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GRASSLAND PROBLEMS IN THE UNITED KINGDOM AND THE NETHERLANDS

Report of a Grassland Symposium
held at the Research and Advisory Institute for
Field Crop and Grassland Husbandry (P.A.W.),
Wageningen on June 12th and 13th, 1967

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LIST OF PARTICIPANTS IN THE GRASSLAND SYMPOSIUM

1. British members

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PROGRAMME

12th June 1967

8.45 a.m. Opening of the Symposium by J.J. Jonker, President of the Netherlands Society for Grassland and Fodder Crops.

Morning session. Chairman M.L. 't Hart

9.00 - 10.30	The nutritive value of conserved forages	D.F. Osbourn W.F. Raymond	S. Iwema
11.00 - 12.30	Forage crop quality and conservation	R.J. Wilkins	P.J.J.Philipsen

Afternoon session. Chairman P.F.J. van Burg

14.00 - 15.30	Factors influencing the mineral composition of herbage	D.C. Whitehead	W.Dijkshoorn
16.00	Visit to the laboratory of the Dept. of Animal Physiology	(Prof. A.M. Frens)	

13th June 1969

Morning session. Chairman G.J. Vervelde

9.00 - 10.30	Simulation of plant and animal growth	P.J. Radford	C.T. de Wit
11.00 - 12.30	The regrowth of plants after defoliation	R.C. Anslow	A. Sonneveld
12.30 - 12.45	Closing of the Symposium.		

Afternoon. Optional excursions

1. Experiment of Th. Alberda in Oostelijk Flevoland on the maximum production of grassland.

2a. Experiments of A. Sonneveld on voluntary intake of fresh grass of different species by heifers and sheep (experimental farm "Droevendaal", Wageningen).

b. Experiments of P.J.J. Philipsen on hay making (experimental farm "De Ossekampen", Wageningen).

THE NUTRITIONAL CHARACTERISTICS OF CONSERVED FORAGES

D.F. Osbourn

It has been found useful at the Grassland Research Institute to consider the three parameters Intake, Digestibility and Utilization of Digested Energy as being the three major components determing the total intake of useful energy. This in turn determines the rate of production and the efficiency of the production process.

These parameters are variously affected when forages are conserved by the processes of conservation, the other feeds fed in conjunction with the conserved forage and the nature of the animal to which the rations are fed.

A. The conservation process

1. Dehydration and physical processing of forages

The effects of dehydration alone are normally small, depressing digestibility slightly, particularly the protein fraction, increasing intake marginally and increasing the efficiency of utilization.

Grinding and pelleting produce marked changes in the digestibility and voluntary intake of dry matter.

The preliminary results of an experiment at Hurley comparing chopped, wafered and ground pelleted forms of processing upon early and late cut materials demonstrate the general findings of a number of experiments (Table 1).

Table 1.

	Physical form		
	Chopped	Wafered	Pelleted
Voluntary intake g D.M./kg L.Wt./day			
Early cut	26.2	31.4	37.6
Late cut	21.8	28.2	36.8
D.M. Digestibility %			
Early cut	72.2	66.1	60.5
Late cut	60.9	54.7	46.2
Intake D.D.M. g/kg L.Wt./day			
Early cut	18.9	20.8	22.8
Late cut	13.3	15.3	17.0

Intake increases as the processing becomes more severe in the destruction of structure and the effect is greater upon the more mature forage than upon the less mature material. Dry matter digestibility declines with increased severity of structural breakdown resulting from processing, and there would not appear to be a very marked interaction with forage maturity. The product of intake and digestibility or digestible dry matter intake is increased by processing in proportion to the severity of the destruction of the physical structure. However, the effect does not interact markedly with maturity. This agrees with the results of Heaney et al (1963), but not with the animal performance results reviewed by Minson (1962) which suggest that the response to grinding and pelleting is inversely related to the production potential of the chopped feed.

The discrepency in the published results may be due to differences arising from the effects of processing on legumes and grasses or as a result of major differences in the efficiency of utilization of digested energy of the different physical forms. This aspect of the subject is currently being examined at the Grassland Research Institute using the comparative slaughter technique.

2. Ensilage of forage crops

In general the digestibility of ensiled forages has been found to be similar to that of the fresh crop ensiled. However, the voluntary intake of silage dry matter is often lower than would be expected from the digestibility of the material. Reduction of the moisture content of the forage prior to ensiling by field wilting often has a considerable effect upon the intake characteristic of the resulting silage and also can effect its digestibility (Table 2).

Table 2.

The effects of in-field wilting prior to ensilage upon the nutritional parameters of the resulting silages compared with barn drying the material.

	Moisture content as fed %	D.M.D. %	V.I. g/kg/day	D.D.M.I. g/kg/day
Silage 1	83.3	77.5 a	21.3 a	16.5 a
2	79.9	77.7 a	22.7 a	17.6 ab
3	78.6	74.5 b	24.9 b	18.5 b
4	70.3	73.2 c	25.2 b	18.5 b
Hay	14.2	71.9 d	32.5 c	23.3 c
S.E.M.		± 0.34	± 0.93	± 0.67

a, b, c etc. means having different suffixes differ

P = 0.05

The effect of wilting has clearly been to increase the voluntary intake of dry matter but also to depress significantly the digestibility of crop silage dry matter. The intake of the most heavily wilted silage is still much less than that of the hay and while extreme wilting was not achieved the results do not, within their limits, suggest that extreme wilting will result in higher intakes than those achieved by moderate wilting.

While wilting provides a partial and not very reliable solution to deficiencies of silage as a sole feed for ruminants it would seem that the precise reason for low intakes should be defined. The magnitude of this problem appears to vary with class of livestock and with the degree of supplementation of the forage material.

B. The effects of concentrate supplements upon the nutritional characteristics of conserved feeds

1. The effect of forage maturity

Blaxter and Wilson (1963) have demonstrated that the differences in the voluntary intake of dry matter existing between early and late cut hays when fed alone may be reversed when fed at high levels of concentrate supplementation.

2. The effects of method of conservation

Experiments with sheep suggest that voluntary intake of dry matter of hay and silage is not reduced at the same rate when these forages are supplemented with barley.
The intake of hay declines by 0.64 units and silage by only 0.26 units for unit intake of barley. These rates of replacements and the different intakes of the conserved forages alone are expressed by the relationships below where Y is the intake of forage dry matter, X the intake of barley dry matter both expressed as g D.M./kg $W^{0.75}$/day

$$\text{Hay} \quad Y = -0.64X + 52.90$$

$$\text{Silage} \quad Y = -0.26X + 38.60$$

Similar results have been found using cattle by Campling and Murdoch (1966). The nutritional parameters of conserved forages particularly intake obviously interact markedly with level of concentrate supplementation.

C. The class of livestock to which the forage is fed

Experiments with sheep and cattle have suggested that the low intake of silages is most commonly observed with young growing animals. Older animals do not respond to the same extent as the young animal (Table 3 & 4).

Table 3.

The voluntary intake of dry matter g/kg $W^{0.75}$/day by lambs and mature wethers offered ryegrass conserved as hay or silage (unpubl. results D.J. Thomson)

	Lambs	Wethers
Silage	57.1	62.3
Hay	80.5	72.4
S.E.M.	± 3.43	

However intake is expressed the difference between the two forms of conservation was greater for lambs than mature sheep.

Table 4.

Live-weight increase of Friesian steers of different ages fed wilted and unwilted silage kg/head/day (Alder and McLeod 1966)

Age of steers (months)	4½	10½	16½
Initial liveweight kg	86	178	348
L.W.I. wilted silage	0.26	0.70	0.95
L.W.I. unwilted silage	0.13	0.41	0.64

Again an interaction appears to occur between age of animal and form of conservation which is evident in their intakes of dry matter and reflected in their live-weight gains (Table 4).

These interactions with age could be caused by varying protein availability and varying protein requirement, but the work of Waldo et al, (1965) would not seem to support such a hypothesis.

D. Some points for discussion

1. The effects of processing particularly the intermediate forms of wafering upon the nutritional value of dried grasses are not at all clear, and require more precise definition if dehydration of forages for ruminant feeds is to become more widespread.

2. The reason for the low intake of silage feeds require more precise definition but the effects of age of animal and level of concentrate supplementation may effect markedly the magnitude of this deficiency in silage feeds.

3. The interaction of supplementation with the forage factors of maturity and method of conservation appear to exert effects upon intake at least as large as the primary effects of maturity and method of conservation.

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GRASSLAND PRODUCTS AND NUTRITIVE EFFECT

S. Iwema

Introduction

Statements about the nutritive value of preserved grassland products are often restricted to the product itself, whereas the interaction animal/feed is left out of consideration. Usually three aspects will suffice: dry matter, starch equivalent and digestible crude-protein. Only the first one is determined, whereas the other two are calculated via regression equations, based on digestion trials.

Three aspects are concerned in the nutritive effect: the intake, digestibility and finally the utilization of the feed by the animal. Data on the digestibility and utilization may partly be recovered from the digestible crude-protein and starch equivalent. However, in this no account is taken of diverging feed intakes or diverging utilization, influenced by factors not measured or immeasurable, or any possible interaction between the feed concerned and the remainder of the daily rations. If the experimental conditions do not deviate too much from those under which the requirement standards have been established, results will be obtained which do not differ much from the expectations. With more extreme feeding, the results may deviate more widely from these expectations.

Feed intake.

Next to the rate of passage through the digestive tract the feed intake is determined by specific properties, which cannot be expressed quantitatively. Palatability and suitability, well-known in human feeding, are probably also important in animal feeding. Hay, silage and dried grass quality may have the same nutritive value, whereas the intake may show considerable differences. Sand contents may sometimes be equally high, but whereas a heterogeneous mixture may cause no trouble at all, a homogeneous mixture may result in a complete refusal. Heated hay and non-heated hay (of different material!) may have the same nutritive value, the nutritive effect, however, may widely differ, regarding intake and utilization. These aspects, mainly in the organoleptic field, demand an answer, which will be difficult to find, however.

Digestibility

Influenced by certain elements, not found by the Weende-method, the passage rate may change considerably, influencing the digestibility and the utilization with it. Sometimes these substances are present in the feed, or almost absent, in other cases the digestibility is affected by constituents in the remainder of the rations. Substances effecting a more rapid passage through the digestive tract than usual, often lead to less complete digestion and utilization of the concerning feed. As yet, little is known about these interactions; however, they may also be the reason for a different valuation of the various preserved grassland products.

Utilization

The utilization of preserved grassland products depend to a considerable extent on processes, occurring in the rumen, influenced by the chemical and physical properties of the feed; next to the presence of volatile fatty acids their mutual rations are important. The effects of these aspects are far-reaching, they even affect animal health. By substances not included in the Weende-system and by nutrient also occurring in the daily rations changes may occur that may show in the utilization. Experiments with long or ground hay, differing in physical properties, have not only shown that there is a difference in intake, digestibility, but also in utilization (with hay meal lower fat contents in the milk). Experiments with moist silage and hay resulted in less fat and protein in the milk, even though the nutritive value supplied was completely equal.

In digestion trials with grassland products often one-sided or almost one sided rations are offered, whereas in practice always mixed concentrate-roughage rations are offered. The results obtained, closely corresponding to the expectations, could be the result of the conditions under which the standards were established.

If nutritive effects - a more correct term for nutritive values - are to be measured, all three aspects will have to be taken into account as well as the possible interactions between intake, digestibility and utilization. A special aspect is the effect of the moisture content of silage on the digestibility, but especially on the utilization and intake. The first is rather easy to measure, the last is neither very difficult (apart from the correct sampling technique of the supplied silages and possible remainders); the utilization, however, raises great difficulties because as yet there is insufficiently known about the function of the rumen.

Very little is known about the specific effect of single concentrates on the nutritive effect of preserved grassland products; since the use of manufactured mixtures is increasing, the tendency to investigate is very limited. Since little is known about the interaction roughage-concentrates, there was little sense until now in investigating the maximum or optimum roughage supplied. With basic mineral pellets possibly enriched with vitamines (A and D) many difficulties may be prevented. With regard to protein and starch equivalent a limitation is not to the point. If the starch equivalent per ha is to be increased this will always be associated with an additional increase in the protein production. A comparison with the U.S.A., where high amounts of maize silage (poor in protein) are supplied and urea is sometimes applied as an additive in silaging, is rather senseless in grass rich areas. As soon as grasses poor in protein and rich in carbohydrates are grown, the problem may be more difficult. At the moment this is not the case. Even if the roughage quality is rather poor, the protein content is usually high enough not to expect considerable effects of urea addition in Western Europe.

DISCUSSION

The discussion is mainly concerned with the starting point of Hurley, viz. to achieve the highest possible yield of digestible energy per acre (cutting at a dry matter digestibility of the grass 70 %). In this case it will be necessary to accept a crude protein content below that required by a ruminant. The nitrogen content could be increased by applying much higher doses of nitrogen fertilizer, but is it sensible to induce luxury consumption of N by plant, when it is comparatively easy to feed the extra nitrogen to the ruminant as urea. It is even doubtful, if the protein supply to cattle via nitrogen fertilization of the herbage indeed is economically satisfactory. For this reason studies are encouraged on the use of urea as a nitrogen supplement with high-energy forages. The Dutch argue, that at this rate we will end by growing maize and beets. On the other hand, it is an open question what is more profitable: a heavy or a light first cut with lower or higher protein contents respectively. In Dutch experiments dry weights of 7 ton dry matter/ha usually show a crude protein content of 13 %. The difference might be caused by differences in growth rate, which in turn might depend on differences in time and quantity of N-fertilization. Apparently at Hurley nitrogen is applied in split applications, but not after each cut.

Next the Dutch views on the merits of chemical methods of assessing digestibility are discussed. At the moment the correlation between the vivo and in vitro digestibility of the dry matter and organic matter is investigated for the various grass species. The calculation is mentioned of the organic matter disgestibility from the contents of cell-wall constituents with the aid of a regression equation which can be used for all types of roughages.

The possibility of calculating the starch equivalent without using the content of crude fibre is mentioned as well.

FORAGE CROP QUALITY AND CONSERVATION

R.J. Wilkins

Some crop factors influencing the efficiency of conservation by dehydration and by fermentation are discussed, and the possible importance of these factors in plant breeding programmes considered.

Dehydration

Loss of crop dry matter occurs through respiration, photochemical degradation, leaching and the breaking off and loss of fragile plants parts. The magnitude of loss is very variable, but generally increases the longer the crop is drying in the field (Watson and Nash, 1960). Consequently losses are normally least for crops cut and directly dried in high temperature driers, and most for grass entirely cured in the field, with losses for barn dried hay between these extremes.

The initial moisture content and the rate at which moisture is lost from the crop will influence the length of the field drying period and the direct energy cost of drying. Experiments with controlled environmental conditions (Shepherd, 1964, 1965; Thaine, 1967) have shown that rate of water loss varies with temperature, relative humidity and rate of air movement. These factors appear also to be important in the field (Nash, 1959; Taylor, 1963). Under controlled conditions, rate of water loss is constant during the initial stages of drying, but then slows. Shepherd (1964) associated slowing in the drying rate of white clover leaves with closure of the stomata. Differences between cropsin rate of water loss during the initial phase of drying are likely to be small, but plant anatomical factors may have a large effect on the rate at which final drying takes place.

Weather conditions prevalent at the time of harvest affect the suitability of a crop for conservation as hay. To take an extreme case, at Hurley the primary growth of Vertas perennial ryegrass cut at 75 % in vitro dry matter digestibility is more easily conserved as hay than is maize of similar digestibility. The environmental potential for evaporation and the frequency of dry spells is higher at the harvest date of the ryegrass and total crop water content is higher in the maize (Table 1).

For the primary growth of perennial grasses delay reaching a particular digestibility (above 65 %) is associated with increase in evaporation at the time of harvest. At a particular digestibility, crop moisture content is generally higher in the earliest maturing grasses, but there is some association between yield and date of harvest at a particular digestibility (Tables 2 and 3). More water may need to be evaporated to obtain a stable storage moisture content from late varieties so it is not clear that late varieties would be conserved as hay more easily than early varieties (Tables 2 and 3).

Ensilage

The main objective in silage making is the attainment within the ensiled mass of sufficient acid concentration to inhibit further microbial activity. Losses will occur in the field and in the silo through respiration, fermentation, oxidation and effluent flow.

In the United Kingdom most silage is made by the fermentation of crop components by indigenous bacteria. In these circumstances, crop attributes may have a large influence on the type of fermentation and characteristics of the resultant silage. The importance of water-soluble carbohydrate content has often been stressed (Watson and Nash, 1960; Murdoch, 1966; Mc.Donald and Whittenbury, 1967). It is not, however, possible to specify exact quantitative requirements for water-soluble carbohydrates. The requirement will be influenced by:

Table 1. Suitability of maize and ryegrass for conservation as hay

	Maize (Inra 270)	Perennial ryegrass (Vertas)
Harvest date	30 Sept.	8 June
Yield (kg/ha)	14,100	9,670
Dry matter digestibility in vitro (%)	76	75
Water content (%)	79	80
Crop water yield (kg/ha)	53,000	38,700
Evaporation from free water surface at date of harvest (mm/day)	1.35	3.70

Table 2. Comparison between early and late varieties cut at 75 % dry matter digestibility in vitro

	Date	Evaporation (mm/day)	Water content (%)	Dry matter yield (kg/ha)	Water yield (kg/ha)
S37 cocksfoot	3 May	2.7	87	3,470	23,200
S24 ryegrass	13 May	3.1	86	6,730	39,700
S23 ryegrass	26 May	3.5	85	6,600	37,400
Vertas ryegrass	8 June	3.9	80	9,670	38,700

Table 3. Comparison between early and late varieties cut at 70 % dry matter digestibility in vitro

	Date	Evaporation (mm/day)	Water content (%)	Dry matter yield (kg/ha)	Water yield (kg/ha)
S37 cocksfoot	17 May	3.2	84	5,830	30,600
S24 ryegrass	25 May	3.5	82	8,560	39,000
S23 ryegrass	9 June	3,9	79	8,830	33,200
Vertas ryegrass	21 June	3.9	82	11,570	52,700

(i) The extent of sugar losses through respiration and oxidation which will be affected by the design of the silo and the method of filling and sealing.

(ii) Crop moisture content. Wieringa (1958) has demonstrated that increases in osmotic pressure resulting from wilting inhibit clostridial development and result in the production of silage stable at high pH.

(iii) Buffering capacity. Crops vary in buffering capacity with legumes generally having a higher buffering capacity than grasses (McDonald and Henderson, 1962; Greenhill, 1964; Playne and McDonald, 1966). To achieve a particular pH, twice as much water-soluble carbohydrate may be fermented in lucerne as in ryegrass.

(iv) Microbial flora. The fermentation products of homolactic and heterolactic bacteria differ (McDonald, Watson and Whittenbury, 1966) and the particular flora developed could lead to twofold variation in the quantity of sugar required to produce a given pH change.

(v) Water-soluble carbohydrates present. With heterolactic fermentation the products from fructose and glucose are different (Whittenbury and McDonald, 1966).

Crops with high sugar content and low buffering capacity are, however, more likely to be ensiled effectively than are crops with low sugar content and high buffering capacity. Wieringa and Hengeveld (1963) suggested that grasses with more than 11 % water-soluble carbohydrate are ensiled effectively.

Crops of similar digestibility differ considerably in water-soluble carbohydrate content, and Cooper (1961) has demonstrated inherent differences between ryegrasses in water-soluble carbohydrate content.

Choice of conservation technique

In Western Europe variation in weather is such that crops cannot be cut at pre-determined growth stage and dried in the field without the possibility of large losses of nutrients. The susceptibility of haymaking to wheather also makes the planning and efficient utilisation of farm resources difficult.

High temperature grass drying systems are not completely independent of weather, because variation in crop moisture content results in big fluctuations in drier through put. The quantity of surface moisture appears to be responsible for much of the unpredictable variation in crop moisture content. Equipment is being developed at the National Institute of Agricultural Engineering to remove surface water mechanically before the crop is dried. This should substantially reduce the effect of weather on crop conservation by high temperature drying.

A combination of high fixed costs, advantages of large scale operation and the marketability of the product, make it likely that in a suitable economic environment the production and artificial drying of crops will be organised in large scale specialist units. A sequence of crops of specific characteristics would then be produced throughout a long drying season.

This conservation technique is not suited to the conservation of flushes of crop growth in excess of the current demands of grazing livestock. These surpluses will be seasonal in occurrence, and it must be likely that they will be conserved more efficiently as high moisture silage than as low moisture hay. The fermentation occurring during ensilage cannot easily be predicted from crop composition, and it seems more rational to manipulate fermentation by the use of chemical and microbial additions rather than by the introduction of good ensiling characteristics into the genotype of the crop.

Conclusion

At a particular digestibility, crops vary in their suitability for conservation. However, the unpredictability of field drying and ensiling, and the possibility of using non-crop inputs in conservation, suggests that attempts to exploit this variation within the context of present conservation techniques may not be justified. Increased use of non-crop inputs will improve conservation efficiency, and allow plant breeders to select for high yield in crops of particular nutritional characteristics.

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SOME QUESTIONS ABOUT THE CONSERVATION OF FORAGE CROPS

Summary of paper by P.J.J. Philipsen

A great number of data should be available concerning various unchangeable conditions like soil, climate ect. to interpret the practical significance of production and quality of forage and the methods of conservation applied. As an example the time of growing and the distribution of the production of a crop over the year or of possible combinations of crops are of major importance to mechanization and labour organization on the farm.

The year production of crops as well as the sensibility of the production for exterior conditions play a great part.

The relation between dry matter production and feeding value and the influence of e.g. the time of cutting on the production of the aftermath are important factors.

On judging the suitability of a crop for conservation purposes one thinks of losses of conservation and the intake of the conserved product by the animals. The question ought to be raised here in how far the crop is suitable for various forms of mechanization, being applied on different types of farms, in other words, in what way the desired rate of mechanization fits in the farm.

Finally the value of the forage should always be compared with alternatives.

DISCUSSION

The discussion mainly concerned the query whether breeders should select for one crop or for a combination of crops greatly satisfying the animal nutrition standards, when conserved.

The difficulties associated with the breeding programme required to achieve this object were obvious. Breeding is time consuming and will grow more difficult as the standards to be met by the present crops are set higher. Selection programmes will grow more complex and time consuming, if, in addition to high production in a minimum number of cuts and satisfactory chemical composition with a good energy/protein ratio, further requirements are set, e.g. with respect to distribution of dry matter production over the year, drying properties, ash content and maybe a further distinction to be made between grasses for grazing and grasses for conserving.

Breeding experts will continue to search for and will continue to urge solutions in this direction.

On the other hand, the more technically minded specialists will investigate methods to change the crop in the desired direction by technical devices. Examples are: affecting the drying properties by bruising, addition of chemicals for conserving (sugar, acids, etc.) as well as for nutritive value (urea, molasses, etc.).

FACTORS INFLUENCING THE MINERAL COMPOSITION OF HERBAGE

D.C. Whitehead

Important factors which, in addition to the soil content of each element, influence the mineral composition of herbage, are listed in Table 1. The magnitude of the influence of each factor on the percentage content of each of the animal nutrient elements is also indicated. Much of the experimental data on which these assessments are based has been summarised elsewhere (Whitehead, 1966 a, b). For some of the items in Table 1 there is a good deal of evidence; for other items very little evidence. For some items the change indicated is consistent; for other items there is considerable variation between experiments. It is assumed that comparisons are made between samples taken from the same site, at an equivalent stage of maturity (except when this is the factor being investigated) and at the same time of year.

For all the elements where a difference between grasses and legumes is indicated, higher contents generally occur in the legumes.

The greatest differences between species within both the grasses and legumes occur in sodium contents. Some grass species, such as timothy and meadow fescue, are inherently low in sodium content, whereas others, such as ryegrass and cocksfoot, may be high or low according to the supply. Recent work with legumes indicates that sainfoin is also low in sodium content, that white clover is very variable and that red clover and lucerne are intermediate. Sainfoin is also lower than the other legumes in calcium content.

The changes with advancing maturity are all decreases, with the possible exception of sodium in legumes.

The effect of fertilizer nitrogen on the contents of elements other than nitrogen is often variable. For phosphorus, potassium, calcium, sulphur and copper, increases resulting from increasing nitrogen supply have been reported from some experiments, and decreases from other experiments. For phosphorus and potassium there is some evidence that increases occur when the supply of these elements is good, and decreases when the supply is poor. For calcium and sulphur the form in which the nitrogen is applied is important. With copper the variation in results is more difficult to explain. Factors which may be involved include (i) the soil supply of copper, (ii) the influence of grazing returns (Whitehead, 1966 b), (iii) the stage of growth at which the samples were taken, since copper content has been shown to be related to nitrogen content (Rasheed and Seeley, 1966) and (iv) the content of copper in the nitrogen fertilizer used - Stoikovska and Cooke (1958) reported a content of 22 ppm in nitro-chalk and 2 ppm in ammonium sulphate.

Fertilizer phosphate has very little effect on the mineral composition of herbage apart from increasing the phosporus content.

Fertilizer potassium, in the commonly used chloride form, increases herbage contents of these two ions, and decreases contents of sodium, magnesium, calcium and sulphur.

Soil pH has a large effect on the contents of the metallic trace elements, particularly manganese and cobalt, which are considerably increased by acid conditions.

With regard to the influence of soil moisture, most reports agree that drought decreases phosphorus content, and that waterlogging increases contents of manganese and cobalt.

An appreciation of the changes in composition brought about by the factors listed in Table 1 is essential when herbage analysis is used for assessing the adequacy of supply of the various nutrient elements for either plants or animals. At Hurley, we now consider that herbage analysis shows promise of being a more reliable means than soil analysis of diagnosing deficiencies affecting the growth of grass swards. However it is

Table 1. Factors influencing the percentage contents of nutrient elements in herbage

	N	P	K	Ca	Mg	S	Na	Cl	Fe	Mn	Zn	Cu	Co	I	Se
Grasses cf. legumes	++	0	0	+++	+	0	0	0	++	0	0	++	++	?	++
Spp. differences within grasses	0	0	0	0	0	0	+++	+	+	+	+	+	+	++	+
Spp. differences within legumes	+	+	0	++	0	+	+++	?	+	0	0	+	0	?	?
Maturity in grasses	+++	+++	++	+	0	+++	0	0	++	0	0	+++	+	+	?
Maturity in white clover	+	+	0	0	0	+	+	0	+	0	0	+	+	?	?
Fertilizer N	+++	+	+	+	+	+	++	+	0	0	+	++	0	+	?
Fertilizer P	0	++	0	0	0	0	0	0	0	0	0	0	0	?	+
Fertilizer K	0	0	+++	+	++	++	+++	+++	0	0	0	0	0	?	?
Soil pH	0	+	0	0	0	0	0	0	++	+++	++	+	+++	?	?
Soil moisture	0	+	0	0	0	0	+	0	0	++	0	0	++	?	?

+++ high values usually $>$100 % greater than low values

++ high values usually 50 - 100 % greater than low values

+ high values usually 20 - 50 % greater than low values

0 high and low values usually differ by $<$20 %

important to take the stage of maturity of the herbage into account, particularly with elements such as phosphorus whose contents decline steadily. With such elements there will be no single critical % value, but a curve of critical values. Although for previously uncut herbage the stage of maturity is fairly readily determined, a greater problem is presented by regrowth herbage. For regrowth, a rapid chemical criterion of maturity is required. Fibre and nitrogen contents are two possibilities, but neither is ideal: fibre because it is chemically imprecise, and nitrogen content because it is very subject to the influence of fertilizer applications. With potassium, whose range of variation with supply is greater than that of phosphorus, and whose change with maturity is less consistent, there is less need to take the precise stage of maturity into account. However critical % values for potassium reported in the literature range between 1.0 and 2.0 % K in the dry matter.

With regard to assessing the likelihood of mineral deficiencies in grazing animals, herbage analysis can give an indication of the total content in the diet. However there is a lack of information on the availability to livestock of the various mineral elements, and on the factors which affect availability. For example, very little is known about the extent to which the % absorption is influenced by the factors listed in Table 1, although there is a certain amount of information for magnesium. The availability of this element is lowest in young herbage with a high nitrogen content, and tends to increase as maturity advances (Kemp et al., 1961; Rook and Campling, 1962). However other experiments (Hodgson and Spedding, 1966; Large and Spedding, 1966) have failed to show any effect of fertilizer nitrogen on the level of serum magnesium in grazing animals. It is clear that there is a need for much further work on the factors influencing the availability to livestock of the mineral elements in herbage.

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SELECTIVE ION UPTAKE AND IONIC BALANCE

Summary of paper by W. Dijkshoorn

Selectivity

Herbage composition reflects ion uptake from the soil relative to the total dry weight produced. If K is released by the soil at a slow rate relative to the demand, the increase in plant weight becomes entirely controlled by the intake and K accumulates at the minimum content of 200 me./kg dry matter. If there is sufficient Na this stimulates further growth of a K deficient ryegrass and K may fall to 100 me./kg while Na accumulates in large excess. But Ca and Mg are unable to accumulate in excess, even in the absence of K, owing to slow uptake and translocation.

This indicates the existence of a monovalent cation uptake system, carrying large amounts of K and Na with strong mutual competition, and a four-ion system, carrying smaller amounts of all cations and without much preference for any of them. These two systems provide the herbage with the salt cations K, Na, Mg and Ca with me. sum C.

Ionic balance

In the tissues, part of the cations C is balanced by the inorganic anions NO_3^-, Cl^-, $H_2PO_4^-$ and $SO_4^=$ which are retained in the ionic form after the metabolic utilization of the greater part of the nitrate and sulphate absorbed. Their me. sum is A. The excess of C over A is balanced by carboxylate anions of the common organic plant acids. The me. of carboxylates in the tissues equals (C-A). With adequate supply (C-A) is maintained at 1000 me./kg dry matter, but there are fertilizer formulas, which make (C-A) to fall to subnormal levels and were found to prevent maximum growth, even if there is sufficient uptake of all essential elements. This indicates nutritional stress on the balance of accumulation, and the (C-A) content as a factor essential for maximum growth.

Attention will be confined to the ionic balance as a tool for systematic investigations on mineral composition and growth in relation to fertilization.

DISCUSSION

Whitehead mentioned contradictory results concerning the effect of nitrogenous fertilizer on the copper content of herbage. Hartmans pointed out that there is a close relationship between crude protein and copper, and that difference in response may have been caused by differences in crude protein level between treatments.

Bosch commented that management (cutting or grazing) may have much influence on the mineral composition of the subsequent cut which was not mentioned by Whitehead. Whitehead, in reply to Bosch said that the returnings from grazing are very important.

Anslow asked if the (C-A) level in grass could be raised to higher values e.g. 1500 me./kg d.m. Dijkshoorn expanded this by stating that such higher values may occur with K shortage in ryegrass supplied with Na, but that values higher or lower than the normal of 1000 me./kg d.m. indicate unbalanced nutrition.

To a further query from Whitehead on critical Cl levels Dijkshoorn said that values higher than 300 me./kg d.m. should be considered undesirable as they could significantly lower the level of (C-A).

Whitehead pointed out that plant analysis for K is indicative of K status only when K is lower than 400 me./kg d.m. When higher than 600 me./kg d.m. K must have been in ample supply. Dijkshoorn further commented that cation supply is mainly delegated to K and that higher levels are required to maintain the level of (C-A) at the normal value.

In reply to the question of Wilson whether there is any means to control the Si content by fertilizer Dijkshoorn said that Si is non-ionic at tissue pH and does not participate in the ionic balance so that Si was not studied.

Whitehead asked about the significance of nitrate: phosphate relationships to which Alberda answered that nitrate correlates with crude protein, the higher the crude protein the greater the proportion of protoplasmatic tissues high in phosphorus.

SIMULATION OF PLANT AND ANIMAL GROWTH

P.J. Radford

Recent work at Hurley on the construction of mathematical models associated with production from grassland has led us to investigate the use of the computer language DYNAMO for simulating biological systems. Our first objective was to construct a simple model of an animal (e.g. a lamb) which itself could be used as a sub-system of a larger more complex biological system. We chose to simulate the production of lambs, initially considering the process as being divided into two stages but with the ultimate intention of combining the resultant models into one. The main features of the first stage of the system being simulated are:

a. lambs taken from the ewe when 24 hours old,

b. offered cold milk substitute at 20 % dry matter ad libitum for the first three weeks,

c. turned out to sainfoin pasture at two weeks of age,

d. milk substitute rationed to 600 g liquid after three weeks,

e. no milk substitute offered from the end of the sixth week,

f. the first stage ends at the end of the seventh week.

Fig. 1 shows the flow diagram of the first stage of the system. It has been drawn according to the conventions given in 'Industrial Dynamics' by Forrester (1961). All inputs to the system are expressed in Digestible Organic Matter but the final output, live weight, is expressed in kg. The level 'Feed in Animal' (FA) performs a similar function to the level 'Plant Reserve' to be found in De Wit's maize model. In effect is is an imaginary reservoir from which nutrient intake is distributed to the various parts of the animal. One important part of the model is that section which converts DOM (above maintenance and activity requirement) into live weight gain. It was found that very little information is available about this conversion factor, expecially for lambs between birth and about 20 kg live weight.

Fig. 2 gives the results of the simulation program based on this stage of the model, together with actual experimental results. The measure of agreement between the two is encouraging.

During the second stage of the lamb production process the animals now seven weeks of age enter a rotational grazing system.
The main features of this system are:

a. The seven paddocks of S23 ryegrass are cut 14 days before entry of the lambs.

b. About 10 % of the total number of lambs form the 'PILOT GROUP'. The purpose of this group is to indicate by their performance the potential live weight gain of animals under the particular conditions of the trial but with no limitation in the quantity of food available to them. These therefore graze each paddock first.

c. The 'MAIN GROUP' of lambs comprising the majority of the lambs follow the pilot group around the paddocks. It is intended to control the rate of gain of these animals at rates not below 80 % of those of the pilot group.

d. The remaining animals form the 'SCAVENGER GROUP'. Since this group graze the paddocks immediately following the main group their intake is restricted by the amount of grass left over.

e. All the three groups are moved to successive paddocks at a specified shifting interval e.g. every four days.

f. At each shifting time the live weight of each animal is measured. If the mean live weight gain of the main group over the last four shifts (16 days) is less than 80 % of the mean live weight gain of the pilot group then a specified number of animals are transferred from the main to the scavenger group.

Fig. 3 shows our 'Typical Lamb' model taken from the first stage. For our present purposes the main feature of the model is the output 'Live Weight' (LW) which is determined by the 'Herbage Available Per Animal' (HAPA). For this reason this whole system will appear in future models as a sub-system indentified by these two parameters.

Fig. 4 is the flow diagram of the second stage of the fat lamb production system. Three 'Typical Lambs' are incorporated in order to simulate the grazing of the pilot, main and scavenger groups respectively. The seven paddocks of the rotational grazing system are adequately represented by the seven 'boxcars' of a DYNAMO 'boxcar train with a 'cyclic shift' i.e. a shifting interval of four days. Information regarding the live weight of the pilot and main groups of animals is stored in the 'linear boxcar trains' (LWB1 and LWB2) in order that the live weight gains over a period of 16 days may be calculated. The gain of the main group is compared with that of the pilot group and various DYNAMO mechanisms enable animals to be transferred from the main to the scavenger groups if the ratic of the gains is less than 80 %. The results of actually running this model are given in Fig. 5. During the second rotation (after 28 days) the main group of animals decline in performance relative to the pilot group. The scavenger group however maintain their potential for growth until the size of the group is increased to the extent that the regrowth of the sward is insufficient to meet their requirements.

A model such as this can be most useful for comparing the effect of different management strategies and enabling one to select the most promising of a number of systems. A further advantage of this type of model is that by changing some of the minor parameters the effect on the whole system are to be found.

Our next step is to join the two stages of lamb growth together in order to produce a single model. This has been achieved quite readily with DYNAMO but such an operation on highlights one of the weaknesses of the language. Quite a large number of dummy variables must be introduced in order to suppress the activity of the rotational grazing section during the weaning stage and vice versa. This exercise challenges one's ingenuity but seems to be rather inefficient. Also the inability of DYNAMO to compute the equivalent of FORTRAN 'DO' loops means that a separate set of equations is needed for each different type of animal in the system although in each case the basic model is identical. Balanced against these disadvantages is the very short running time needed for a DYNAMO programme as compared with other simulation languages. However one or two new digital simulation languages seem very promising and we are currently investigating the use of DSL/90.

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Fig 1.

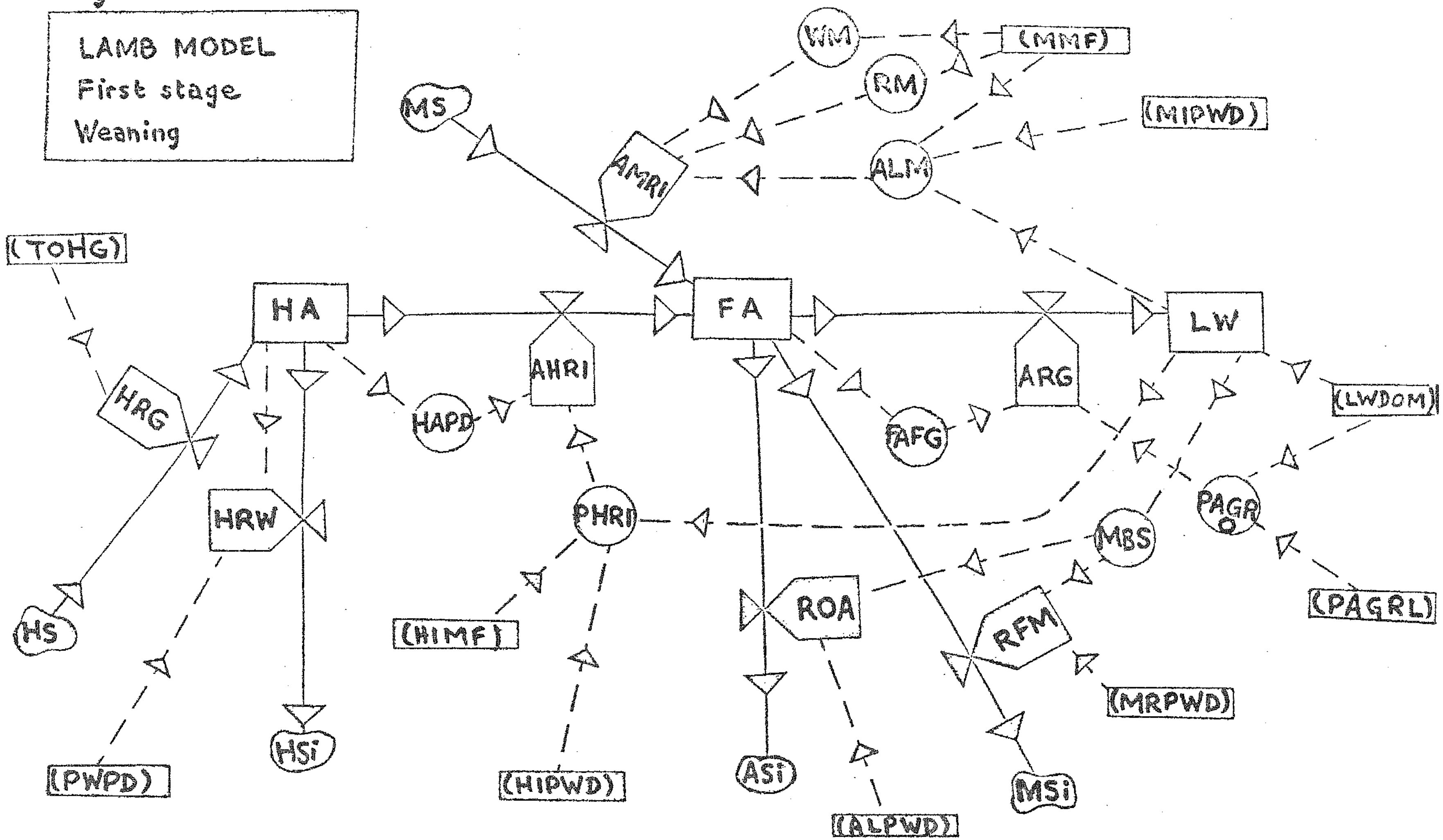

LAMB MODEL
First stage
Weaning
MS
AMRI
WM
RM
ALM
(MMF)
(MIPWD)
(TOHG)
HA
FA
LW
HRG
HRW
AHRI
HAPD
ARG
FAFG
PHRI
MBS
PAGRO
(LWDOM)
(PAGRL)
ROA
RFM
(MRPWD)
HS
(HIMF)
(PWPD)
HSi
(HIPWD)
ASi
(ALPWD)
MSi

Fig. 2. PAGE 12 C15PJR

LW=W, LWG=G, HA=H, AHRI=I, AMRI=M

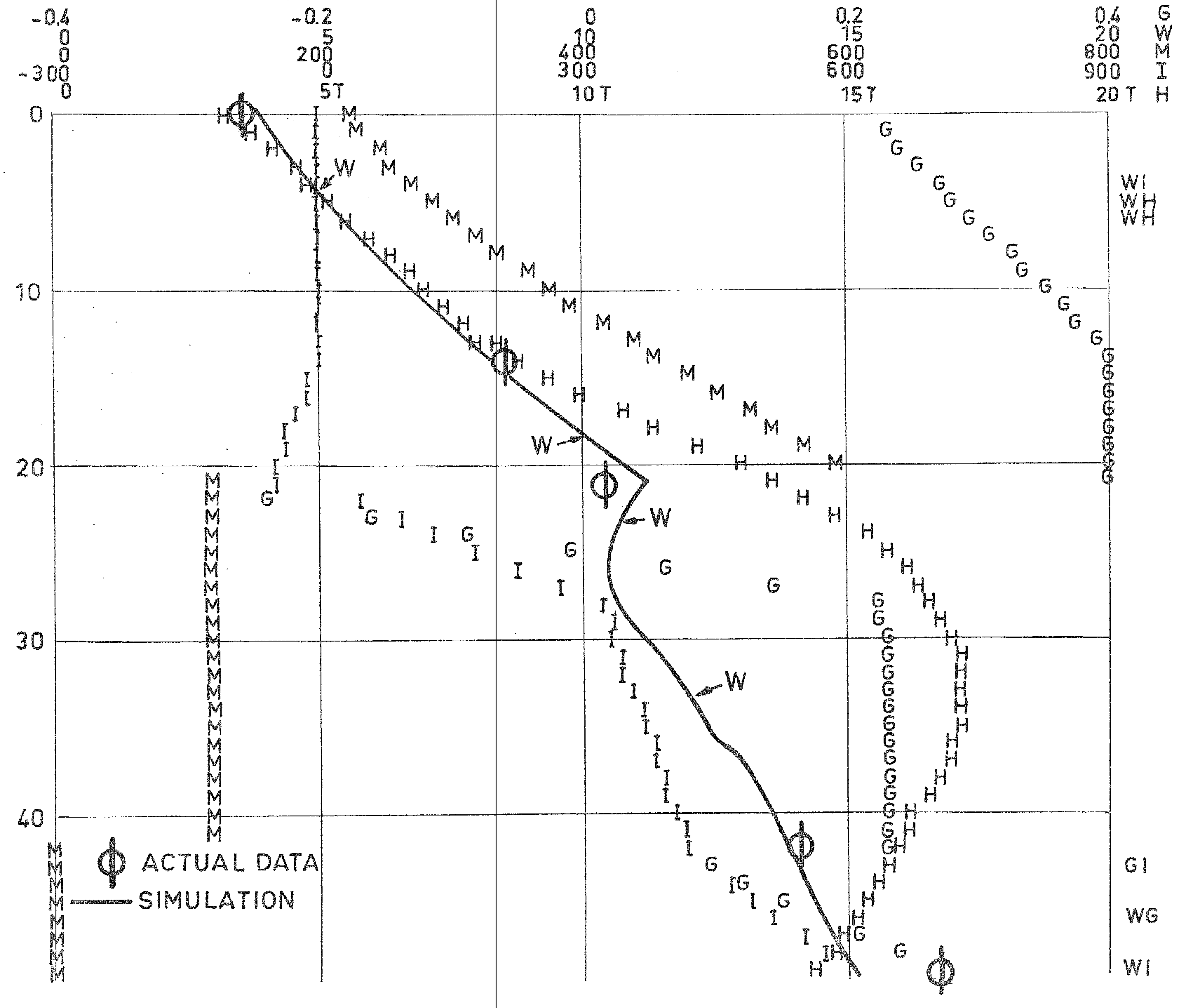
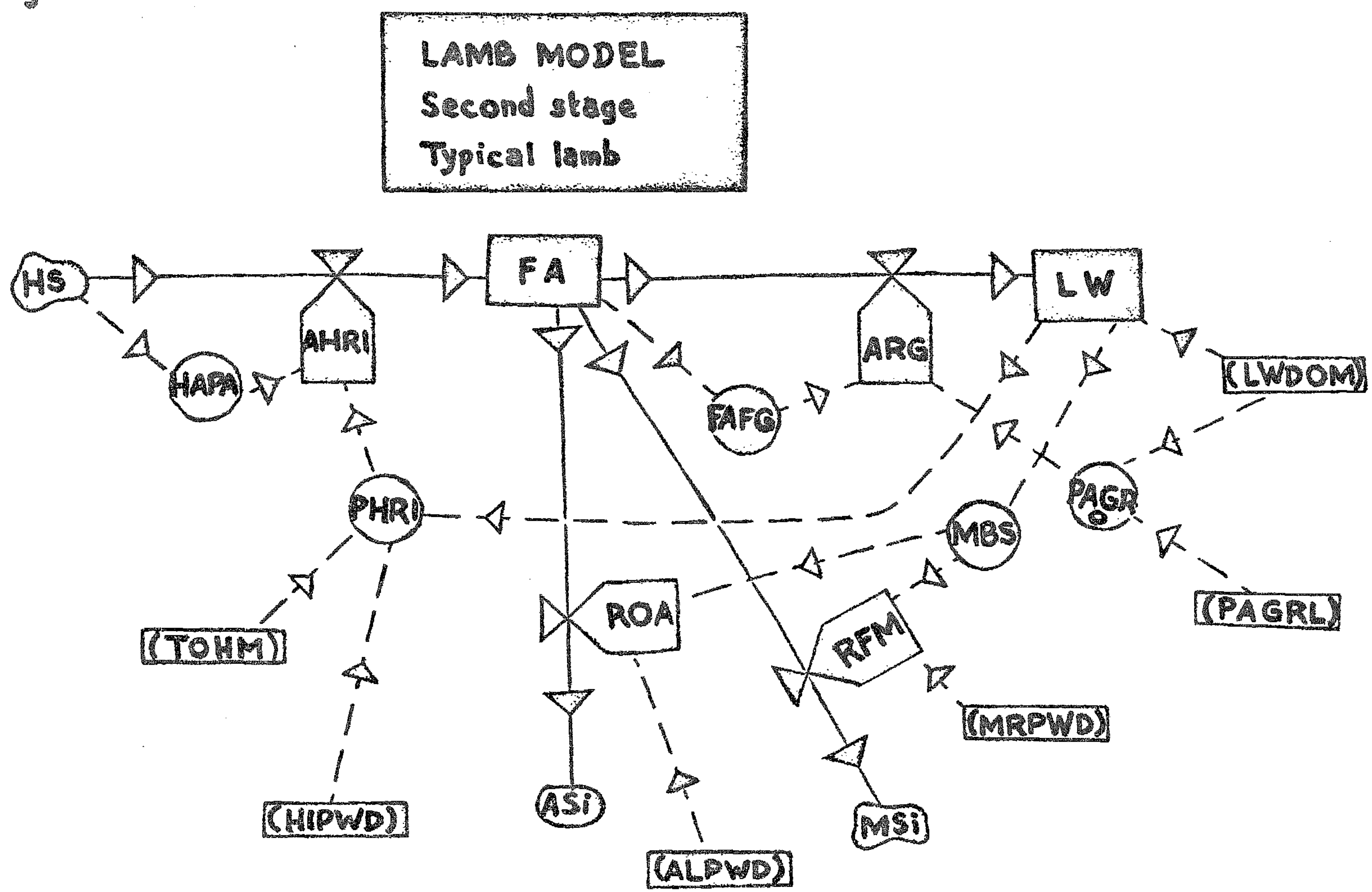


Fig 3.



LAMB MODEL
Second stage
Typical lamb
HS
HAPA
AHRI
FA
FAFG
ARG
LW
(LWDOM)
PAGR
(PAGRL)
MBS
PHRI
(TOHM)
(HIPWD)
ROA
RFM
(MRPWD)
ASi
(ALPWD)
MSi

Fig 4.

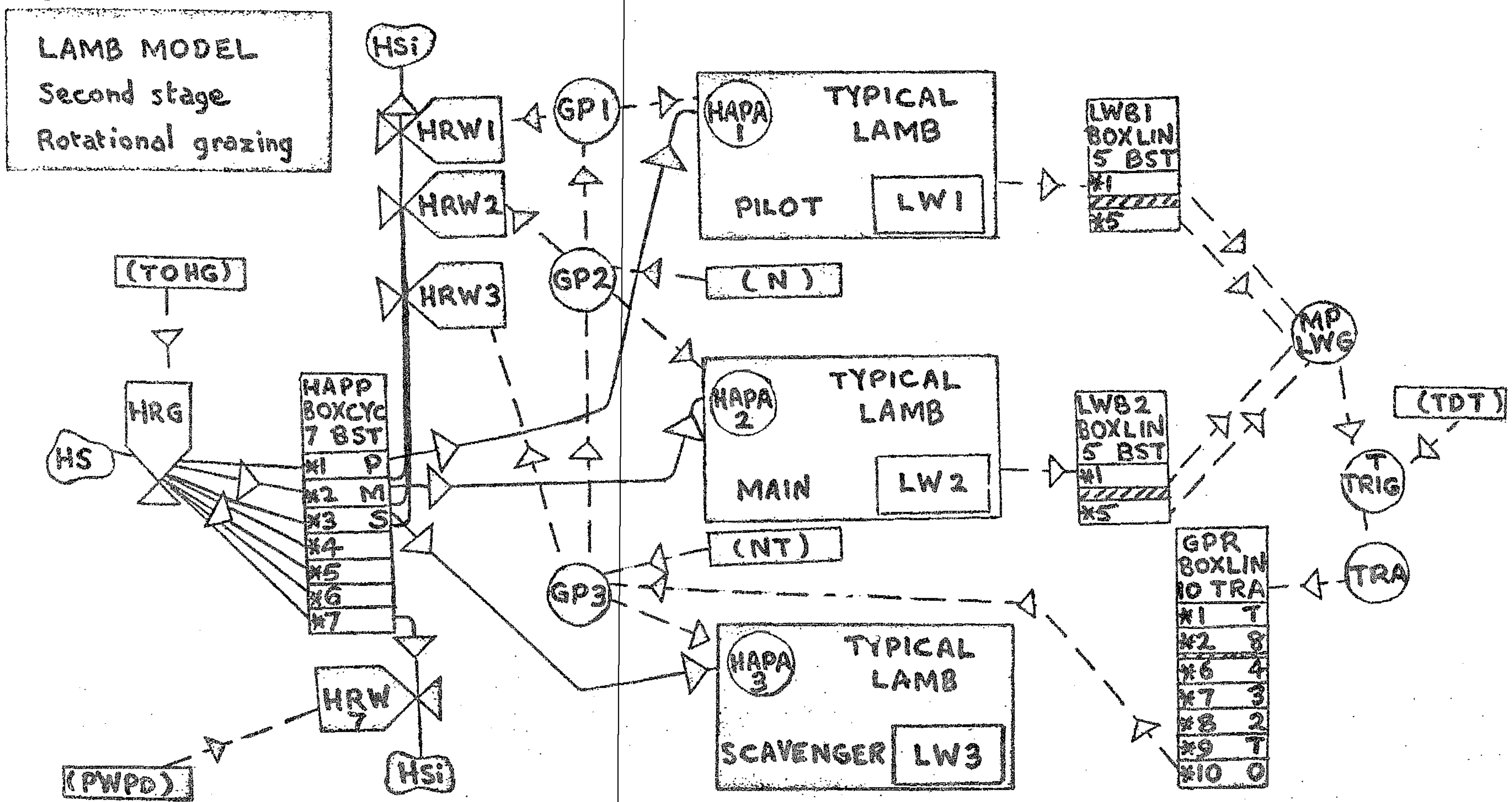
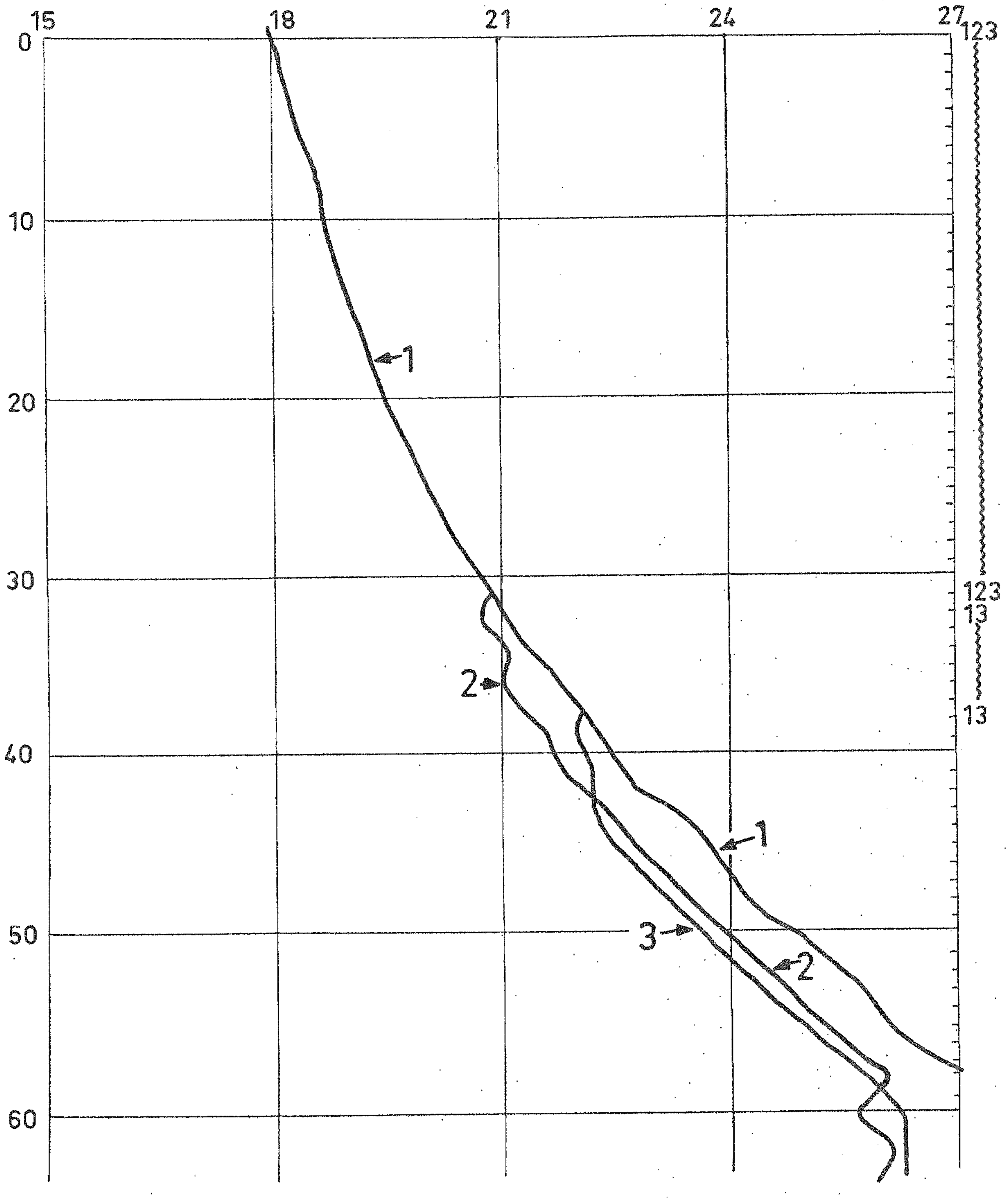

LAMB MODEL
Second stage
Rotational grazing
HSi
HRW1
HRW2
HRW3
(TOHG)
HRG
HS
HAPP BOXCYC 7 BST
*1 P
*2 M
*3 S
*4
*5
*6
*7
HRW 7
(PWPD)
HSi
GP1
GP2
GP3
(N)
(NT)
HAPA 1
TYPICAL LAMB
PILOT
LW1
HAPA 2
TYPICAL LAMB
MAIN
LW2
HAPA 3
TYPICAL LAMB
SCAVENGER
LW3
LWB1 BOXLIN 5 BST
*1
*5
LWB2 BOXLIN 5 BST
*1
*5
MP LWG
T TRIG
(TDT)
TRA
GPR BOXLIN 10 TRA
*1 T
*2 8
*6 4
*7 3
*8 2
*9 T
*10 0

Fig. 5.   PAGE 6   022 PJR

LW1 = 1, LW2=2, LW3=3,



DYNAMO MNEMONICS FOR LAMB MODELS AS IN FIGS. 1 – 6

	TYPE	
AGR_1	R	ACTUAL GROWTH RATE PILOT
AGR_2	R	ACTUAL GROWTH RATE MAIN
AGR_3	R	ACTUAL GROWTH RATE SCAVENGER
AHRI	R	ACTUAL HERBAGE RATE OF INTAKE
ALMIR	A	AD-LIB MILK INTAKE RATE
ALMMF	A	AD-LIB MILK MANAGEMENT FACTOR
ALMMX	C	AD-LIB MILK MANAGEMENT FACTOR (INITIAL VALUE)
ALMMY	C	AD-LIB MILK MANAGEMENT FACTOR (SUBSEQUENT VALUE)
ALPWD	C	ACTIVITY LEVEL PER METABOLIC WEIGHT PER DAY
AMRI	R	ACTUAL MILK RATE OF INTAKE
ARG	R	ACTUAL RATE OF GROWTH
BST	A	BOXCAR SHIFTING TIME
FA	L	FEED IN ANIMAL
FAAFG	A	FEED IN ANIMAL AVAILABLE FOR GROWTH PER DAY
FAFG	A	FEED AVAILABLE FOR GROWTH
FAX	C	FEED IN ANIMAL(X)
FST	C	FIRST SHIFTING TIME
GP	A	GRAZING PRESSURE
GPR	B	GRAZING PRESSURE REGULATOR
GRI	A	GROWTH RATE INDICATOR
HA	L	HERBAGE AVAILABLE
HAPA	A	HERBAGE AVAILABLE PER ANIMAL
HAPD	A	HERBAGE AVAILABILITY PER DAY
HAPP	B	HERBAGE AVAILABLE PER PLOT
HAPPY	C	HERBAGE AVAILABLE PER PLOT (INITIAL VALUE)
HIMF	A	HERBAGE INTAKE MANAGEMENT FACTOR
HIPWD	C	HERBAGE INTAKE PER WEIGHT PER DAY
HRG	R	HERBAGE RATE OF GROWTH
HRW	R	HERBAGE RATE OF WASTAGE
LMBS	A	LOGN METABOLIC BODY SIZE
LW	L	LIVE WEIGHT
LWB	B	LIVE WEIGHT BOXCAR
LWDOM	C	LIVEWEIGHT TO DIGESTIBLE ORGANIC MATTER CONVERSION FACTOR
LWG	S	LIVE WEIGHT GAIN
MBS	A	METABOLIC BODY SIZE
MIPD	A	MILK INTAKE PER DAY
MIPWD	C	MILK INTAKE PER WEIGHT PER DAY
MPLWG	A	MAIN TO PILOT LIVE WEIGHT GAIN RATIO
MRPWD	C	MAINTENANCE RATE PER METABOLIC WEIGHT PER DAY
~~N~~	~~C~~	~~TOTAL NUMBER OF LAMBS~~
NT	C	NUMBER TRANSFERRED
PAGRL	A	POTENTIAL ABSOLUTE GROWTH RATE LIVEWEIGHT
PAGRO	A	POTENTIAL ABSOLUTE GROWTH RATE (ORGANIC MATTER)
PHRI	A	POTENTIAL HERBAGE RATE OF INTAKE
PWPAD	C	PROPORTION WASTED PER ANIMAL DAY
PWPD	C	PROPORTION WASTED PER DAY
RGC	C	ROTATIONAL GRAZING CONSTANT
RGI	A	ROTATIONAL GRAZING INDICATOR
ROA	R	RATE OF ACTIVITY
ROGP	A	RECIPROCAL OF GRAZING PRESSURE
RFM	R	RATE FOR MAINTENANCE
RMR	A	RATIONED MILK RATE
SGI	A	SAINFOIN GRAZING INDICATOR
SIPWD	A	SAINFOIN INTAKE PER UNIT WEIGHT PER DAY
SRG	R	SAINFOIN RATE OF GROWTH
SST	C	SECOND SHIFTING TIME
TDT	A	TRANSFER DECISION TIME
TIME	L	TIME
TLWDM*	C	TABLE OF LIVE WEIGHT TO D.O.M. CONVERSION FACTOR
TMSI	A	TRANSFER FROM MAIN TO SCAVENGER INDICATOR
TOHG*	C	TABLE OF HERBAGE GROWTH
TOHM*	C	TABLE OF HERBAGE MANAGEMENT
TOSG*	C	TABLE OF SAINFOIN GROWTH
TRA	A	TRANSFER NOW
TTRIG	A	TRANSFER TRIGGER MECHANISM
WMR	A	WITHDRAWN MILK RATE

DISCUSSION (after De Wit's comments)

A question was raised regarding the simplicity of the typical lamb model presented by Radford compared to the very detailed model of the maize plant presented by De Wit.

In reply Radford pointed out that the two types of models were geared to slightly different applications. The lamb models were of most value when used as sub-systems of complicated farm management models where often the most important factors affecting the system were management decisions. He cited an explanation taken from MILSUM (1966) where it is shown that although, cells, organs, humans, families and communities are all interrelated systems and sub-systems, very little information regarding the response of cummunities can be deduced from a very detailed and precise knowledge of cells. However, a knowledge of families and humans would be of great value when studying communities. It is simply a case of deciding how deep one needs to go before the extra information produces a negligible effect on the output of the systems as a whole. He proposed to construct models at many different levels to be used for different purposes.

De Wit added that when considering the more general system then one could include in the model summaries of the results of the more remote sub-systems. It was certainly pointless to include all the fine detail of each sub-system within the larger, coarser system. For example the correct way of producing the model of a grazing system was not necessarily to combine the detailed physiological model of the grass plant with an equally detailed model of the animal.

Osbourn asked if any feature of homeostatic control had been incorporated in the lamb model. If not would the absence of such a component have caused the departure of the results of the model from the experimental results.

Radford suspected that the departure of the model from reality was bound up with the lack of knowledge of the digestible organic matter to live weight gain conversion factor especially at the change over from milk to mixed feeding. With regard to the possibility of compensatory growth of the animals after they had lost weight Radford stated that any available information on this subject could quite easily be incorporated in this model but to date his information was that there was little data to support this theory.

THE REGROWTH OF PLANTS AFTER DEFOLIATION

R.C. Anslow

The majority of experiments which have studied the effect of cutting on grass growth agree in demonstrating a reduction in the total annual yield as crops are cut more frequently, at least more frequently than twice or three times a year. Such an experiment, comparing rates of herbage production of perennial ryegrass cut either 3 or 6 weekly, is summarized in Fig. 1 (taken from Anslow, 1967).

From this, it can be seen that the higher total yield from 6-weekly cutting (11,600 kg/ha) than from 3-weekly (7,000 kg/ha) arose from a higher rate of production the whole season through. Plots which changed from 3- to 6-weekly cutting on successively later dates rapidly assumed the same rate of production as those plots which had been cut throughout at this frequency. The seasonal pattern of production was not very different at one frequency or the other.

Explanations for such effects as these may not necessarily involve major differences in the rate of net assimilation of crops cut at different frequencies. We are only considering in such experiments differences in the production of dry matter above the height of cutting, this is a fairly small part of the total weight above the soil surface, and the proportion which it forms of the total weight of the aerial parts of the crop is demonstrated in Fig. 2. This shows the proportion of the aerial parts of a late-flowering variety of perennial ryegrass which were removed by cutting approximately once a month. The proportion, at most about 60 %, was found to be more variable than this in an earlier-flowering variety and in cocksfoot and timothy. Crops from the experiment described previously (Fig. 1) were analysed to show the distribution of the total dry-matter in successive strata above soil level. This showed that plots cut every 6 weeks could have as much as 82 % of their dry weight above 5 cm from the soil surface in early June and that the proportion could remain at about 60 % until September. However, plots cut every 3 weeks had at most 61 % above cutting height in May and the proportion fell to around 40 % for most of the summer.

Such differences as these in the efficiency of the harvesting process may explain a large part of the reduction in yield associated with frequent cutting. It is not immediately necessary to consider how the physiology of the sward has been altered to explain differences in agricultural production.

However, it is unlikely that such a major interference with the crop and its environment would be without some influence on the growth of each grass plant or each tiller and it is necessary for us to consider how the crop can respond to the incidence of cutting. The extent to which we see any response at all will depend on the severity of cutting, how close it is to soil level and how frequently it is repeated.

The following list includes some ways in which cutting could influence the crop and subsequently we will consider how the grass plant is known to be capable of responding to such influences.
Cutting entails:

(a) the removal of some fraction of previously synthesized tissue, which may itself be increasing in weight or may be exporting assimilates to other parts of the plant (Williams, 1964). It may, however, involve the removal of tissue which is losing weight through anabolic processes (Navasero and Tanaka, 1966), through microbial decomposition or through abscission from the parent plant.

(b) the removal of a considerable quantity of mineral nutrients in various degrees of assimilation, nutrients in respect of which the plant is usually in a state of stress.

(c) a reduction in the light-intercepting capacity of the crop and, probably, a change in the age-distribution pattern of the leaves in the crop. The upper layers of a sward appear to contain a preponderant amount of leaf area of young leaves and the more horizontal older leaves largely occupy the lower strata. The rate of net assimilation of the leaves left behind after cutting could be less than that before cutting (Pearce, Brown and Blaser, 1965) due to the higher average age of the expanded leaf area. Alternatively it could be higher than formerly because of the higher average illumination per sq. cm of leaf surface after cutting.

(d) a change in the micro-environment of the crop resulting largely from the increase in the proportion of daylight which reaches soil level following cutting. This is likely to lead to higher soil temperatures and to higher temperatures of those plant parts which occur near soil level (Mitchell and Bieleski, 1964). The rate of metabolism of these parts could well be increased and this could be particularly relevant as the vegetative shoot apices are mostly within a few mm of the soil surface. The increased temperature of the soil surface and the improved rate of diffusion of water vapour following removal of the crop canopy could lead to more rapid drying of the surface with possible repercussions on root activity and availability of nutrients. The rate of diffusion of carbon dioxide among the leaves remaining after cutting is likely to be higher than in an uncut crop and there would be less likelihood of diurnal deficits occuring in such swards. There are indications of the possible extent of these factors from the literature but there is a need for a fuller description of the environment in swards of contrasting structure and work is beginning at Hurley to provide such information.

From what we know of the physiology of the grass plant, cutting can lead to:

(a) a possible interruption in the outward extension of the root system which may involve a halt in root growth for days or weeks (Crider, 1955; Garwood, 1965). There is also the possibility that the adsorption of nutrients from the soil solution by existing parts of the root system might cease after cutting (Davidson and Milthorpe, 1966).

(b) a reduction, at low levels of soil moisture, in the uptake of water (Jantii and Heinonen, 1957). This, however, has not been recorded in experiments at Hurley in which water was lost at a constant rate before and after cutting (Garwood and Williams, 1967).

(c) a reduction in the concentration of soluble carbohydrates in stem bases (del Pozo Ibanez, 1963), presumably due to an excess of respiration over photosynthesis.

(d) an interruption in the process of formation of new tillers, in some species at least (del Pozo Ibanez, 1963).

(e) in some situations, a reduction in the rate at which new leaves appear on a tiller (see Anslow, 1966).

There are thus many ways in which the rate of growth of a sward could be affected by cutting, a number of ways in which the effect of cutting could be perceived and a number of ways in which the plants in the crop could respond to the altered environment. The actual effect, in a particular circumstance, would most likely depend on which conditions were most limiting to plant growth.

However, the growth of a crop is an integrated response so that, for instance, deficiency of nitrogen in the soil environment could finally make its effect felt in a reduced capacity of the crop to intercept daylight. The chief need for experimental evidence at present is a determination of the relative importance of these various influences and responses in a range of field situations and to outline the ways in which the plant responds as an integrated system.

One point that has arisen from much of this kind of work is that the growth system of the crop contains a considerable buffering capacity, an ability to accommodate variation in many forms of treatment so that imposed treatments often produce less marked results than might be expected (Humphreys and Robinson, 1966). The characteristic population of a grass crop is probably a basic factor in this inertia, a low density of plants per unit area leading to correspondingly bigger plants, more tillers resulting in smaller tillers and rapidly appearing leaves being narrower and shorter than those appearing more slowly.

An example of this inertia in a grass crop as it relates to its response to defoliation is shown in the following experiment, which was designed to investigate the relative importance of leaves of different ages to the growth of a crop of perennial ryegrass. Previous work had shown that few tillers in such swards have more than 3 green leaves. Fig. 3 demonstrates this point, showing that throughout the year 80 % of all tillers had either two or three green leaves. Leaving crops longer than one month, as was followed in the experiment from which these data were collected, does not perceptibly increase the number of leaves per tiller. Any leaf in excess of the expanding leaf and two expanded leaves shows signs of yellowing.

From experiments using labelled carbon in the carbon dioxide around the leaf we know that a leaf begins to export assimilates before it is fully expanded and after expansion it exports at first mostly to the apical meristem and the developing leaves and, towards the end of its life, mostly to the roots (Williams, 1964). There is no evidence that an old leaf ever again imports assimilates. These data are at present mostly qualitative and mostly refer to either individual tillers or to young, individual plants. In a dense crop, the rates of assimilation of the older leaves may be very low, due to the ontogenetic fall in rate of assimilation with age (Jewiss and Woledge, 1967) and due to their occurrence, so we suspect, in regions of poor illumination and possibly of restricted carbon dioxide diffusion.

The relative importance of these three green leaves to the rate of dry-matter production was examined by removing the lamina of particular leaves from each tiller in a 30 x 30 cm plot in June. Leaves were removed so as to leave behind plots with either an expanding leaf and two expanded leaves on each tiller (treatment A), or an expanding leaf and the last fully expanded leaf (treatment B) or an expanding leaf only (treatment C).

At this time of year, the leaf sheaths in this species are very short and are mostly covered by dead leaf sheaths so that the great majority of the photosynthetic ability of each leaf unit was removed when the lamina was detached.

During regrowth after the first defoliation, tillers were examined every few days in treatment C and the number of expanded leaves on 50 random tillers was found. When this number showed an average of one per tiller the defoliation routine was repeated on all plots of these three treatments. At each harvest, leaves were dried and weighed. Between June and October, there were seven harvests; after the last one the crop was cut at ground level, and tillers were counted, dried and weighed.

Two other treatments were also included in the experiment. In D, the herbage was clipped off with shears, leaving a stubble about 5 cm high and the clipping was repeated on alternate defoliations of A, B and C so that there were 3 clippings over the whole period. In E, the sward was left untouched except to clip off inflorescences on a number of occasions.

The total dry-matter production from each treatment therefore consists of the leaves, if any, removed at each clipping, the weight of any inflorescences clipped off and the crop remaining after the last harvest. Fig. 4 shows the results. The weight of foliage removed was very similar in the four treatments A, B, C and D. The weight of inflorescences removed was a very small proportion of the total weight and the weight of crop left after the last harvest accounted for almost all the differences in the total weights recorded.

Of the selectively defoliated treatments, the one in which leaves were removed only when senescent changes were visible (A) produced the greatest amount of dry-matter but this was not significantly greater than B and total dry-matter was significantly depressed only when all fully-expanded leaves were repeatedly removed (C).

Differences in leaf area were not measured but C would appear to have had only 20 % of the leaf area of A immediately after each defoliation and measurements of light intensity in each crop demonstrate that light interception in C was far from complete. Since the total dry-matter formed is not greatly different between A and B and C, the net assimilation rate of leaves in C must have been much higher than in A.

Cutting the grass sward approximately once a month, as in D, was seen to be as severe in its effect on growth as removing all fully expanded leaves within a few days of their full expansion. This indicates that removal of all the youngest foliage, although infrequently, imposed a considerable check to the growth of the crop.

In the untouched swards (treatment E) there had obviously been a considerable loss of weight through decomposition. From knowledge of the number of leaves which had probably emerged from June to October and knowing how many leaves were present at the end of the experiment, it was possible to make an assessment of the probable loss of weight through decomposition. This appears to indicate that such a treatment had produced the highest yield of all and, in fact, even without the addition of the estimate of loss through decomposition, its production was as great as that of treatment A. This result appears to be illogical if permitting leaves to remain on the plant from B to A had no significant effect on growth but leaving them longer still did so, although it is possible that decomposing leaves provide some benefit to those growing. It must be pointed out that the comparison of E with A, B or C is not straightforward. These latter swards were subject to intensive and repeated handling which might be expected to have reduced their growth below that of less disturbed swards, such as E. It is impossible to know how much this influence did occur but it might have been considerable. Treatment D was also handled much less than A, B or C so that perhaps the reduction in yield caused by clipping should be greater than the figures indicate.

It does not seem likely that the depression in growth caused by removing leaves at earlier stages of development can be explained by a reduced uptake of mineral nutrients. There was a much higher concentration of nitrogen and of potassium in the herbage and in the crop remaining where leaves had been removed at earlier stages and the total quantity of nitrogen and potassium recovered in herbage was greater in these treatments than in A or E. It appears therefore that the results shown depend chiefly on the differences in the period during which leaves were present and were active in carbon assimilation on each tiller. In spite of the demonstration of such an effect, the chief single conclusion from the experiment relates to the buffering capacity of the growth processes in the grass crop in which changes in the area of the assimilatory surface can be compensated to a considerable degree by changes in the rate of assimilation of the foliage remaining.

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Because Sonneveld was absent through illness, the paper of Anslow was answered by Alberda. He discussed the shape of the growth curve after defoliation and the possibility of predicting the total herbage production for a given cutting scheme.
A paper dedicated to this subject has been published in the Neth.J.agric. Sci. 16 (1968) 142-53.

DISCUSSION

On a question of Wilson whether Anslow would agree that the slow rate of growth that Alberda had indicated for the initial regrowth period actually occurs in swards, Anslow answered that growth rate is hard to define because it may refer to the whole plant, the aerial parts on the production above cutting height.

As to the sharp decrease of the apparent rate of dry-matter production in the field some time after reaching a closed canopy, especially in the second half of the season (see Alberda: J. Br. Grassl. Soc. 20 (1965) 41-48), De Wit said that the increased respiration could not account for this. Contrary to the meaning of Alberda and De Wit, Anslow and 't Hart believe that decomposition is an important factor.

In reply to a question of Woodford Alberda confirmed that growth can be considerably reduced by handling.

Fig. 1. The rate of production of herbage and the emergence of inflorescences from plots of perennial ryegrass cut at intervals of either 3 or 6 weeks.

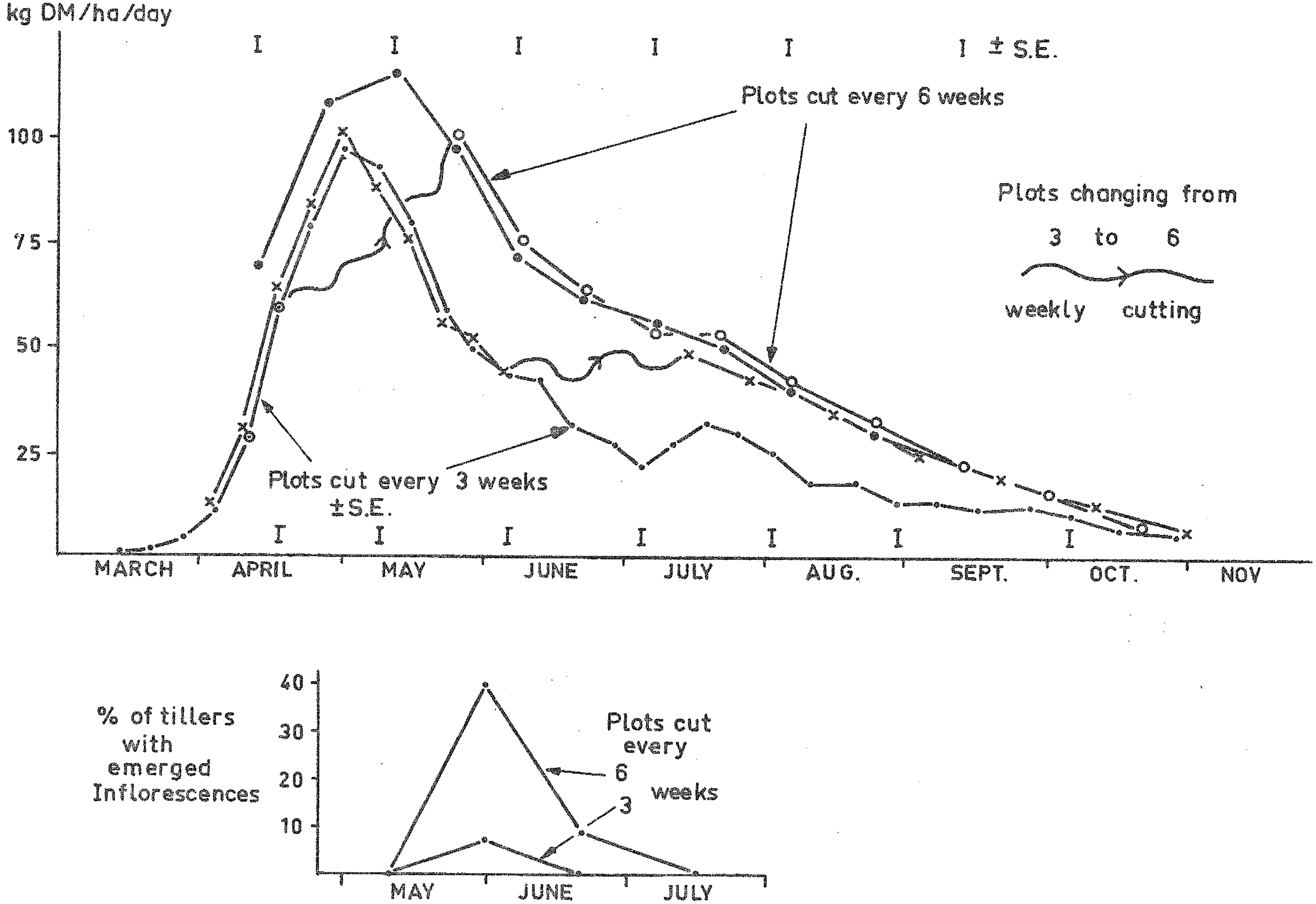

Fig. 2 The proportion of the aerial parts of perennial ryegrass (S.23) which can be removed by cutting at 4 cm. above soil level, approximately once a month

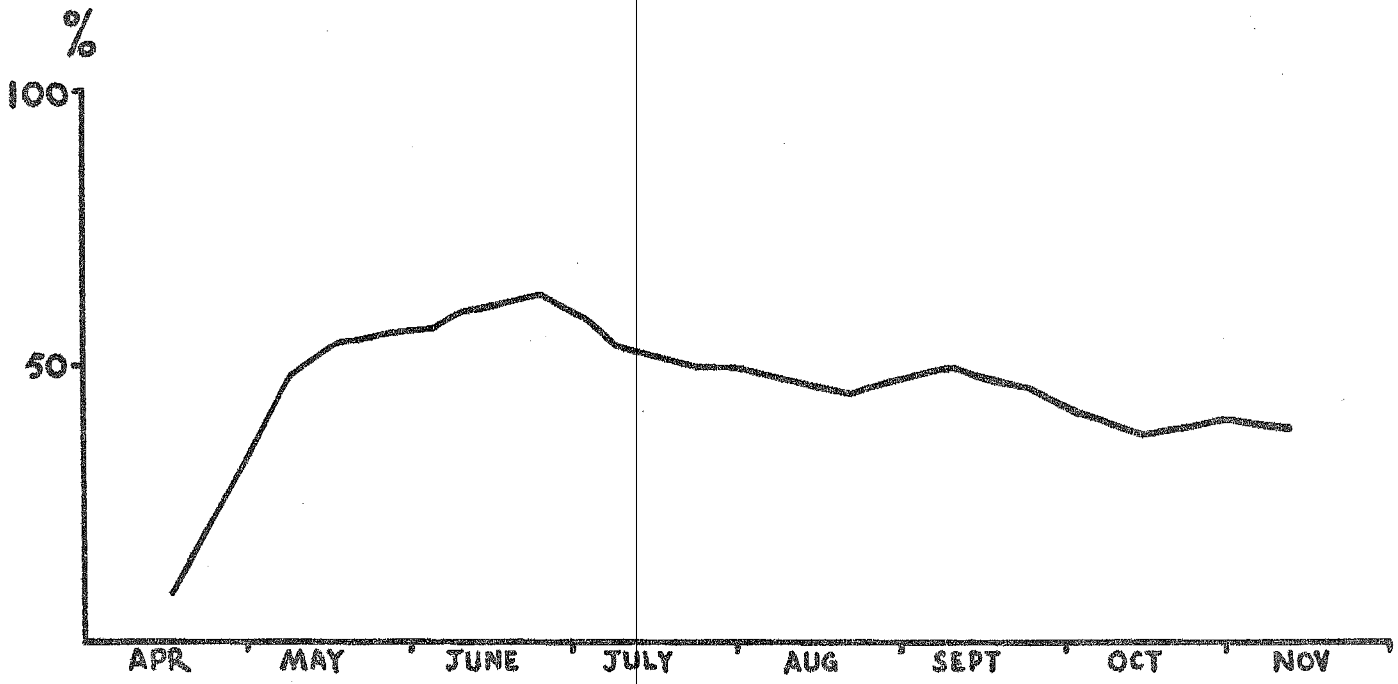

Fig.3 The proportion of tillers in perennial ryegrass (S.24) with 1, 2, 3 or 4 green leaves per tiller in plots cut approximately once a month.

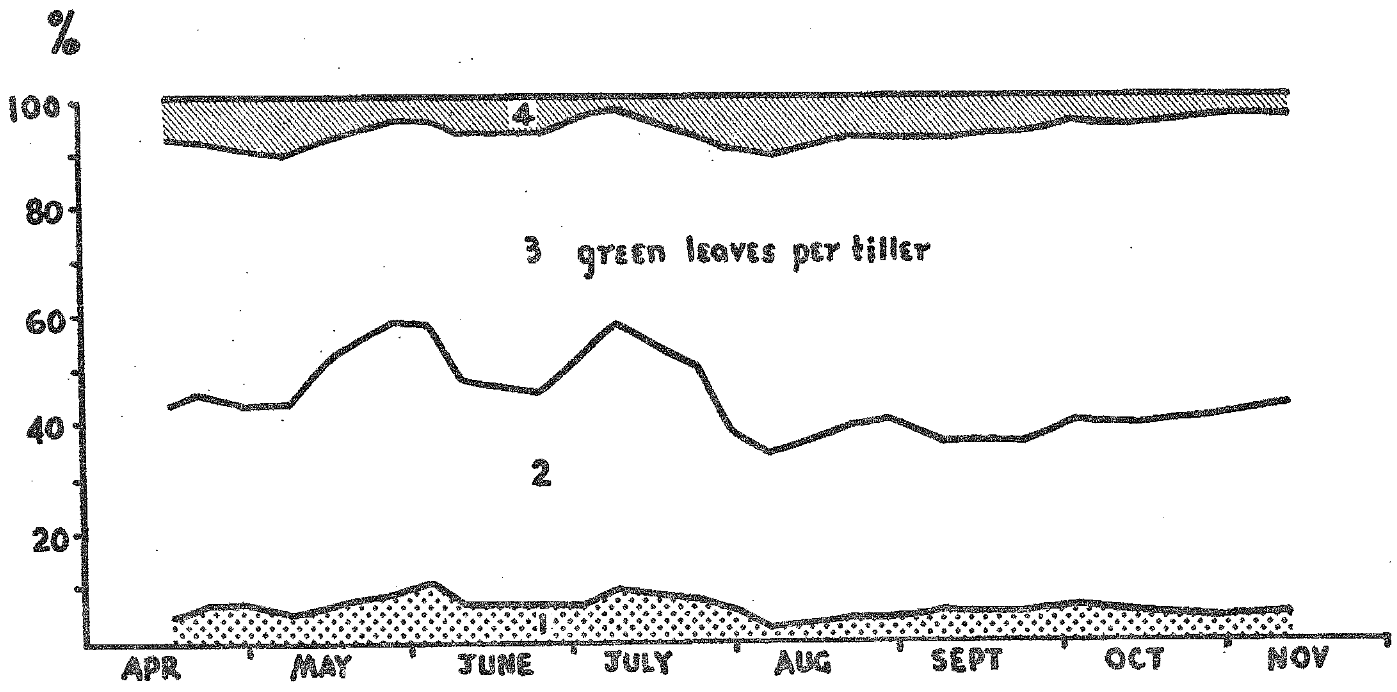

Fig.4

Production of dry matter by swards of perennial ryegrass, differing in average age of foliage.