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The Available Energy of Timothy Hay

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The increasing interest and importance attaching to the study of the nutrition of domestic animals, as well as of man, from the standpoint of the energy involved induced the Pennsylvania Experiment Station to undertake the construction of a respiration-calorimeter upon the plan devised by Atwater & Rosa, bnt enlarged and modified to admit of experiments upon cattle. In the construction and operation of this expensive apparatus, the Station has enjoyed the cooperation of the Bureau of Animal Industry of the U. S. Department of Agriculture, and with the permission of its Chief, Dr. D. E. Salmon, the following preliminary report of some of the results is presented. Acknowlegment should also be made of the skill and faithfulness of our assistants, Messrs. C. W. Norris, J. B. Robb, T. M. Carpenter and N. W. Buckhout, in the execution of the laborious respiration and calorimetric experiments and of the cooperation of the Chemical Division of the Station, under the direction of Dr. Wm. Frear, in the examination of feeds and excreta, Dr. C. A. Browne, Jr., having had general charge of the reception and care of samples and having executed the determinations of carbon and hydrogen, while the determinations of heats of combustion have been made by Mr. Norris.

The experiment constitutes a study of the energy-content of timothy hay (this material having been selected because it constitutes a fairly definite farm product) and of the use made of this energy in the organism of cattle. Although few in number, the results seem to us worthy of consideration in the light of suggestions for further investigation, while they possess a certain interest also as being, so far as we are aware, the first direct determininations of the heat production of a farm animal.

At the outset, one or two definitions seem desirable. The heat of combustion of a material like timothy hay measures the total amount of kinetic energy which we can obtain from it. This quanity is commonly spoken of as the potential energy or "gross energy" of the hay. By no means all of this gross energy is capable of being used by the animal organism. A considerable proportion of it reappears as potential energy in the various excreta, solid, liquid and gaseous, of the animal, and therefore escapes from the body entirely unused for its purposes. By subtracting the quantity of potential energy thus rejected by the body from the total amount supplied in the food we obtain the amount which is capable of conversion into the kinetic form in the organism. This portion has been somewhat commonly designated as "available" energy, or more specifically as "gross available" energy to indicate that it represents the maximum amount available for any purpose. We shall see presently, however, that there are not wanting indications that a portion of this so-called available energy may in some instances be of no direct use to the organism; that is, that it may neither serve immediately to maintain the vital processes nor add to the store of potential energy in the body, but simply increase the heat production of the animal. We therefore venture to propose the substitution for the term available energy, of the term *metabolizable* energy as equivalent to energy of food minus energy of excreta. Although not particularly euphonious, this term has the advantage of expressing the facts of the case, while avoiding any implications regarding the uses to which this energy is put in the body, as well as the necessity of using the word available in two senses.

Rubner's well-known experiments[1] with dogs and

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[1]Zeit. f. Biol., 19, 312.

other animals showed that, at or below the maintenance requirement, nearly pure nutrients could be substituted in the metabolism of the animal for the ingredients of body tissue, and that they were valuable for this purpose approximately in proportion to their metabolizable energy as above defined. For example, Rubner found that when nearly pure proteids were given to a fasting dog, the amount of proteids destroyed in the body was largely increased, but that a correspondingly smaller amount of fat was oxidized, and further that the proteids replaced fat in inverse proportion to their content of metabolizable energy. Under these conditions there was, of course, no increase in the total amount of heat produced in the body but simply a substitution of one kind of fuel for another. Rubner experimented with fats and carbohydrates as well as with proteids and found the same law to hold, while in a single experiment he also substituted carbohydrates for fats in the food in a corresponding ratio. This law of the substitution of nutrients in the manner just indicated is called by Rubner the law of isodynamic replacement and the relative values of the nutrients as deduced from it, isodynamic values. Rubner experimented chiefly with carnivora, but his law has been generally assumed to apply to all animals. Thus Kellner[2], in his extensive investigations upon cattle, regards the results which he obtained for the metabolizable energy of various materials as representing their value as part of the maintenance ration and speaks of them as replacement values (*Vertretungswerte*).

It has been well established by the investigations of Zuntz and others that there is a not inconsiderable expenditure of energy in the digestion and assimilation of the food. This energy must ultimately assume the form of heat in the body, the amount of heat produced depending on the kind and amount of food consumed. This would seem to imply an *increase* in the heat production with increasing quantities of food, and therefore to contradict the law of isodynamic replacement. Rubner explains this apparent discrepancy by the

[2] Landw. Vers. Stat., **53**, 440.

hypothesis that the heat into which the energy expended in digestion and assimilation is ultimately converted is substituted in the body for an equivalent amount of heat which would otherwise be produced by oxidation of body substance, so that there is no increase in the total heat production.

Rubner's conclusions have exerted a profound influence upon the science of nutrition, but at the same time their value lies more largely in the point of view which they opened up than in their exact numerical accuracy. As just stated, isodynamic replacement implies that there is no increase in heat production with an increasing amount of food. As a matter of fact, however, the great majority of Rubner's experiments do show more or less increase in the heat production, the only exceptions being a single experiment with fat, and three or four upon cane sugar, some of which Rubner himself considers of doubtful value. From theoretical considerations the writer has been led to question the entire applicability of Rubner's law to herbivorous animals, and especially to ruminants with their large expenditure of energy in digestive work, and the experiment here reported was planned to test the equivalence of the metabolizable energy of hay and that of body tissue.

Four different amounts of timothy hay, with the addition of a small uniform amount (400 grms.) of linseed meal, were fed to the same steer, weighing about 400 Kgs. Each ration was fed for two weeks, during the second of which the visible excreta were collected quantitatively and during which the animal passed 48 hours in the respiration-calorimeter at the uniform temperature of 18.2° C. for the determination of gaseous excreta and heat production.

Passing over the details of the experiments, only the final results as regards energy are presented here, as follows:—

	Period A.		Period B.		Period C.		Period D.	
	Outgo Cals.	Income Cals.	Outgo Cals.	Income Cals.	Outgo Cals.	Income Cals.	Outgo Cals.	Income Cals.
Feed		14923		20297		25198		29647
Excreta:								
Feces	6446		8590		11477		14276	
Urine	863		974		1125		1220	
Methane	996		1251		1374		1896	
Metabolizable	*6618*		*9482*		*11222*		*12255*	
	14923	14923	20297	20297	25198	25198	29647	29647
Metabolizable		6618		9482		11222		12255
Heat produced	9067		10206		10606		11183	
Gain or loss		*2449*		*724*	*616*		*1072*	
	9067	9067	10206	10206	11222	11222	12255	12255

Comparing the four periods, we note at once that with increasing amounts of feed the heat production also shows a material increase, which should not be the case if isodynamic replacement took place in accordance with Rubner's theory.

Proceeding now to consider the results quantitatively, we may for simplicity set aside the energy of the excreta and compare directly the amount of metabolizable energy

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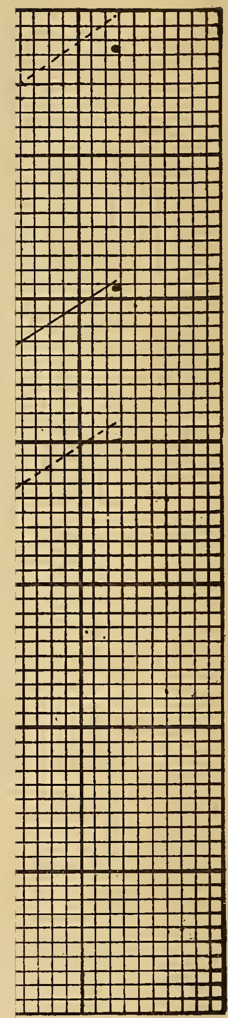


12000 Cals. 13000 Cals.

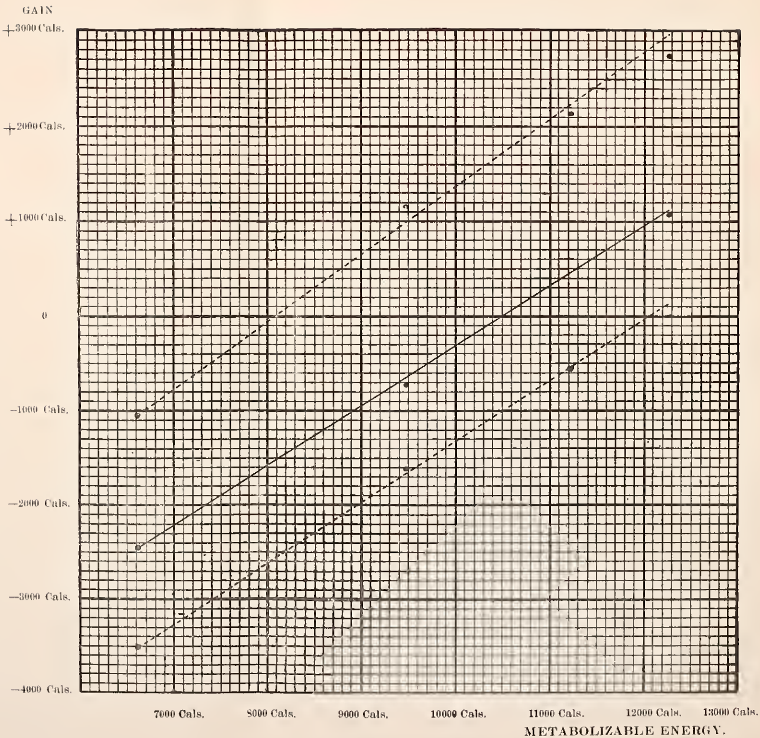
IZABLE ENERGY.

furnished the animal in each period with the nutritive effect produced. This effect is measured by the extent to which loss of tissue was prevented below the maintenance ration, or by the increased gain above maintenance, and may be compared in the different periods by regarding the ration of Period A as a basal ration and subtracting the results for that period from those of the other three.

Thus, comparing Periods A and B, we find that in Period B 2864 Cals. of metabolizable energy were added to the basal ration and diminished the loss of tissue by 1725 Cals., or in other words that 60.24 per cent. of the additional metabolizable energy supplied was used for maintenance, while 39.76 per cent. gave rise to the production of heat which was in excess of the needs of the animal, so far as maintaining the body temperature was concerned, since the normal temperature was maintained on the lesser supply of metabolizable energy.

The results of similar comparisons for each of the three periods are contained in the following table, and are also represented graphically by the full line in the accompanying diagram, in wnich the abscissae represent the quantities of metabolizable energy supplied to the animal and the ordinates the resulting gain or loss of energy by the body. The points show the results for each period and the line the average result:

	Metabolizable Energy. Cals.	Gain of Tissue. Cals.	Gain in per cent. of Metabolizable
Period B	9482	— 724	
" A	6618	—2449	
Difference	2864	1725	60.24
Period C	11222	+ 616	
" A	6618	—2449	
Difference	4604	3065	66.57
Period D	12255	+1072	
" A	6618	—2449	
Difference	5637	3521	62.46
Average			63.09


GAIN
+3000 Cals.
+2000 Cals.
+1000 Cals.
0
-1000 Cals.
-2000 Cals.
-3000 Cals.
-4000 Cals.
7000 Cals.
8000 Cals.
9000 Cals.
10000 Cals.
11000 Cals.
12000 Cals.
13000 Cals.
METABOLIZABLE ENERGY.

It is obvious that in each case a considerable proportion of the metabolizable energy of the added food was used for other purposes than the maintenance of body tissue, the amount thus expended ranging, in round numbers, from 33% to 40%, and averaging 37%. In other words, the metabolizable energy of the hay had only about 63% of the nutritive value which the theory of isodynamic replacement would ascribe to it. The same fact is, of course, indicated in the graphic representation by the fact that the line representing the average results make an angle of more than 45 degrees with the vertical.

The facts that the external conditions, particularly temperature and relative humidity, were almost absolutely identical in the four periods, and that the smallest amount of heat produced was sufficient to prevent any material fall of body temperature for two weeks, seem to negative the supposition that the additional heat evolved in the later periods was a mere production of heat for its own sake.

There was no noticeable difference in the several periods as regards the muscular activity of the animal, with the exception of differences in the amount of time passed respectively in the standing and lying posture. This difference, however, was not inconsiderable, the number of minutes per 24 hours passed in the standing position ranging, during the eight days of the respiration trials, from 675 to 1026. The muscular exertion necessary to maintain the standing posture is an important source of heat. In this experiment the amount of heat given off from the animal by radiation and conduction and brought out of the calorimeter in the water current has been computed separately for the periods when the animal was standing or lying, omitting from the computation all periods of less than three hours. The ratio of heat given off while lying to that given off while standing was as follows:

Period A	1 : 1.321
Period B	1 : 1.332
Period C	1 : 1.296
Period D	1 : 1,286

We have no means of comparing in a similar way the heat given off by the animal as latent heat of water vapor. If, however, we make the not improbable assumption that this amount was proportional to that given off by radiation and conduction, we may compute the total amount of heat produced respectively in the lying and the standing position per minute or per 24 hours with the following results:

HEAT PRODUCTION (PER 24 HOURS).

	Observed. Cals.	Computed Lying. Cals.	Computed Standing. Cals.
Period A	9067	7664	10125
" B	10206	8325	11088
" C	10606	9086	11772
" D	11183	9512	12232

Comparing these computed amounts of heat, we can also compute the gain or loss of tissue and its relation to the metabolizable energy supplied, in the same manner as before, with the results contained in the following tables and represented by the broken lines in the diagram:

	Metabolizable Energy. Cal.	Gain, Lying. Cal.	Gain in per cent. of Metabolizable
Period B	9482	+1157	
" A	6618	−1046	
Difference	2864	2203	76.92
Period C	11222	+2136	
" A	6618	−1046	
Difference	4604	3182	69.12
Period D	12255	+2743	
" A	6618	−1046	
Difference	5637	3789	67.22
Average			71.09

	Metabolizable Energy. Cal.	Gain, Standing. Cal.	Gain in per cent. of Metabolizable
Period B	9482	—1606	
" A	6618	—3507	
Difference	2864	1901	66.51
Period C	11222	— 550	
" A	6618	—3511	
Difference	4604	2961	63.31
Period D	12255	+ 23	
" A	6618	—3511	
Difference	5637	3534	62.70
Average			64.51

According to these figures, if our animal had passed all his time in the recumbent posture he would have gained upon each ration except the first one, while, on the other hand, if he had spent all his time standing, he would have lost upon every ration except the heaviest. It is scarcely necessary to do more than call attention to the practical importance attaching to this large difference between the metabolism of the animal in the two positions. Its bearing upon the differences observed in the productive power of different animals, as well as upon questions of practical management, is obvious.

But while the absolute results thus computed differ materially from each other and from those actually observed, the elimination in this way of the influence of varying amounts of muscular exertion does not materially affect the main result. There is still a large percentage of the metabolizable energy which is not used for constructive purposes, although the proportion appears to be somewhat less when lying than when standing. The most natural supposition is that this energy is expended in the digestion and assimilation of the food. Apparently the amount of heat thus produced, even on the lowest ration, was so large as to reach or pass the limit of possible substitution for heat which would otherwise be produced by the oxidation of tissue. As food was added above this amount, the heat resulting from its digestion and assimilation was necessarily in excess of the needs of the organism under the conditions of the experiment and became simply an excretum.

If this interpretation of the results is correct, it has important theoretical bearings. It becomes evident, in the first place, that the maintenance requirement of cattle is a question of tissue replacement rather than of heat production, and, therefore, that the value of a given feeding stuff for maintenance depends upon the availability of its energy. We may, for instance, regard it as at least very probable that the work of digestion and assimilation in the case of a material like corn meal would be materially less than in the case of hay; or, in other words, that a larger percentage of its energy would be availab e for the maintenance of tissue. It would follow from this that in case of a ration consisting largely of grain a less amount of material or of metabolizable energy would be required for maintenance than in the case of a ration consisting exclusively of coarse fodder. In other words, the maintenance ration is a variable rather than a constant, depending upon the kind of food used. It may be noted that this conclusion has already been indicated by the experiments upon the maintenance ration of cattle made at this Station in 1896–7.[3]

Furthermore, if the heat production upon the maintenance ration is in excess of the requirements of the animal, it seems unlikely that small variations in the stable temperature to which the animal is exposed will have the effect upon the maintenance requirement which is ordinarily attributed to them. Still less is this likely to be the case with fattening cattle, where the amount of food and the consequent heat production are largely in excess of the maintenance ration.

Another important point indicated by our results is that the availability of the metabolizable energy of the food for tissue building is approximately constant within the range of the experiment, or, in other words, that the gain is a linear function of the amount of metabolizable

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[3]Bulletin 42, p 159.

energy supplied. While this is not exactly true, the variations from it, as shown by the diagram, are comparatively small, and probably within the limits of experimental error. We should anticipate that the *muscular* work of digestion would be approximately proportional to the total dry matter supplied. As the figures show, the proportion of the total energy of the hay which was found to be metabolizable diminished as the amount was increased, the difference arising chiefly from differences in digestibility. Since, nevertheless, the total expenditure of energy in digestion and assimilation appears to be approximately proportional to the metabolizable energy, it seems evident that a large share of this expenditure must be for the work of assimilation. Probably a very large factor in it is the loss of energy in the methane fermentation.

Still another indication afforded by our results is that the availibility of the metabolizable energy was substantially the same above and below the maintenance requirement. This is indicated both by a comparison of the actual results in Periods C and D, and also by a comparison of the computed results lying and standing. We might anticipate that the conversion of the assimilated food into tissue would require a still further expenditure of energy, and that consequently the availability above the maintenance requirement would be less than that below it. Our experiments, as noted, afford no clear indication of such a difference; indeed the availability above the maintenance requirement, as computed from from the results while lying down, is greater than that below the maintenance requirement as computed from the results while standing, In view, however, of the assumptions involved in the computation, too much weight should not be laid upon this point, and we present it rather as a suggestion for future research than as a conclusion. It may be noted also in this connection that Kellner's experiments in which meadow hay was added to a basal ration showed a utilization of the metabolizable energy for fattening of less than 42 per cent, as compared with the 63 per cent. of availability found in our experiments.

The results of our work, then, may be briefly summarized as follows, it being understood that they are presented tentatively, and that they apply primarily to the conditions of this experiment, namely, a rather high stall temperature and comparatively light rations consisting chiefly of coarse fodder:

1. The nutritive value of timothy hay, either for maintenance or production, was not measured by its metabolizable energy, but was in every case materially less. In other words the digestible nutrients of the hay did not replace body tissue in isodynamic proportions.

2. The work of digestion and assimilation in the case of timothy hay appears to be so great that at, or even below, the maintenance requirement, the heat production of the animal is in excess of the amount needed for the maintenance of body temperature.

3. The availability of the metabolizable energy of timothy hay, within the range of these experiments, appears to be a linear function of its amount.

4. The experiments afford no clear indication that the availability is less above than below the maintenance requirement.