots, 75 gr. each, of air-dry peas were kept in constant temperature room A for a week, in five Dewar flasks. Thermometers, bottles of boiled distilled water, and of saturated aqueous solutions of mercuric bichloride, had been placed in room A at the same time, and were therefore of like temperature. Each lot of peas was then thoroughly washed in the bichloride solution, rinsed twice with boiled distilled water, and covered with 100 cc. of boiled distilled water in each flask. (The rinsing water came from the laboratory and had a temperature 2° C. higher than that put in the flasks to start germination.)

The temperatures were:

Flask 1, therm. 1, 17.4°
“ 2 “ 2, 17.3
“ 3 “ 3, 16.9
“ 4 “ 4, 18.4
“ 6 “ 6, 17.5

MARCH 27, 10 A.M.; ROOM 16.25°

1.....	18.9°	-37.0 cc.	Absorbed 63.0 cc. aq.
2.....	18.7	-44.0	“ 56.0
3.....	17.55	-40.5	“ 59.5
4.....	18.3	-45.4	“ 54.6
6.....	18.4	-45.5	“ 54.5

I poured off the unabsorbed water in each flask as indicated above, showing that each lot of 75 gr. of air-dry peas had absorbed the number of cc. of water above stated. The rise in temperature in each flask showed the liberation of heat. Reckoning the heat equivalents already found of the pieces of apparatus, the peas, and the water, we find that there were liberated in each flask the following quantities of heat, plus whatever had been lost by radiation through the flasks, by leakage through the cotton plugs, etc., in the first 22.5 hours of the experiment, namely:

1.....	1.5°	218.55 calories
2.....	1.4	96.00
4.....	0.00	0.00
6.....	0.9	129.75
Average ..		130.68 calories

MARCH 28, 10 A.M.; ROOM 16.25°

	No.	Temp.	Gain in 24 hrs.	Total gain
1.....	23.8°	4.9°	6.4°	
2.....	24.7	6.0	7.4	
3.....	20.4	2.85	3.5	
4.....	21.2	2.9	2.9	
6.....	22.1	3.7	4.6	
Average.....		4.07	4.96	482.71

MARCH 29, 9:30 A.M.; ROOM 16.2°

1.....	32.3°	8.5°	14.9°	
2.....	38.55	13.85	21.25	
3.....	25.00	4.6	8.1	
4.....	25.9	4.7	7.6	
6.....	29.4	7.3	11.9	
Average.....		7.79	12.95	923.90

MARCH 30, 9:00 A.M.; ROOM 16.2°

1.....	39.0°	6.7°	21.6°	
2.....	45.1	6.55	27.80	
3.....	30.25	5.25	13.35	
4.....	31.8	5.9	13.5	
6.....	36.7	7.3	19.2	
Average.....		6.34	19.09	751.93

MARCH 31, 1909, 9:30 A.M.; ROOM 16.1°

1.....	40.9°	1.9°	23.5°	
2.....	50.8	5.7	33.5	
3.....	32.6	2.35	16.7	
4.....	32.3	0.50	14.0	
6.....	37.25	0.55	19.75	
Average.....		2.20	21.49	260.92

APRIL 1, 1909, 9:30 A.M.; ROOM 16.4°

1.....	41.3°	0.4°	23.9°	
2.....	52.55	1.75	35.25	
3.....	33.1	0.5	17.2	
4.....	30.7	-1.6	12.4	
6.....	34.8	-2.45	17.3	
Average.....		-0.28	21.21	-33.16

APRIL 2, 1909, 9:30 A.M.; ROOM 16.5°

1.....	44.3°	3.0°	26.9°	
2.....	53.3	0.75	36.0	
3.....	33.8	0.7	17.9	
4.....	30.6	-0.1	12.3	
6.....	33.7	-1.1	16.2	
Average.....		0.65	21.86	77.09

At this point the experiment was stopped and the flasks emptied. The peas in no. 4 showed practically no molding or fermentation. The odor was entirely pleasant, and the radicles of these germinating seeds were long and fine. Flask 2 was found to contain very rotten peas; the peas in flask 1 were fairly rotten; in flasks 3 and 6 the peas were about equally bad, but decidedly less rotten than in 1. This result agrees with the experience of HANNIG, who says: "Nach Erfahrungen des Referenten kann eine Sterilisierung von Samen durch Schütteln in Sublimatlösung alleine nicht erzielt werden, sondern nur dadurch, dass die Samen zuerst mit verdünntem Alkohol oder ausgekochtem Wasser behandelt werden, um die an den Spalten der Samen haftenden Luftblasen zu entfernen."⁵ Only experience led me to believe in the possibility of sterilizing by HANNIG's method. Owing to the long duration of these experiments, complete sterilization becomes as difficult as it is desirable. I find no help in this particular in SCHROEDER's recent paper,⁶ although for other plants and for briefer times his directions are most welcome.

Adding together the daily gains in heat, we find that, up to the sixth day, on which more heat was lost by radiation than gained in respiration, there had been liberated 2550 calories which had not been lost or converted into work. On the sixth day 33.16 calories more were lost in radiation (or otherwise) than had been liberated during that time in respiration. But when the experiment was stopped on the seventh day, this loss had been made up, and there had been an average total gain of 2593.63 calories in each flask, after all corrections for absorption of heat by the materials con-

⁵ Rev. in Zeitschr. Bot. 1:202. 1909.

⁶ SCHROEDER, H., Die Widerstandsfähigkeit die Weizen- und Gerstenkorns gegen Gifte und ihre Bedeutung für die Sterilisation. Centralbl. Bakteriöl. 2:28. 1910.

cerned had been made. This amounted to a gain of 370 calories per day, when the seven days are averaged, or 4.93 calories per day for each gram of peas. The comparative daily changes in room temperatures, flask temperatures, and the number of calories liberated, are shown on the accompanying diagram (fig. 5).

FIG. 5.—Graphic representation of the amount of heat liberated by germinating peas

A comparison of these figures with those of BONNIER's classical paper⁷ shows at once that my figures are lower than his. For example, he says (p. 12), "1 kilogramme de graines germant dégage en 1 minute 59 calories." The greatest average gain in heat in my experiment was on the fourth day, in which 923.9 calories were accumulated in 23.5 hours. Calling this 924 calories and 24 hours,

⁷ BONNIER, G., Recherches sur la chaleur végétale. Ann. Sci. Nat. Bot. VII. 18:12. 1893.

we get 8.55 calories per minute for a kilo of peas. But one sees at once that in BONNIER's experiments only short intervals of time were employed (36 minutes for the above quoted experiment), whereas my experiments lasted for nearly or quite one week. In fact, I made no effort to "break the record," and was not aware of the record until I figured my results in order to compare them with BONNIER's. I venture to think, however, that my experiments supplement those of BONNIER by showing the continued liberation and loss of great quantities of heat by germinating peas, and presumably by other plants or their parts, for a time and not merely minute by minute. I need hardly say that the experiment above described in detail is only one of many, the results of which are so similar that it is unnecessary to report them.

The quantity of heat liberated by certain animals

Having some curiosity about the liberation and loss of heat by animals, as compared with plants, I made the following experiments. One was with two salamanders lent me by the Department of Physiology of this University. I put them in separate drained Dewar flasks, and left them for 24 hours in the laboratory. The temperature in the flasks fluctuated with the room temperature, so nearly in the same way as if no animals had been in the flasks, that I did not continue the experiment. I report it with no further comment than this, namely, that the salamanders must have exhaled some warmth, but it was inappreciable.

The other experiment was very striking. Into cotton-plugged drained Dewar flask 14, which weighed 167.2 gr., I put a very lively mouse. The weight at the end of the experiment was 186.5 gr.; therefore, the mouse weighed 19.3 gr. As no excretion, solid or liquid, had taken place during the experiment, whatever loss of weight had occurred was due to exhalation and evaporation only. The thermometer readings for a half hour, beginning at once after putting the mouse in the flask, were as follow, the room temperature remaining stationary at 20° C.

During this half-hour of time, therefore, this mouse gave off by radiation and exhalation an amount of heat sufficient to raise the temperature within the apparatus 13.95° C. As previously stated,

the average of 10 determinations shows that it takes 24.8 calories to raise the temperature of flask 14, with thermometer 6 and a cotton plug, 1° C. Hence the heat *given off* by this mouse in 30

Time	Temperature	Time	Temperature
2:30 P.M.	22.6°	2:47.5 P.M.	32.0°
2:34 23.1		2:48 32.2	
2:35 24.3		2:48.5 32.4	
2:35.5 24.6		2:49 32.6	
2:36 25.1		2:49.5 32.7	
2:36.5 25.4		2:50 32.9	
2:37 25.7		2:50.5 33.1	
2:37.5 26.2		2:51 33.2	
2:38 26.4		2:51.5 33.6	
2:38.5 26.7		2:52 33.9	
2:39 27.1		2:52.5 34.1	
2:39.5 27.5		2:53 34.5	
2:40 27.9		2:53.5 34.8	
2:40.5 28.3		2:54 35.0	
2:41 28.7		2:54.5 35.2	
2:41.5 29.0		2:55 35.35	
2:42 29.2		2:55.5 35.5	
2:42.5 29.4		2:56 35.6	
2:43 29.6		2:56.5 35.7	
2:43.5 29.9		2:57 35.9	
2:44 30.1		2:57.5 36.05	
2:44.5 30.5		2:58 36.3	
2:45 30.7		2:58.5 36.1	
2:45.5 31.0		2:59 36.2	
2:46 31.2		2:59.5 36.4	
2:46.5 31.5		3:00 36.55	
2:47 31.7			

minutes amounts to 345.96 calories at least. This takes no account of the amount of heat lost in this time by this set of apparatus, being given off to the air; nor does it include any estimate of the heat retained by the body of the mouse. The body temperature of a mouse I do not know, nor do I know whether the body temperature rose during the experiment. This amount of heat, therefore, is simply what is absolutely lost to the animal, an amount equal to 11.19 calories per minute. The rise in temperature is indicated by fig. 6.

Does the age of the seed affect the heat yield?

I do not know that any successful attempt has been made to answer this question, in spite of the theoretical and practical importance which are evident on a moment's reflection. If the

heat yield bears a fairly uniform relation to the age of the seed, this may be the cause, or it may merely be the reflection or symptom or result of that chain of causes, which finally deprives the seed of its germinating power. Even so, it is important to determine whether this is the case or not. And if it can be shown that the

FIG. 6.—Rise in temperature in flask 14, in which a mouse was confined

heat yield is proportional, or inversely proportional, to the age of the seed, other things being equal, and a convenient method can be employed for determining this, we shall have, for the first time, a means of ascertaining the age and the viability of seeds. Those who have had any experience in buying seed have also known the

disappointment in fine-looking but worthless seed which failed to germinate. The Pure Food and Drugs Act has made it necessary to take fewer articles which come under its operation on faith or on the word of the dealer. But there being no convenient way of testing the quality of seeds, they are as unreliable as ever. It is highly desirable, therefore, from a practical standpoint, to have a method of testing seeds as to their germinating power. Such a method must be reasonably accurate and convenient. I believe it will be found that Dewar flasks may be adapted to this use, and I wish to furnish a certain amount of evidence now in favor of this belief, hoping to be able to determine the matter before long.

Peas retain their germinating power much longer than many other seeds, longer than the ordinary grains, for example.⁸ They are even less suitable, therefore, for experimental investigation of this matter than many other seeds. I happen to have in my laboratory, however, peas bought in 1908, 1910, and 1911. Each lot must have been of the preceding year's crop, or older; but owing to the large yearly demand for pea seed, probably very little old stock of this sort is carried over, and I believe, therefore, that the seeds in my laboratory are, most of them at least, of the crops of 1907, 1909, and 1910. The variety is commercially known as "American Wonder," an "extra early." The following table shows the behavior of these three crops in Dewar flasks this year, in constant temperature room A. The flasks and thermometers were sterilized by washing with concentrated aqueous solution of corrosive sublimate, and subsequently rinsed three times with sterile distilled water. The peas were weighed, air-dry, in 80 gr. lots and put, with 100 cc. boiled distilled water, in each of the flasks to be used. The boiled water and the peas, as well as all the parts of the apparatus, were kept in the constant temperature room for at least 24 hours before an experiment was set up. The water was drawn off at the end of the first day.

To this table I should like to add the figures reported in my first paper describing the use of Dewar flasks as respiration calorimeters,⁹ for these figures were obtained by using the same 1907 crop of peas.

⁸ PFEFFER, W., *Pflanzenphysiologie* 22: p. 327 and the literature there cited.

⁹ PEIRCE, G. J., A new respiration calorimeter. *BOT. GAZ.* 46:199. 1905.

JANUARY 19-23, 1911; CROP OF 1910

		1st day	2d day	3d day	4th day	5th day
Flask 7.....	17.8°	18.7°	21.8°	27.8°	31.1°	
Flask 8.....	17.8	18.5	22.3	26.9	31.5	
Flask 13.....	17.7	18.5	22.4	26.4	33.0	
Average gain		1.33	4.93	9.8	14.63	

JANUARY 25-28, 1911; CROP OF 1909

Flask 9.....	17.0°	17.9°	22.7°	25.3°		
Flask 10.....	17.5	18.4	23.7	26.4		
Flask 11.....	17.1	19.0	23.1	24.9		
Flask 12.....	17.0	18.0	24.2	27.9		
Flask 13.....	17.0	19.5	25.15	28.1		
Average gain		1.44	6.72	9.4		

JANUARY 31-FEBRUARY 5, 1911; CROP OF 1907

Flask 10.....	17.2°	17.8°	21.8°	25.8°	29.1°	32.8°
Flask 11.....	17.1	17.8	19.4	23.7	23.6	25.2
Flask 12.....	17.1	17.6	19.3	21.3	23.2	24.4
Flask 13.....	17.2	17.8	22.2	26.8	30.8	35.4
Average gain		0.6	3.52	7.25	9.52	12.3

It should be said that the following temperatures were obtained under the far from uniform conditions of the laboratory, for I did not at that time have a constant temperature room.

APRIL 29-MAY 2, 1908; CROP OF 1907

Flask 1.....	22.7°	27.0°	33.4°	36.8°		
Flask 2.....	21.6	25.7	35.1	40.5		
Flask 3.....	22.1	27.3	35.3	41.4		
Flask 4.....	22.4	27.4	35.0	38.8		
Flask 6.....	22.3	26.5	34.5	40.0		
Average gain		5.56	12.44	17.3		

Assuming the correctness of these figures (and both the 1908 and 1911 figures above given are among many that might be given) and making all due allowances for the differences in temperatures between the laboratory and the constant temperature room, one must admit there appears to be a decided difference in the amounts

of heat given off. The flasks used in 1908 were inferior as insulators to those in use in 1911; hence the 1908 figures are not as high as they would have been if more efficient insulators had been employed. So far as these figures show, therefore, it appears that the amount of heat liberated by germinating peas decreases with

FIG. 7.—Heat yields of peas of different ages

their age. If this be true, the amount of heat liberated may then be used as the index of the age or freshness of seeds.

The accompanying diagram (fig. 7) represents the above figures in the form of curves. The difference between the curves of 1907 peas in 1908 and 1911 is even more striking than the figures on which they are based.

It does not by any means follow that the other processes of the

plant decline proportionally with the liberation of heat. Experience shows that old seeds germinate less well than fresh. The foregoing experiments show that the heat yield is less in old than in fresh peas. One record of mine, made up of many measurements, connects growth with these other two processes.

FIG. 8.—Lengths of seedling peas of same number of days' growth, but of different age of seed.

Peas which had been sprouted and kept for four days in Dewar flasks were subsequently put in moist sand to continue germination. The peas were of two lots, those of the 1907 crop and those of the 1909 crop. One week later they were carefully taken up and measured. The average length of the 1909 seedlings was 9.70 cm., of the 1907 seedlings 3.52 cm. The latter is scarcely more than 60 per cent of the former. The seedlings from the older seeds made less than two-thirds the growth of the seedlings from fresher seeds in the same length of time and under the same conditions. The accompanying diagram shows this graphically (fig. 8).

If the result just now described were not consistent with the difference in heat yields according to the age and freshness of pea seeds, I should place no reliance whatever on it. As it is, I do not understand why I did not test such an interesting result by repeated experiment, but I have not yet done so. The question seems to me to deserve further examination.

The possible significance of heat liberation in respiration

From the foregoing experiments, whether on germinating seeds or on warm-blooded animals, it appears that there is a much greater release of energy in the form of heat than can be or is used as such by the organism. Admitting that, under the extraordinary conditions of the experiment, the mouse previously described may not have behaved normally in any respect, and that the production and loss of heat may have been excessive, it is nevertheless evident

that the loss of heat by a warm-blooded animal is very great. When we reflect that all of the heat lost is liberated from the food of the animal, that the loss by radiation will vary with the temperature of the environment and the efficiency of the animal's covering as an insulator, whether this be hair, feathers, subcutaneous fat, or clothing, and that the loss by exhalation will also vary with the rate of exhalation, then we must realize that very much of the heat liberated in respiration is lost. What percentage this is in the case of a mouse I do not know, and it is hardly necessary to know at the moment. It is evident that if the liberation of heat is the essential result of respiration, respiration must be an excessively wasteful process.

Having once conceived respiration to be primarily for furnishing the living organism with energy in the form of heat, I am constrained now to regard it very differently. That it is the chief means of liberating energy still seems to me most probable; but apart from the production and maintenance of a body temperature apparently most favorable to the other functions collectively, the liberation of heat in respiration appears to be wasteful. It may be as useless as it is inevitable.

The material products of respiration vary with the food, with the materials oxidized, directly or indirectly, in the body. Intracellular respiration, or the catabolic processes, the end products of which are oxides and heat, may not only produce within the cell the optimum temperature for its activities and liberate energy at once converted into work, but they may also neutralize (destroy) substances which would otherwise be or become injurious to it. The oxidation of these substances would necessarily be accompanied by heat liberation. The heat thus liberated must be either converted into work or given off, lest again the organism suffer. We may, therefore, conceive the heat liberated in respiration to be of two sorts: a part of it useful in certain organisms, or even certain cells, in maintaining a bodily or cellular temperature which is the optimum or so-called "normal"; and another part, in excess of this first part, which is waste, to be gotten rid of as promptly as any other waste. It is a dangerous product, as the organism in fever shows.

We may, then, regard the end products of respiration, the

oxides and the heat, as wastes. Although inevitable they are not essential; some of them, possibly all, are dangerous, and for this reason to be eliminated as quickly as possible.

The bodies of animals are compact masses compared to the bodies of plants. From the extensive surface of the plant body radiation is rapid; from the limited surface of the higher animals, it is slow. The plant needs no forced draft to carry off its waste heat; the massive animal does. The submersed animal is in a medium which quickly absorbs heat; it needs little else than the water it lives in to relieve it of its waste heat, as well as its waste oxides. Its simple circulatory system is adequate. But air absorbs little heat; it is indeed a fair insulator as compared with water, as the bather in cold water knows by experience.

The liberation of heat may be used, like carbon dioxide, by the physiologist as a gauge of the activity of respiration, but like carbon dioxide, it must be regarded by him as an end product, a waste, and not the essential product. The essential product of respiration may be energy, but if so, it is that energy which is immediately convertible, and is converted into work by the organism. On the other hand, respiration may be essentially a process of purification, in which useless or injurious substances are converted into forms which can be eliminated. The liberation of energy accompanies these oxidations. Some of this energy may be useful and used; much of it is useless and is eliminated. Elimination by radiation is sufficient in organisms of extensive area in proportion to their mass. Radiation is insufficient for organisms of small area in proportion to the mass. In these the circulatory and so-called respiratory systems are employed to eliminate heat as well as the material products.

In this study of heat liberation, therefore, I believe I have been occupied with an unessential, although inevitable, feature of the process of respiration. The essential part of the process of respiration is much more likely to be found to be chemical and not physical. And if this is made any more evident by this study, my work is not in vain.

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