

NUTRITIONAL FACTORS INVOLVED IN WOOL PRODUCTION BY MERINO SHEEP

I. THE INFLUENCE OF FODDER INTAKE ON THE RATE OF WOOL GROWTH

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Summary

The rate of wool growth (weight of wool produced per unit time), determined in seven sheep subjected to four levels of food intake, increased 400-600 per cent. from the lowest to the highest level of feeding and this change was reflected in both the mean length and in the mean diameter of the fibres, the relationship between these variables being characteristic of the individual sheep. The fibre diameter distributions were also affected, the individual fibres responding up to the limit of their capacities in proportion to their cross-sectional areas.

The nutritional factors involved in these changes were assessed from complete energy and nitrogen balances and the findings were interpreted in light of existing knowledge of the physiology of amino acid utilization.

From the amino acid constitutions of the proteins in the diet and in the main products of these transactions (wool and flesh) it was estimated that the cystine and methionine content of the protein of diet 541 would limit to 27 per cent. the efficiency of its conversion to wool. Under the conditions of the experiment the efficiency of the utilization of the sulphur-containing amino acids for wool production was at its highest, 47 per cent., when the best wool producer was in strongly positive energy balance, and at its lowest, 14 per cent., when the poorest producers were close to energy equilibrium.

From these observations it was concluded that a Merino sheep grazing on natural pastures would rarely, if ever, exhibit its full wool producing propensity and, as a corollary, that the rate of wool production by a grazing sheep would vary considerably with the seasonal changes in its nutritional environment, and that this would be reflected in its wool staple. Experimental evidence to support this conclusion is submitted.

I. INTRODUCTION

The ultimate nutritional conditions that determine the rate of wool growth are, with little doubt, the concentration and composition of the assemblage of amino acids in the tissue-fluids which surround the wool follicles. The quota of the amino acids and simple peptids absorbed from the intestine which thus eventually becomes available to serve as a substrate for wool production is influenced by physiological interactions that might be expected, *a priori*, to alter with the nutritional state of the sheep.

The supply of amino acids is determined initially by the quantity and quality of the protein ingested in the fodder, and this, under certain circumstances, may be augmented with amino acids from the digestion products of the protein elaborated from simpler nitrogenous substances by the microflora of the rumen; its fate,

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however, depends mainly on the state of the energy balance of the animal. When the energy requirements are met completely by the oxidation of constituents other than the protein of the ration, the supply of substrate is influenced according to whether the relative rates of absorption and of utilization by synthetic processes allow the concentration of amino acids in the blood stream to rise above the deamination threshold. The quota that escapes deamination serves the organism's demands for amino acids, and, at any level of nitrogen equilibrium, may be depleted by the protein syntheses involved in growth, pregnancy, and lactation – with which processes the proliferating cells in the follicles would have to compete. When the available energy of the ration approximates closely the energy dissipated by the animal, the protein digestion products are drawn on heavily to serve as fuel, and so the removal of amino acids from the systemic circulation for this purpose seriously depletes the substrate. When the animal is frankly in negative energy balance and is drawing on its own tissues to make up the deficit, the factors that determine the amino acid supply to the follicles are influenced by the increased nitrogen turnover arising from the hydrolysis of tissue proteins. Under these circumstances, the supply of substrate may be augmented; if the concentration of protein in the fodder is low and the ration is reduced to a level that is grossly insufficient to meet the energy requirements, the rate of wool growth tends to increase for a period above that which prevailed when the ration was just enough to maintain the animal in energy equilibrium.

These considerations of the intermediary metabolic processes known to be involved in the utilization of amino acids indicate that the nutritional factors which primarily influence wool production are the protein available from the ration, the quality of this protein, and the intake of other dietary constituents which are capable of providing for the energy demands* of the animal. The former variables determine the total substrate of amino acids and its composition, and the latter that portion of it which eventually becomes available for the competing protein syntheses involved in wool production, growth, pregnancy, lactation, etc.

The experiment described below, which was designed originally to study changes in the energy transactions of the sheep at different levels of feeding, afforded an opportunity to estimate the influence of nutrition on wool production under conditions in which there was a precise knowledge of the state of the energy balance. It provided also a means of assessing the magnitude of the processes that compete for the amino acids absorbed from the fodder.

As the composition of the diet in these experiments was constant, both the available energy and available protein altered proportionately when the level of intake was changed.

* It is not feasible to estimate directly the actual amount of energy that is dissipated by the synthetic processes involved in wool production, but from what is known of the thermodynamics of amino acid condensations this should be small. The amount of metabolizable energy which is drawn upon for wool production *per se* is thus unlikely to exceed materially the combustible energy of the wool fibre and of the secretions which accompany it—a quantity which in these experiments was never more than 3 per cent. of the metabolizable energy derived from the rations.

II. EXPERIMENTAL PROCEDURE

The animals that were employed, the experimental regime to which they were subjected, the diet on which they were fed, and the various procedures that were used to determine their nutritional status have been described in a previous paper (Marston 1948). In brief, seven strong-wooled (Anama strain) Merino ewes were fed with a fodder, diet 541 (a mixture of 5 parts of crushed wheat, 4 parts of chaffed lucerne hay, and 1 part of cane molasses, compressed into pellets) at 4 levels which ranged in stages, according to the available energy intake, from approximately $\frac{1}{2}$ maintenance to 2 maintenance. In the following discussion, periods, 1, 2, 3, and 4 refer to the 14 days of the 9th and 10th weeks on the approximate levels of fodder intake $\frac{1}{2}$, 1, $1\frac{1}{2}$, and 2 maintenance, respectively — they do not indicate the order in which the fodder was presented to the animals. Complete energy and nitrogen balance sheets were derived from the analytical data.

The comparative wool growth was determined directly. The wool produced on 15 cm. x 10 cm. areas delineated by tattoo on either shoulder of each individual was collected at fortnightly intervals by shaving; it was treated as previously described (Marston 1935). The total wool production was computed from the dry weight of wool collected, the skin area ($A = 0.117W^{0.59}$ where A = skin area in m.², and W = wt. in kg. of the ewe fasted 72 hr. from maintenance level) and the predetermined ratio of the wool grown per unit area on the patch to that grown over the whole skin area which, for this strain, was close to 1.4.

The mean fibre diameters of the samples were determined by measuring the sharply focused, magnified image (500x) of the dry fibres embedded in cedar oil. In each case, 1,000 fibres were measured at random.

III. RESULTS

(a) *The Rate of Change in the Wool Growth Supervening on an Alteration of the Level of Feeding*

Preliminary experiments indicated that an alteration in the rate of wool growth followed immediately a change in the level of fodder intake, but it was evident that a considerable period elapsed before the rate of wool production became constant. In the main experiment here under discussion, the ewes were fed at each level for a period of 10 weeks, the collections from which the balance data were derived being made over the 14 days of the 9th and 10th weeks of this cycle. The wool was collected from the tattooed areas at fortnightly intervals throughout and the data derived from these consecutive collections proved conclusively that equilibrium between the level of intake of this particular fodder and the rate of wool production became established only after the lapse of 3 months, or more, subsequent to the relatively large changes in the level of feeding that were imposed.

This phenomenon is illustrated in Figure 1 by the performance of two typical cases, No. 572 and No. 547, selected at random from the experimental animals. Prior to the experiment, both had been fed for some months on rations

which ensured a slight positive energy balance, and under these conditions ewe No. 572 produced 1.62 g. wool/150 cm.²/14 days and ewe No. 547, 1.70 g. wool/150 cm.²/14 days on the tattooed areas. At the beginning of the experiment the fodder was changed to diet 541 which was fed at the 2M level to No. 572 and at the $\frac{1}{2}$ M level to No. 547. The rate of wool production of the former increased, and that of the latter decreased, but it is clear from the observations of the wool grown in the subsequent periods (Fig. 1) that in neither case was a steady state rapidly attained. Although the food intake was constant for each 10-week

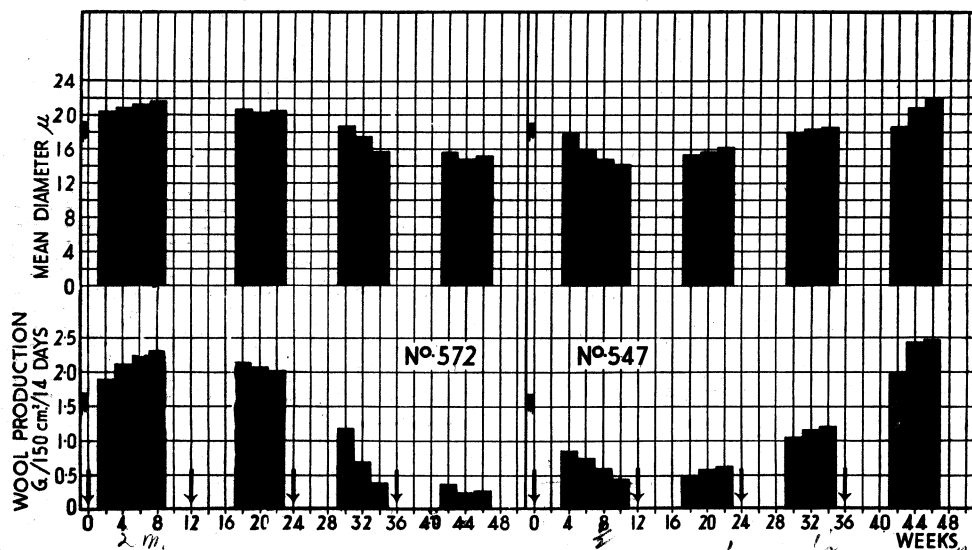


Fig. 1.—The relative slowness in the establishment of an equilibrium between food intake and the rate of wool growth is shown. The fodder was changed at 0 weeks to diet 541 which was fed to No. 572 at 2M level and to No. 547 at $\frac{1}{2}$ M level. The rate of wool growth continued to change for a considerable period after each alteration of fodder intake and tended slowly to approach an asymptote which would imply a state of nutritional equilibrium. This phenomenon supervenes on each alteration of fodder intake level (indicated by arrows). The levels of intake were approximately 2, $1\frac{1}{2}$, 1, and $\frac{1}{2}$ maintenance in respect to the energy available from the ration. The changes for No. 572 were made at intervals of 12 weeks in that order and for No. 547 in the reverse order.

step, the rate of wool growth altered slowly during this period and tended gradually towards the asymptote which would signify that nutritional equilibrium had been established. The observed changes in the rate of wool production which supervened on subsequent alterations of the level of fodder intake, whether the levels of intake were increased or decreased, reflected the same phenomenon.

The nature of the physiological processes responsible for this lag in the establishment of nutritional equilibrium changed according to the level of feeding: at the lowest level, steady depletion of the fat reserves was the major factor which determined the quantity of amino acids drawn upon for fuel, and so the quota that became available for wool production; and at the levels above maintenance, synthetic processes other than wool production were mainly responsible for depletion of the substrate. In neither case was their influence

constant. Nutritional equilibrium was impossible at the lowest level of feeding, and at the higher levels, a steady state could be reached only if the laying down of tissue protein either proceeded at a constant rate, or ceased altogether as it would when the animal had attained its maximum capacity to store protein. The extent to which these factors operated during the collection periods that began 8 weeks subsequent to each change in intake level may be derived from the nitrogen and energy balances discussed below.

(b) *The Relationship between Food Intake and the Rate of Wool Production*

The general phenomenon of the dependence of the rate of wool production upon the level of feeding is obvious from the data set out in Table 1 and Figure 2. These indicate the relative rates of wool growth over the 14 days of the 9th and 10th weeks after each change in the level of food intake; the first three ewes

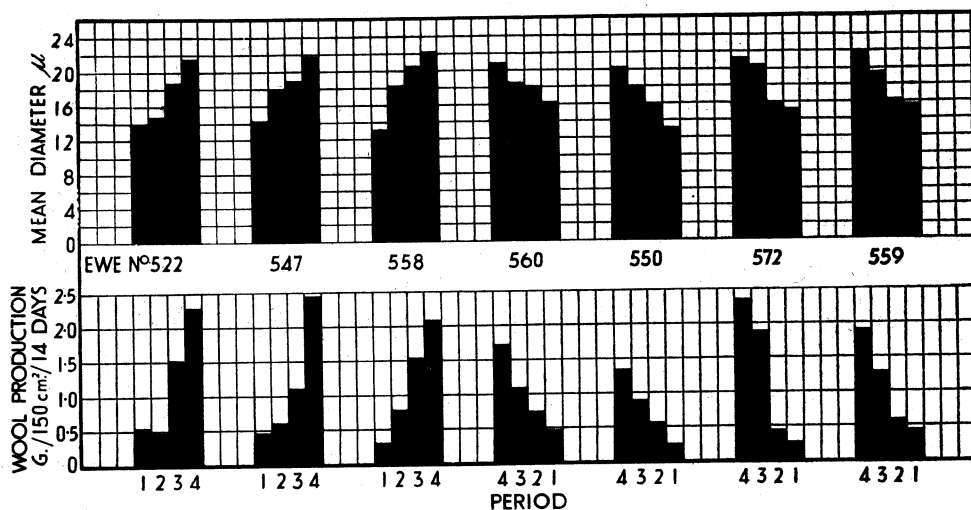


Fig. 2.—The influence of the level of fodder intake on the rate of wool production and mean diameter of the fibres is shown. The available energy intake from diet 541 was approximately $\frac{1}{2}$, 1, $1\frac{1}{2}$, and 2 maintenance, and the available protein intake was approximately 25, 50, 75, and 100 g. per day, for periods 1, 2, 3, and 4 respectively. The levels of feeding were changed in ascending steps for Nos. 522, 547, and 558, and in descending steps for Nos. 560, 550, 572, and 559. The ration was fed for 8 weeks prior to the beginning of each of the periods reported.

were fed in ascending stages and the other four in descending stages. The daily intakes of nitrogen over each of the 10-week intervals and the state of the nitrogen and energy balances during the 14 days of the periods, in which the wools referred to in Table 1 and Figure 2 were collected, are set out in Table 2.

(c) *The Rate of Wool Production in Relationship to the Energy and Nitrogen Balances of the Ewes fed on Diet 541*

During the 12 months of the observations each of the ewes traversed the physiological states that were mentioned in the introduction to this paper; their nutritional status ranged from one of frankly negative energy balance in which

TABLE 1
THE RATE OF WOOL GROWTH AT DIFFERENT NUTRITIONAL LEVELS

Sheep No. and Surface Area	Period	Dry Clean Wool Fibre			
		W (obs.) g.	Weight g./day	D, Mean Diameter μ	Relative Length
		(1)	(2)	(3)	(4)
522 (0.87 m. ²)	1	0.50	1.5	13.85 $\pm$ 0.124	100
	2	0.49	1.4	14.75 $\pm$ 0.136	86
	3	1.55	4.6	18.79 $\pm$ 0.159	168
	4	2.35	7.0	21.60 $\pm$ 0.175	193
547 (0.85 m. ²)	1	0.46	1.3	14.84 $\pm$ 0.060	100
	2	0.60	1.7	16.35 $\pm$ 0.073	107
	3	1.22	3.5	18.84 $\pm$ 0.076	165
	4	2.48	7.2	21.80 $\pm$ 0.080	250
558 (0.84 m. ²)	1	0.40	1.1	13.18 $\pm$ 0.105	100
	2	0.50	1.4	15.15 $\pm$ 0.125	95
	3	1.68	4.8	20.62 $\pm$ 0.147	172
	4	2.65	7.6	22.27 $\pm$ 0.136	232
550 (1.05 m. ²)	1	0.27	1.0	13.13 $\pm$ 0.092	100
	2	0.57	2.0	15.81 $\pm$ 0.106	145
	3	0.91	3.2	17.80 $\pm$ 0.116	183
	4	1.34	4.8	20.17 $\pm$ 0.122	210
559 (1.05 m. ²)	1	0.45	1.6	15.73 $\pm$ 0.128	100
	2	0.48	1.7	16.27 $\pm$ 0.129	99
	3	1.24	4.4	19.56 $\pm$ 0.149	178
	4	1.83	6.5	22.00 $\pm$ 0.139	208
572 (1.05 m. ²)	1	0.43	1.5	15.40 $\pm$ 0.143	100
	2	0.48	1.7	15.95 $\pm$ 0.165	104
	3	1.98	7.1	20.53 $\pm$ 0.189	260
	4	2.45	8.7	21.42 $\pm$ 0.202	295
560 (1.00 m. ²)	1	0.48	1.6	16.08 $\pm$ 0.134	100
	2	0.75	2.5	18.05 $\pm$ 0.138	124
	3	1.18	4.0	18.69 $\pm$ 0.154	182
	4	1.58	5.4	20.83 $\pm$ 0.148	196

(1) = observed weight of clean dry wool produced on 150 cm.²/14 days.

(2) = weight of clean dry wool produced/day, computed from (1), *vide* text.

(3) = mean diameter of fibres on patch.

(4) = relative mean length of fibres computed from W/D^2 , period 1 being taken as 100.

they were drawing on their own tissues to the extent of approximately 500 kg. cal./day, through two intermediate levels, to one of strongly positive energy balance which favoured the rapid production of tissue protein and fat. The supply of protein from the fodder was increased approximately 400 per cent.

from the lowest to the highest level of feeding (Table 2), but coincident with this increase the overall nutritional status was altered in favour of other physiological processes which competed seriously with the follicles for the supply of substrate. The rate of wool production under these conditions was clearly the resultant of a number of variables, the nature of which changed with the level of feeding — the substrate of amino acids was depleted at the lower levels to provide fuel to meet the energy demands, and at the higher levels, to provide for the competing

TABLE 2
NITROGEN BALANCE AND WOOL GROWTH OF SHEEP ON DIET 541

Sheep No.	Period	Intake (g.N/24 hr.) N_i	Faeces (g.N/24 hr.) N_f	Urine (g.N/24 hr.) N_u	Available N (g.N/24 hr.) N_a	N Balance (g.N/24 hr.) N_b	Wool (g.N/24 hr.) N_w	Energy Balance (kg.cal./24 hr.)
522	1	3.67	0.69	5.22	5.47	-2.24	0.25	-405
	2	8.08	1.44	5.88	6.64	+0.76	0.24	-20
	3	12.90	3.06	7.32	9.84	+2.52	0.77	+250
	4	19.83	4.19	10.00	15.64	+5.64	1.17	+780
547	1	3.48	0.64	5.45	5.67	-2.61	0.22	-430
	2	7.86	1.48	5.71	6.38	+0.67	0.29	-35
	3	12.51	2.53	7.44	9.98	+2.54	0.59	+380
	4	19.26	3.81	9.77	15.45	+5.68	1.20	+715
558	1	3.38	0.60	5.00	5.19	-2.22	0.19	-395
	2	7.97	1.90	5.80	6.07	+0.27	0.24	-70
	3	12.60	2.78	7.22	9.82	+2.60	0.81	+230
	4	18.20	4.30	9.38	13.90	+4.52	1.28	+715
550	1	4.18	0.63	5.19	5.35	-1.64	0.16	-480
	2	9.55	1.65	7.50	7.90	+0.40	0.34	-30
	3	15.05	2.60	10.45	12.45	+2.00	0.54	+280
	4	18.85	4.10	12.10	14.75	+2.65	0.80	+640
559	1	3.95	0.72	4.79	5.06	-1.56	0.27	-500
	2	9.42	1.65	7.80	7.77	-0.03	0.29	-100
	3	15.55	3.14	10.35	12.41	+2.06	0.74	+230
	4	20.30	5.52	11.45	14.78	+3.33	1.10	+730
572	1	4.62	0.73	6.10	6.36	-2.21	0.26	-430
	2	9.42	2.02	7.15	7.40	+0.25	0.29	-30
	3	15.20	2.81	10.25	12.39	+2.14	1.19	+270
	4	19.80	5.38	11.30	14.42	+3.12	1.47	+560

In period 1 of each series when the animals were frankly in negative balance the available nitrogen, N_a , is expressed as the nitrogen in the urine, N_u , plus the nitrogen in the wool, N_w , which under these circumstances is the nitrogen turnover. In all other periods N_a is the nitrogen intake, N_i , minus the nitrogen in the faeces, N_f . The nitrogen balance, N_b , in each case is $N_i - (N_f + N_w)$. The nitrogen in the wool, N_w , is computed (*vide* text) from the wool collected by shaving 150 cm.² patches outlined by tattoo lines on either shoulder, the nitrogen content of pure dry wool keratin being taken as 16.8 per cent. The energy balance figures are those reported by Marston (1948). The levels of feeding were changed in ascending steps for

Nos. 522, 547, and 558, and in descending steps for Nos. 550, 559, and 572.

syntheses involved in the laying down of tissue protein. Thus the relationships between the rates of wool production and the intakes of protein (or, more precisely, of that part of the ingested protein which became available to the animals), although roughly linear (*vide* Fig. 3.) were not simple ones.

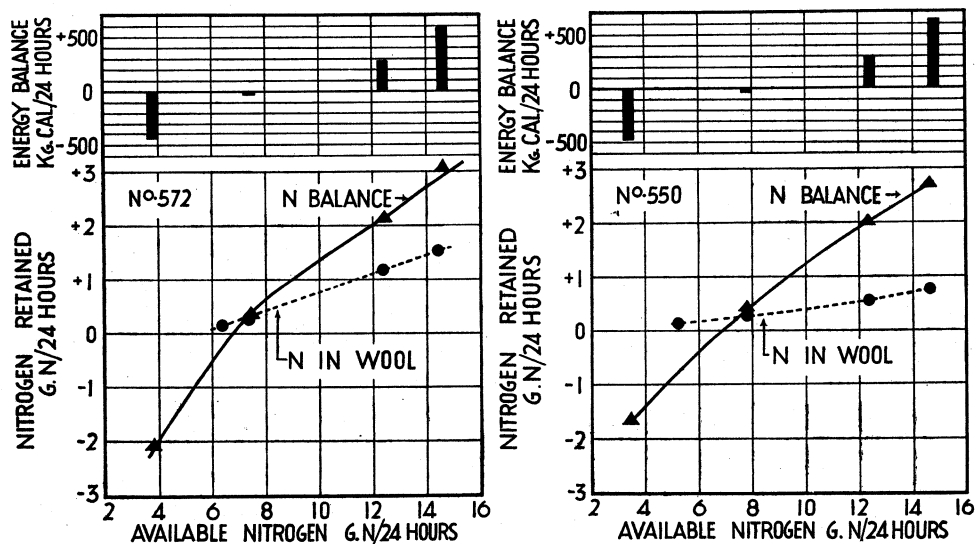


Fig. 3.—The difference in the wool producing efficiency of ewes No. 572 and No. 550 over a range of practically identical nutritional conditions is shown. Neither ewe expressed its full capacity as a wool producer under the conditions imposed. Above the maintenance level of fodder intake the relative rates of the synthesis of wool keratin and muscle protein are indicated respectively by the nitrogen in the wool and the difference between this and the total nitrogen retained. For animals in frankly negative balance, the nitrogen available for wool production was computed (*vide* footnote to Table 2) from the nitrogen in the urine plus the nitrogen in the wool. Under such conditions this is a close estimate of the nitrogen turnover. The amino acids arising from the tissue proteins which are degraded when the animal is in negative energy balance add to the substrate available for wool growth — when a sheep is living entirely at the expense of its own tissues, after prolonged fasting, its wool continues to grow at a considerable rate — and so at fodder intake levels below maintenance (those of period 1) the rate of wool growth bears a closer relationship to the nitrogen turnover estimated in this way than to the nitrogen available from the fodder. In the curves which refer to the state of nitrogen balance of the animals, however, the “available nitrogen” at the intake level of period 1, as at all other levels, is computed from the difference between the nitrogen in the fodder and the nitrogen in the faeces. This is a reasonably close estimate of the nitrogen in that part of the fodder that is digested and absorbed. The relatively small contribution made to the faecal nitrogen by nitrogenous constituents excreted into the bowel and not reabsorbed has been neglected in these considerations.

At high levels of protein intake the increment in the rate of wool growth might be expected to diminish towards an asymptote which would be defined by the maximum capacity of the follicles to utilize amino acids.* There was no

* Although this maximum is primarily a hereditary characteristic of the individual it may be influenced materially by early nutritional history, for obviously a sheep that has been stunted through malnutrition during its period of rapid growth would never express its full hereditary propensity as a wool producer.

evidence, however, that the maximum rate of wool production was approached in the range of nutritional conditions to which the experimental animals were subjected: the relationship between wool production and protein intake remained, in every case, approximately linear at intake levels above maintenance. It may be concluded that under these conditions the rate of wool growth was limited not by the maximum ability of the follicles to utilize amino acids but by the supply of raw materials for the synthesis of keratin.

(d) *The Efficiency of the Merino as a Converter of Protein to Wool Fleece*

At the highest level of feeding when the protein intake was comparatively large and the state of the energy balance was such as to minimize the immediate call on the amino acids for fuel, the nitrogen retained in the wool was less than 10 per cent. of the nitrogen absorbed from the ration — it varied between 10 per cent. of the available nitrogen (No. 572) and 5.4 per cent. (No. 550). Thus it is evident that the capacity of the ingested protein to provide the essential amino acids for the synthesis of wool keratin was seriously limited. Although at the higher levels of food intake a considerable drain on the substrate of amino acids was imposed by the syntheses involved in flesh formation, this complication did not materially alter the situation. The extent of the depletion may be determined with reasonable accuracy from the difference between the total nitrogen retention and the nitrogen content of the wool produced (*vide* Table 2); if the nitrogen available to the follicles is estimated in this way, the efficiency of its conversion to wool was at its highest, 12 per cent., in No. 558 which was laying down flesh during period 4 more rapidly than any of the other animals, and at its lowest, 6.2 per cent., in No. 550 which throughout was the poorest wool producer.

The capacity of diet 541 to provide essential amino acids for wool and flesh production respectively may be estimated from the composition of the main proteins concerned in these transactions (Table 3). It is apparent that the sulphur-containing amino acids, cystine and methionine, would impose the first limiting factor for the synthesis of keratin from the assemblage of amino acids available from diet 541. The overall composition of this substrate would be influenced by differences in the digestibility of the proteins from the wheat and the lucerne, but the error involved in assessing, from the composition of the diet and the nitrogen absorbed, its ability to provide the essential amino acids for wool production would be negligible as the proteins from lucerne and wheat have practically an identical capacity to provide cystine.*

If the potential cystine were transferred quantitatively to wool keratin the overall efficiency of conversion of the amino acids from diet 541 could not exceed 27 per cent. The proportions converted were much lower than this. The greatest observed efficiency was achieved by No. 558. At the highest level of feeding this

* It is within the scope of the animal organism to produce cystine from methionine through the intermediary thio-ether, $\text{H-S-(}\beta\text{-amino-}\beta\text{-carboxyethyl)-homocysteine}$: the serine involved in this conversion being formed *in vivo* either from other amino acids or by transamination. The potential capacity of an amino acid mixture to supply cystine to the animal is thus the sum of its contents of methionine and cystine, 1 mol. of methionine being capable of transformation to 1 mol. (80 per cent. of its weight) of cystine. The reaction is not reversible (for review of literature see Marston 1946, p. 207, *et seq.*).

TABLE 3

THE DISTRIBUTION OF AMINO ACIDS IN THE PROTEIN SOURCES OF DIET 541 AND THE PRODUCTS OF THE NUTRITIONAL TRANSACTIONS

Amino Acid	Per cent. of Amino Acid Nitrogen in Total Nitrogen of				
	Whole Wheat Protein (1)	Lucerne Protein (2)	Diet 541 Protein (3)*	Wool Protein (4)	Whole Muscle Protein (5)
Cystine	1.3(b)	1.2(d)	1.2	9.0(e)	0.8(a)
†Methionine	1.5(b)	1.3(d)	1.4	0.4(f)	1.9(a)
†Threonine	2.4(b)	4.0(b)	3.4	4.7(f)	3.9(a)
Arginine	8.4(b)	15.1(d)	12.5	20.0(e)	15.3(a)
†Histidine	3.6(b)	2.3(d)	2.8	1.1(e)	4.1(a)
†Lysine	3.2(b)	6.6(d)	5.2	3.2(e)	10.4(a)
†Tryptophan	1.0(b)	1.8(d)	1.5	0.6(e)	1.0(b)
†Phenylalanine	3.0(b)	2.4(b)	2.6	1.9(f)	2.6(b)
Tyrosine	2.3(b)	2.5(d)	2.4	2.0(e)	1.5(b)
†Leucine	4.5(b)	7.4(b)	6.2	17.2(f)	5.3(b)
Isoleucine	2.4(b)	3.6(b)	3.1		4.2(b)
†Valine	3.4(b)	4.5(b)	4.1	3.4(f)	4.3(b)

* Computed from (1) and (2) on basis 100 g. of diet 541 contained 2.3 g. protein N of which 0.92 g. N (40 per cent.) was supplied by wheat and 1.4g. N (60 per cent.) by lucerne.

† Essential amino acids.

‡ The sum of leucine and its isomer.

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animal bound in its wool 47 per cent. of the potential cystine available in the substrate that remained after requirements for flesh formation** had been subtracted from the total amino acids absorbed. The efficiency *decreased* materially at lower levels of food intake. In period 4, the highest level, it ranged between 47 per cent. and 24 per cent.; in period 3 it ranged between 40 per cent. and 19 per cent.; and at the approximate maintenance of period 2 it ranged between 18 per cent. and 14 per cent. The low efficiency of conversion at maintenance level is simply explained by the relatively great call on the amino acids to serve as fuel to support the basal energy requirements. This call was not inconsiderable at the intermediate level of feeding, period 3, for under these conditions the combustible energy of the absorbed amino acids either approximated closely or actually exceeded the calorific value of the retained nutrients.

As the follicles have little or no capacity to store their requirements of amino acids, wool growth is essentially dependent on the concentration of amino acids in the tissue fluids. The continual high concentration of amino acids in the

** Assessed, *vide supra*, from the difference between the total nitrogen balance and the nitrogen in the wool.

systemic blood stream which apparently is necessary to sustain maximum wool growth tends to favour wastage of the substrate by oxidative deamination, even at food intakes which ensure a strongly positive energy balance. This tendency is enhanced by the considerable diurnal variations in the rate of absorption of amino acids from the intestine. The relative rates of absorption of amino acids and of their utilization by the follicles probably comprise the main factor responsible for the low efficiency of utilization of the sulphur-containing amino acids observed at the highest levels of feeding in these experiments.

(e) The Influence of Fodder Intake on the Dimensions of the Wool Fibre

As there was no evidence that any of the follicles ceased to function during the period of observation — there was no sign of cast fibres in the staple even at the lowest level of production — it may be assumed that the density of the fibre population on the area from which the wool was collected remained the same at all levels of feeding and so the relative change in the mean length of the fibres at any level of feeding may be derived, provided the specific gravity of the fibres remains unaltered, from the expression, $L = W/kD^2$, where L = the mean length, D = the mean diameter, and W = the weight produced in the observed period, k being a constant. The data relevant to the influence of fodder intake on the dimensions of the fibre are set out in Table 1.

It is obvious that the rate of wool production is contingent on a change in the mean diameter of the fibres: as $W = kD^2L$, W being related to D by a function considerably in excess of D^2 , an alteration in mean diameter of the fibres reflects a relatively large change in the rate of wool production.

The variance of the fibre diameter population was also subject to the level of food intake — “g” statistics revealed that the fibre diameter distributions, which in every case tended to be skewed towards the stronger classes became, as the rate of wool growth increased, more asymmetrical and more platykurtic. The findings suggest that the finer classes change over a more restricted range than the stronger classes; apparently, with an alteration in the rate of growth, each fibre is influenced up to the limit of its capacity in proportion to the area of its cross section. Detailed analyses of these variations will be discussed in another paper.

(f) Wool Production by Grazing Sheep

From the above considerations of the physiological factors involved in wool production, it would appear unlikely that a high-producing Merino sheep could ever express its full propensity for wool production while grazing on natural pastures.

Few pastures, at any stage of their growth, would be capable of providing the nutritional requirements for maximum wool production. When their protein content is greatest the fodder plants are young and succulent and the sward is usually wet; in these circumstances the quantity of the available fodder with which a sheep can deal is limited by the water in (and on*) the pastures. When

* To derive its energy requirements from constituents other than the available protein of wet young pastures a sheep would, of necessity, ingest between 6 and 10 litres of water each day.

they are dry, their protein content is low and less easily assimilated from the lignified plant cells. The bulk of this relatively indigestible fodder that a sheep would need to consume in order to provide the full complement of amino acids for maximum wool production, exceeds the capacity of its digestive organs. Under these extremes of grazing conditions the situation is complicated further by the inability of the sheep to fulfil its basal energy requirement even when it has fed to repletion. The supply of amino acids which otherwise would provide a substrate for wool production is then depleted to serve as fuel.

The ability of a pasture to provide the nutritional requirements for maximum wool growth, if it were ever capable of achieving this, would be transitory; and so it may be concluded that the wool production of a grazing Merino is usually, if not always, limited by the nutritional quality of its fodder.

Considerable changes in the rate of wool production might thus be expected to supervene on the seasonal fluctuations in the chemical composition of the pastures. These changes would be reflected in the mean diameter of the wool fibres.

This phenomenon, which is prevalent under natural grazing conditions in Australia, is evident from the observations set out in Figure 4. The mean fibre diameters of the wool grown on areas delineated by tattoo lines on the shoulders of a group of ten high-producing Merino ewes were determined* at monthly intervals for two years. The animals were of the same breeding as those employed in the experiments described above. They were members of the Division's breeding flock and grazed with it on the natural pastures of the Adelaide foothills. The performances of the three reported in Figure 4 are representative of the range of variations observed. The very considerable seasonal change in the fibre diameters of all is obvious, and although no quantitative measure of the chemical composition of the pastures was attempted, it is clear that the changes in the fibre diameters reflected very closely the nutritive quality of the fodder of which there was always a large excess available to the animals.

As the experimental observations discussed above have proven that the rate of wool growth in this type of Merino is proportional to a function considerably greater than the square of the mean fibre diameter, the relative changes in the rates at which wool was produced at different times of the year by the grazing flock were obviously large. By comparison with the performance of the individuals fed under laboratory conditions, it would appear that the nutritional state of the grazing ewes varied with the season over a range which at its lowest was somewhat better than that of period 2, and at its highest materially superior to period 4 (*vide supra*), the former being reached in midwinter and the latter in late spring and early summer. The actual nutritive quality of the fodder if judged from the chemical composition of the dried pasture clips would have been greatest in midwinter when the fodder plants were in their earlier stages

* The mean diameter was derived by measuring at random the dried clean fibres (*vide supra*) from a sample collected by clipping the 15 cm. x 10 cm. area with very fine hair-clippers, the patch having been clipped similarly a week previously. Each reported mean and its variance thus refers to approximately one week's growth at the time indicated. Five hundred fibres were measured in each case.

of growth. The pastures then, however, were usually sodden with moisture and so the *quantity of dry matter consumed by the grazing animal*, and not the quality of the fodder, became the first limiting factor. The steady decline in the

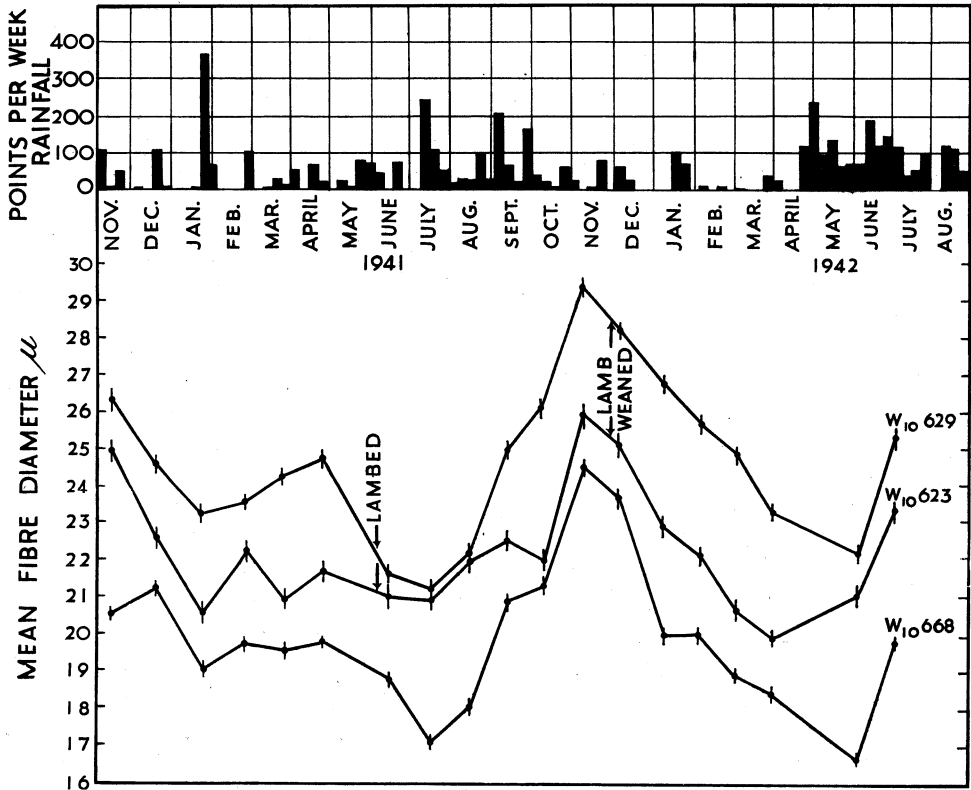


Fig. 4.—The seasonal variation in wool production by sheep grazing on natural pastures composed essentially of annual species is shown. The mean fibre diameters of the wool grown on areas delineated on the shoulders of each animal are plotted as points with $\pm$ P.E. indicated by the length of the line on either side. The change in mean fibre diameter between the winter level (June-August) and that of the flush of spring (Oct.-Nov.) implies approximately a fourfold increase in rate of wool production.

Ewes No. 629 and No. 623 carried lambs. Ewe No. 668 did not lamb in 1941. A supplement of barley (4 oz. per day) was available to all ewes from January 21 to July 3, 1941, and from January 5 to July 7, 1942.

rate of wool growth during the summer reflected the decreasing nutritional quality of the available fodder. The sheep is a selective feeder and so would deplete the dry, standing pasture of its most nutritive constituents.

IV. GENERAL CONCLUSIONS

The efficiency with which a high-producing Merino sheep converts its fodder protein to wool fleece obviously is influenced by a number of physiological factors, and while there can be no doubt that the initial nutritional limitation is imposed by the potential capacity of the fodder to provide cystine, the ultimate supply of essential amino acids that becomes available to the follicles

is clearly subject to competitive reactions which change both in nature and extent with the overall nutritional status of the animal.

It may be concluded from the above experimental observations that wool production is practically always limited by nutritional factors. Both the quantity and quality of the fodder consumed by a grazing sheep vary over a wide range according to the season, and these variations are reflected in the fleece by alterations both in the length and in the mean diameter of the wool fibres. The response of individual follicles is by no means constant, and so alteration of the nutritional level of the sheep leads to a marked change in the nature of the fibre diameter distribution curve. Thus, attempts to classify a sheep by the mean and variance of the fibre diameters of its wool fleece are not convincing. It would not be justifiable from the elaborate data of these experiments either to assess precisely the wool-producing propensity of any of the individuals or to predict the way in which these sheep would react to a nutritional environment distinct from the observed range.

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