

A critical appraisal of some grassland models

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Grassland and ecosystem models have been proliferating since the beginning of the IBP in 1968. From a rather ambitious beginning, total ecosystem and even less comprehensive grassland models have become increasingly complex so that the task of comprehending someone else's models has become a formidable, if not an impossible task. True, the actual intellectual exercise in ecological holism has increased awareness of certain aspects of grassland systems that would otherwise have been ignored (Noy-Meir, 1975a). This is useful in itself but is essentially a spin-off that hardly justifies the scale of effort involved in the more complex ecosystem models. Many reported modelling efforts conclude with a declaration that the results are reasonable but the model needs further development; and that there are large gaps in our knowledge of the processes that make the systems run (Patten, 1971). Many are sitting ducks for withering criticism like that of Passioura (1973).

And yet, the enthusiasm that produced many of these complex abstractions of grassland systems cannot be dismissed as misguided preoccupation with computerized science fiction because the challenge is real and the approach is intuitively promising. How else will the burgeoning explosion of research results in biology, and grassland science in particular, be marshalled into a usable, integrated form, meaningful beyond the restrictions of the individual analytical disciplines? There certainly is an overshoot of complexity and an undershoot of sound conceptualization, but many of these 'first generation' ecosystem-like models can be seen as exploratory exercises that are more like tests of a new methodology than applications of it. Now, after the international flurry of modelling activity has thrown up a growing pride of models on grassland and related systems, is it not time to have a closer look at some of them in order to see what has been achieved that is already of general interest and what pitfalls should be avoided? A comprehensive and balanced review, especially of the larger models, is called for, but will not be attempted here. The comparative study presented instead is intended as no more than an

introduction to a critical appraisal of grassland modelling that should become a permanent feature of such activity. The more pointed the criticism the greater the chance that the quality and status of grassland models will rise to a level that will make possible undisputed contributions to the understanding and management of grassland, and gain the grudging respect of anti-modellers.

What justification is there for grassland models?

Biological system models are said to be a means of hypothesis testing and as such are a research tool (Patten, 1970). They are also said to be the means whereby basic research results in plant physiology, soil science and agrometeorology are efficiently extrapolated to field conditions (de Wit, 1970). Grassland modellers often claim that, for them, modelling is all of this too, but mainly a management tool (Arnold & Bennett, 1975). One can object that if crop canopy models have reached a higher level of complexity, often very sophisticated complexity, without yet becoming management tools, how can such a claim be seriously made for a grassland system where the grazing animal and its interaction with the growing pasture add greatly to the potential complexity of the system? The stock rejoinder is that if the farmer relies on available knowledge, experience, intuition and faith to manage the complexities of the system and often does so successfully, surely the application of a much more powerful battery of information and experience in an objective and dynamic reasoning scheme should be even more successful. The implication is that the criterion of scientific rigour has been replaced by one of pragmatic usefulness. Unfortunately hardly any grassland models have shown that they stand by the second criterion, which may be an even sterner master than the first.

It seems therefore, that grassland models today can be justified not on performance but on promise. A slim justification indeed, but the need is so obvious, and the alternatives so few and so demanding, that the promise will have to be proved vain before grassland modelling is given up.

The grassland system

A representation of the basic elements in a grassland system is given

in Fig. 1. The elements or state variables that are defined as part of the system interact with each other while the driving variables act unidirectionally on the system. The management variables have a more ambiguous status: they can be fixed and independent of the dynamics of the system or they can be flexible and dependent on information feedback, in which case they would be part of the system.

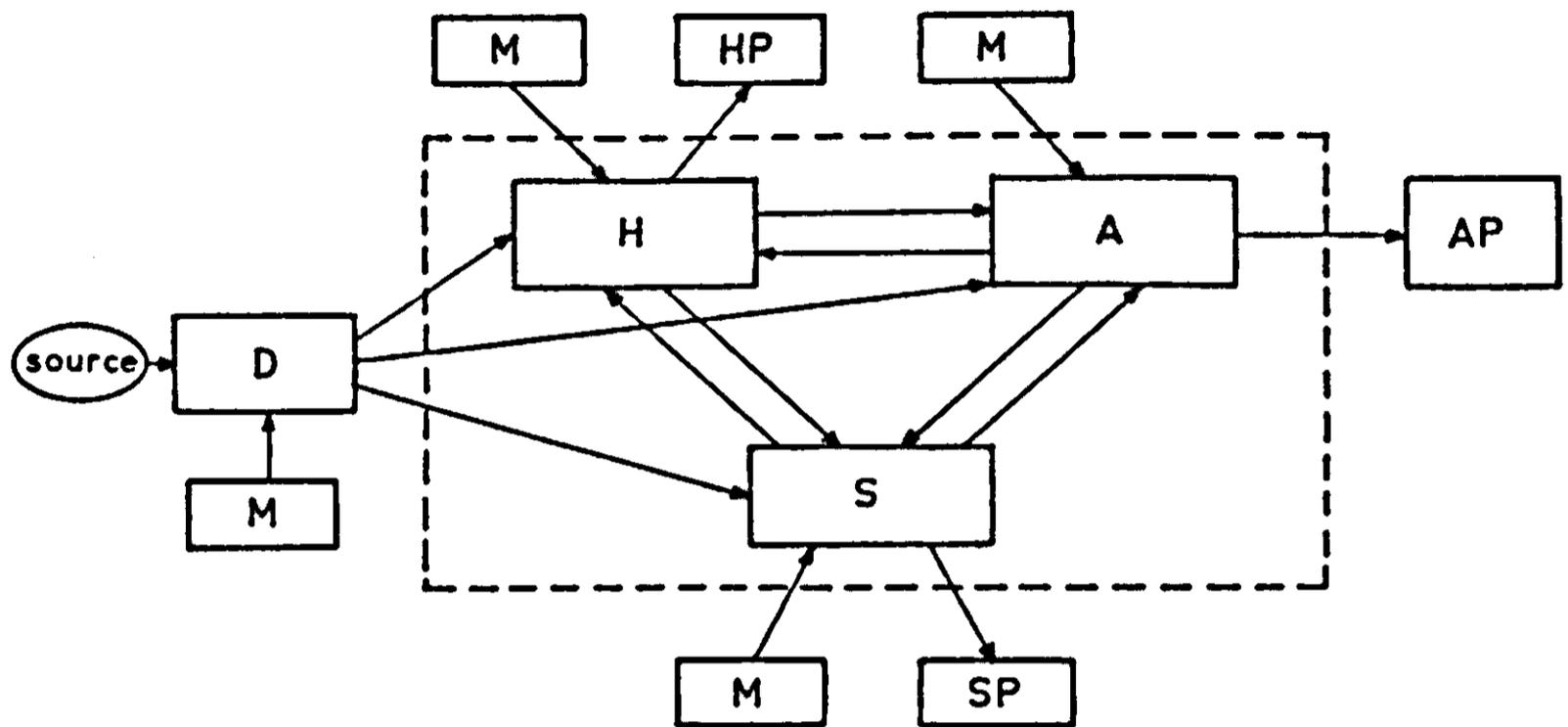
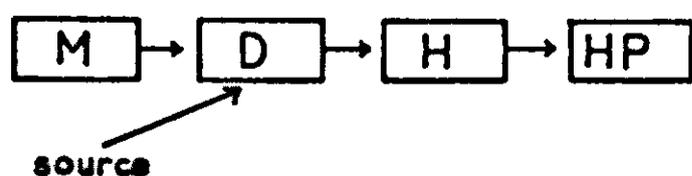


Fig. 1 | Some relationships between variables in a grassland system. (D = driving variable; M = management; H = herbage; A = animal; S = soil; HP = herbage output; AP = animal output; SP = soil output. ----- system boundary).

Management of the driving variables implies practices like irrigation and windbreaks; management of the herbage includes grazing systems, reseeding, haymaking and artificial forage desiccation; management of the animal includes supplementary feeding and protection from the elements; management of the soil includes chemical fertilization and cultivation. The outputs are obvious, those of soil including runoff, deep drainage and eroded soil. Even in such a highly simplified representation, it is clear that the interactions or feedbacks are numerous and complex. A crop canopy model that assumes moisture and nutrients to be non-limiting (as many do) treats the following relationships defined in Fig. 1:



These are 4 links only, compared to 9 when soil is added as a variable and 15 when animals are added. As most serious crop canopy models are already very complex, it is clear, *a priori*, that a grassland model will have to simplify many of the interrelationships to stay comprehensible and manageable. Simplification in this context means either omitting processes considered secondary or irrelevant to the main objective or reducing the number of component elements of a process and replacing them with a single empirical relationship or table. These elements become forcing functions or 'black boxes' unaffected by feedback from the rest of the system. As 'system' and 'feedback' are, in a sense, almost synonymous this procedure which is basic to biological modelling, reduces the sensitivity, generality, and in some cases, even the validity of a model. The alternative, severe circumscription of the scope of the model, has been chosen by many crop canopy modellers but it is cold comfort for the grassland modellers interested in pasture, animal and management interactions. Noy-Meir (1975c), however, has shown that the comfort may not be so cold, after all.

A list of some crop, grassland and ecosystem models selected to represent different levels of complexity and different approaches to the analysis of grassland systems, is given in Table 1. Growth models have received much more attention till now than have grassland models. Some of them are discussed here as background and reference to the discussion on grassland and ecosystem models.

Review of some growth, grassland and ecosystem models

The BACROS Model

BACROS, or basic crop simulator (de Wit et al., 1970 and 1976) is a detailed physiological process model that has been developed over a number of years by a continuing process of validation and experimentation. It assumes moisture and nutrients to be non-limiting but radiation and CO₂ content of the incoming air to be variable. The model simulates the photosynthesis and distribution of assimilate between shoot, root and respiration of specific crop canopies. It does not simulate morphogenetic change in the plant, so that leaf area must be entered as input. The model has been used mainly to help develop hypotheses about growth processes and direct an integrated research effort. The resolution of the model is very fine, the time constant being of the

Table 1 Some models and the system relationships they treat.

Model type	Name	System relationships treated (see Fig. 1)	Reference
Growth models (Crops and other spp.)	BACROS	D-H	Wit, C. T. de et al., 1976
	SPAM	D-(S)-H	Lemon, E. R. et al., 1971
	ARID CROP	D-S-H	Keulen, H. van, 1975
	Dryas empirical	D-H	Whitfield, D. W. A., 1972a
	Dryas process	D-H	Whitfield, D. W. A., 1972b
	Hurley-irrigation	D-S-H	Brockington, N. R., 1971
Grassland models (growth grazing)	Hurley, ewe-lamb	(D)-H-A-HP-AP	Edelsten, P. R. et al., 1973
	LEYFARM	D-S-H-A-AP	Arnold, G. W. et al., 1972, 1974a, b
	Armisdale	D-S-H-A-AP	Vickery, P. J. and D. A. Hedges, 1972a, b
	Simple, analytical	H-A	Noy-Meir, I., 1975a, b, c
Ecosystem models	PASTOR	D-S-H _f -A-AP	Goodall, D. W., 1967, 1973
	NEGEV	D-S-H _f -A _f -AP	Seligman, N. G. et al., 1971
Ecosystem models	PWNEE	D-S-H _f -A _f	Patten, B. C., 1972
	ISLE ROYALE	(D)-H-A ₁ -A ₂	Beyer, W. A. et al., 1973

Subscripts, i or integers, indicate that more than one species is involved.

order of a few minutes. The results of the simulation are generally very close to the measured results, in most cases within $\pm 10\%$ of the actual hourly photosynthesis rate. This model is cited here as an example of the tremendous effort that is needed to obtain accurate results from a basic model of even a limited aspect of crop growth. Even such a model requires an independent determination of a fundamental variable like leaf area. A fixed proportionality between shoot weight and leaf-area does not materially reduce accuracy in many situations, especially as the canopy becomes closed, but can introduce considerable error through positive feedback when leaf-area is low.

The SPAM Model

SPAM (Soil Plant Atmosphere Model; Lemon et al., 1971; Stewart & Lemon, 1969) is a similar process model developed specifically for corn but in principle adaptable to other crops too. It does not regard soil moisture as necessarily non-limiting and has photosynthesis dependent on soil moisture too. Essentially it is a micro-meteorological photosynthesis model of the type that is attracting much attention in many parts of the world. It, like BACROS, is an example of the detail and complexity of photosynthetic canopy models. Expanding them on the present level of detail to include morphogenesis, phenology, non-optimal soil moisture and nutrient conditions will make them so complex that, besides computer limitations, they will be extremely difficult to manipulate and comprehend. At that stage, simulation will become self-defeating in that it will probably create more problems than it will solve. Thus for more comprehensive models, and certainly for grassland models, certain elements of the basic models will have to be reduced or simplified.

The ARID CROP Model

A possible approach is used in ARID CROP (van Keulen, 1975). This is an application of BACROS to conditions where soil moisture is not necessarily optimal. It draws most attention to the water status of the soil as moisture enters, passes through it and is withdrawn by evaporation and transpiration. In order to exploit the plant physiological depth of BACROS and yet avoid becoming bogged down by its complexity, a simplifying concept was necessary to link the two models. The con-

cept chosen was first proposed by de Wit (1959) and is based on the observation that growth and transpiration are closely related; CO₂ uptake and moisture loss are regulated by the stomata, but moisture loss will also depend on the evaporative conditions. Thus in order to relate moisture loss to CO₂ uptake it must be corrected for the current potential evaporation. Thus,

$$G = M \frac{E}{E_0},$$

G = growth (or CO₂ uptake)

E = actual transpiration

E_0 = potential transpiration

M = proportionality or transpiration factor

The value of the transpiration coefficient (M) can be determined by BACROS for a given plant species and given radiation conditions. Thus, this detailed physiological process model enters ARID CROP as a single coefficient. The concept has the added advantage that M is an experimentally verifiable parameter. It can therefore also be used without reference to BACROS. It is now left to determine the actual transpiration, which in fact is what ARID CROP does by simulating the rooting depth of the crop, soil moisture and canopy cover.

This approach assumes that there is no feedback from ARID CROP onto M which is dependent solely on the radiation conditions and the species. If M was dependent on soil moisture changes too, its determination would have had to be included in ARID CROP. It is therefore fundamental to this type of solution, that the link variable developed by the basic model does not depend materially on feedback from the applied model. It then becomes a driving variable in the applied models. Such an approach has been called 'hierarchical modelling' (van Keulen, 1975).

ARID CROP has been tested on data from the Northern Negev of Israel (van Keulen, 1975) and has been found accurate, also to within 10% of the observed final yield. There are, however, deviations during the growing season in that early growth is overestimated and late growth underestimated. This problem will have to be solved before full confidence can be placed in ARID CROP as a source of input to an even more comprehensive model. It runs at present on the

assumption that nutrients are non-limiting. Development to include the effects of nitrogen limitation is under way.

Here we have an example of development of a grassland model step by step from a basic plant physiological process model to more and more comprehensive applied models.

The Dryas empirical and the Dryas process models

The two following models (Whitfield, D.W.A., 1972a, b) illustrate an aspect of accuracy and resolution in plant growth models. The first one, an empirical model of growth of the shrub *Dryas integrifolia*, calculates net assimilation from radiation input and the measured (or interpolated) amount of *Dryas* photosynthetic tissue. The relationship between net assimilation and radiation is determined for different phenological states and is then used as a set of functions or tables in the model. It is estimated that the seasonal net photosynthesis calculated by the model is accurate to within 5% of what is measured in the field. The second model, a process model, is still in the development stage but includes a fairly detailed treatment of the energy budget and water relations, photosynthesis and respiration, translocation and allocation of carbohydrates and nitrogen, decomposition of dead leaves and nitrogen cycling. The driving variables, temperature, relative humidity, wind speed and incoming radiation, are entered on an hourly basis. In order to run the model, parameter values are determined by field experiments, taken from literature or guessed. The model result for dry biomass increase agrees with measured data for the beginning of the season but then deviates strongly in the later season. This is ascribed to the "lack of any attempt to represent hormonal control of growth or seasonal variation of such processes as gross photosynthesis". The carbohydrate content of the plant is rather stable in the experimental data, but shows strong seasonal variation in the model results.

The process model is clearly a more sophisticated and thus a more interesting one to the physiologist. Yet the results in terms of biomass increase are much less satisfactory than those of the empirical model. The reason is that the empirical model uses as input, data which are closely related to the final result. The process model uses more plant specific data (parameters, initial values) and more detailed micro-meteorological data, but these are also more distantly related to the

final result. The closer one comes back to the data and looks at leaf temperatures, for instance, the better the approximation to reality. BACROS, which is also a process model, has indeed achieved much closer agreement with observation in many situations, but that only after a much larger effort had been invested in experimental determination of relationship between variables and model development. The point of this discussion is that accuracy and resolution of a model are often inversely related, if by accuracy we mean the agreement between model output and observation and by resolution, the number of simulated processes that separate the input and output variables. Thus, if one is constructing a more complex model it would be sounder to invest the main experimental and modelling effort into those selected processes which are of central interest and rely on actual data or data-hugging simulations for the elements of peripheral interest. The resultant increase in model managability is achieved at a cost of flexibility and generality. In addition it must be clearly established that the data entered are not particularly sensitive to feedback from other parts of the model. Such an approach has been used in the Hurley models.

The Hurley irrigation model

The Hurley grassland irrigation model (Brockington, 1971) determines the effect of irrigation on dry matter yield of grassland in England. Nutrients, including nitrogen, are assumed to be available in the top layer only. When moisture is depleted from this layer and the sward depends on moisture from the lower soil layers, it is starved of nitrogen even though there may still be some available in the upper soil layer. The emphasis in this study is the effect of moisture depletion in the top layer on potential growth. Thus potential growth, which is defined here as growth when moisture is non-limiting in both soil layers, is entered as a table derived from observed data. Moisture deficiencies in the soil layers are then combined into a water factor which serves as a reduction factor on potential growth. The results of the model agree very well with experimental data in some years so that it was regarded as sufficiently reliable to be used for a series of irrigation strategy studies. Here too, accuracy goes with low resolution. The limitations, however, must be recognized. For instance, if drying of the top layer was accompanied by decrease of the grass cover so that a return to optimal

soil moisture conditions would not produce potential growth till the cover was restored, then the model results would not apply because potential growth would then become dependent on feedback from the model. Such an effect has been neglected, probably because the problem was not thought to be serious, even though there were discrepancies between the model and observed results in one of the verification years reported that could have been due to just such an effect. The approach in this model is thus highly empirical and as such it is of limited generality. This need not be a serious objection in cases like this because the alternative is to do experiments of a much more limited scope on a site no less specific than the model.

The Hurley ewe-lamb Model

It becomes more difficult to use such simplifications successfully in cases where the scope or objective of the model is more ambitious. A case in point is the Hurley ewe-lamb model (Edelsten et al., 1973). The structure of the model is given in Fig. 2. Here the emphasis is on the management of the flock of sheep by manipulating the grazing rotation, supplementary feeding and silage cuts from the vegetation.

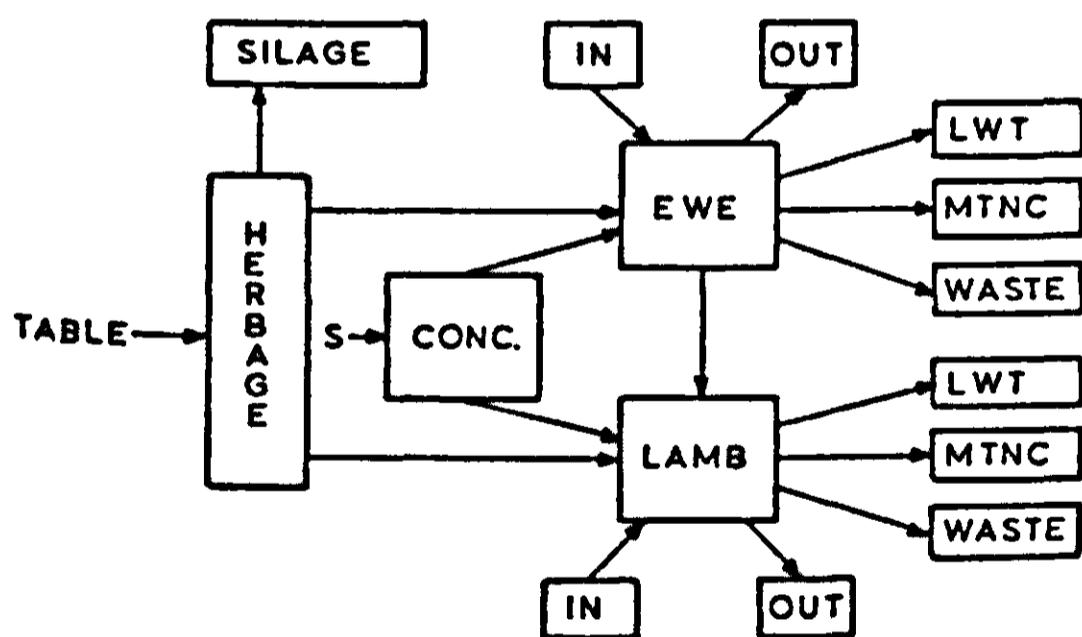


Fig. 2 | Structural relationships in the Hurley ewe-lamb model. (After Edelsten et al., 1973).

Growth rate of the vegetation under grazing conditions is entered as a season specific table (Fig. 3) constructed from observed data. When paddocks are not being grazed, growth is calculated by means of an

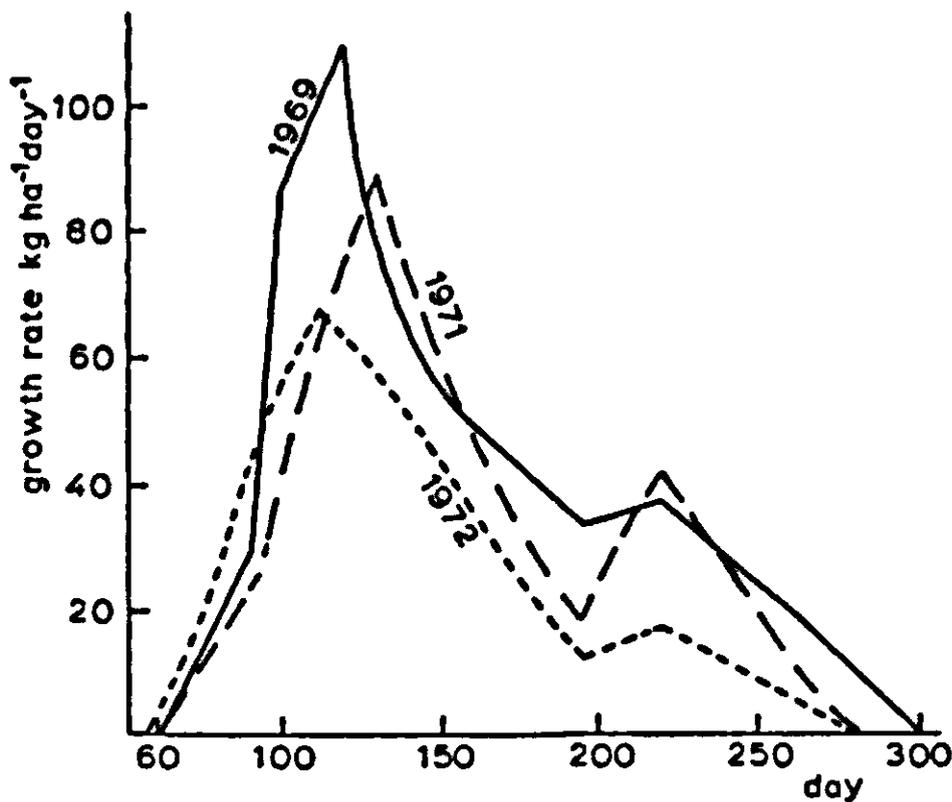


Fig. 3 | Growth rate functions of grazed pasture used in the Hurley ewe-lamb model. (After Edelsten et al., 1973).

algorithm based on the seasonal rates. It is thus assumed that there is no feedback of grazing effects from the model on herbage growth and that growth undisturbed by grazing is independent of different conditions from year to year. Whatever effect grazing had on growth, it was regarded as constant and independent of the management or stocking densities defined in the model. Such an assumption obviously limits the scope of the model to those cases where this condition holds. Some results of this model are given in Table 2. The growth rates of the

Table 2 Some results of the Hurley ewe-lamb model.

	Experimental results			Model results		
Stocking rates (ewes ha ⁻¹)	14	17	20	14	17	20
Ave. growth rate-lambs (g day ⁻¹)	189	186	167	212	182	167
Silage produced (tons DM ha ⁻¹)	0.96	0.96	0.96	1.5	1.5	1.5
Concentrates fed (kg lamb ⁻¹)	2.8	6.2	9.8	1.1	30.7	35.6

lambs are close to observed, especially at the higher stocking densities. This accuracy is built into the model as the management of the herd was set to attain acceptable growth rates. Management included concentrate feeding which is influenced by the amount of feed grazed off the pasture. The amount of concentrate simulated was rather different to that observed; there was also a large discrepancy in the amount of silage harvested.

This model is being developed and the results are from an early version. They do show that some conceptual weaknesses need to be identified and rectified. This will most probably be done as the development of the model progresses. An obvious area of weakness to look at more closely would seem to be the feedback of grazing on herbage growth and the assumptions on which undisturbed growth are based. If the weaknesses can be removed by minor adjustments then possibly the use of the herbage growth tables could still be maintained. If not, then it could well be that a more detailed herbage growth model that could simulate the effect of grazing on growth rates would be required.

The LEYFARM Model

LEYFARM (Arnold & Campbell, 1972. Arnold et al., 1974a, b) is a moderately complex, comprehensive model that in its present form, simulates grazed, annual (legume) pasture from seed germination through growth, flowering, seed formation, death, decay and consumption through grazing, to the softening of hard seeds for the next season's germination. The moisture balance in the soil and the grazing animal are simulated in detail. The model is unabashedly empirical and as the objective is to study grazing management, it regards statistical relationships for describing many of the component processes as sufficient at this stage. It makes wide, if not indiscriminate, use of the experimental data available. Considerable attention is given to the seeds which are formed as hard seeds and have to soften before they can germinate. Germination takes place in waves and the separate waves are monitored to form the basis for calculating a mean emergence day (MERGD) and a mean weighted flowering day. These days are used to determine the weight of individual seeds, the yield of seeds and the rate of ageing of the herbage. After germination and establishment, growth is initiated by converting germinated seed into live biomass (weight of seedlings = $0.5 \times$ weight of germinated seed). From

then on and until all live biomass eventually dies, the pasture grows at a daily growth rate, dies at a daily death rate. The live and dead material are consumed by sheep selectively and the dead material also decays.

Here only the growth of the germinated pasture without grazing will be considered so as to keep the discussion circumscribed and compatible with the foregoing sections.

The daily growth rate (DGR) is determined as follows:

$$\text{DGR} = \text{POTGR} \times \text{RADF} \times \text{R} \times \text{AGE} \times \text{TEMP}$$

The potential growth (POTGR) is entered as a function of dry weight of green matter (GRNMAT) in kg ha^{-1} (Fig. 4). The form of the function used implies approximately exponential growth till 1000 kg ha^{-1} and linear growth thereafter. The maximum growth rate approaches $126 \text{ kg ha}^{-1} \text{ day}^{-1}$. This value is somewhat less than

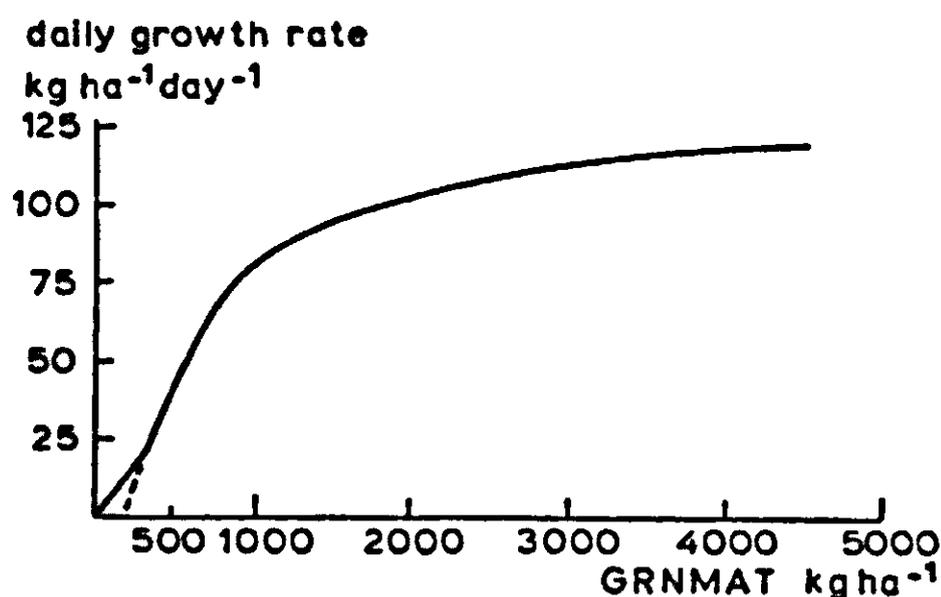


Fig. 4 | LEYFARM: Potential daily growth rate as a function of amount of live biomass (GRNMAT). (Derived from Arnold et al., 1974b).

potential growth measured under similar climatic conditions but with a mixed grass-forb sward (van Keulen, 1975). It probably reflects the higher respiration costs involved in producing the high level of protein in plants like the annual legumes modelled in LEYFARM (Penning de Vries, 1973). The linear increase in growth when live biomass is below $500 \text{ kg GRNMAT ha}^{-1}$ implies that growth rate increase per unit GRNMAT (the relative growth rate) is less than it is just above 500 kg GRNMAT . The reason for such a patchy construction is not clear but is probably related to the data used and could be a rough

approximation of exponential growth at low GRNMAT values.

The radiation factor (RF) is a function with two variables, radiation (RAD) ($\text{cal cm}^{-2} \text{ day}^{-1}$) and GRNMAT (Fig. 5). The dependence on radiation when the canopy is fully developed (7000 kg ha^{-1}) is linear, a rather rough approximation in semi-arid conditions. $\text{RF} = -0.5$ when $\text{RAD} = 0$, implies an excessive dark respiration rate. When GRNMAT is low, growth is virtually independent of radiation, even when $\text{RAD} = 0$ (Fig. 5). This is not reasonable but may not have had an important effect on the results if low radiation values are rare.

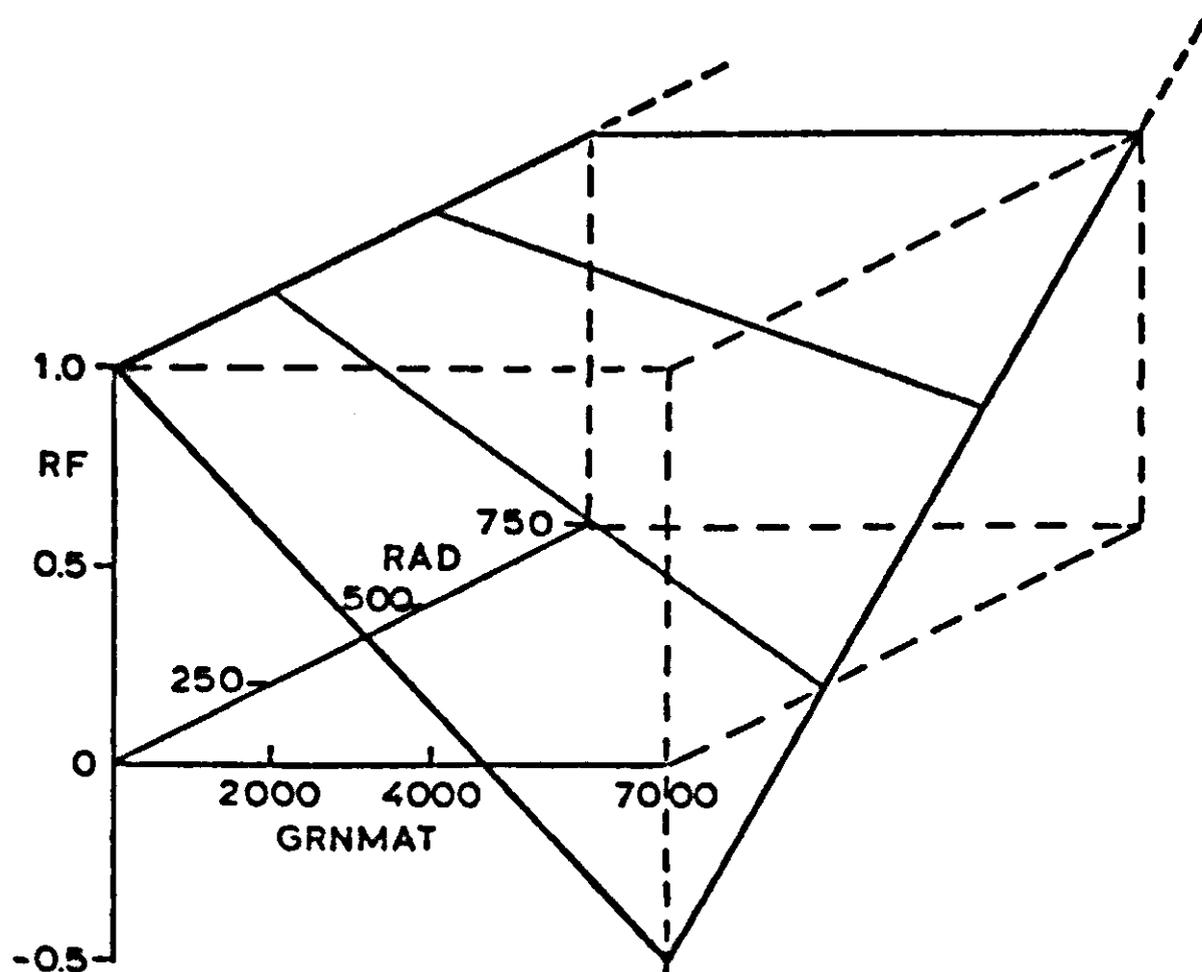


Fig. 5 | LEYFARM: Dependence of radiation factor (RF) on live biomass (GRNMAT) and radiation intensity (RAD in $\text{cals cm}^{-2} \text{ day}^{-1}$). (Derived from Arnold et al., 1974b).

The effect of soil moisture on growth is mediated by $R = E/E_0$, where E = actual evapotranspiration; E_0 = potential evapotranspiration. When LAI is less than 1, E is split into transpiration, E_t , and evaporation from bare soil E_b . Then,

$$E = \text{LAI} \times E_t + (1 - \text{LAI}) \times E_b, \quad \text{LAI} < 1$$

$$\text{LAI} = \text{GRNMAT}/1000$$

E_t and E_b are determined by a special soil water sub-routine (Carbon & Galbraith, 1975).

When LAI is less than one, the growth reduction factor, R, is calculated from the transpiring vegetation only. Thus,

$$R = E_t / (E_0 \times \text{LAI}), \quad \text{LAI} < 1.$$

It may have been simpler and more realistic to relate R to the cover of the vegetation as follows:

$$R = E_t / (E_0 \times \text{COVER})$$

$$\text{COVER} = 1 - \text{EXP}(-0.5 \times \text{LAI}) \quad (\text{van Keulen, 1975}).$$

The age factor is dependent on a function of MERGD and number of days after flowering (Fig. 6).

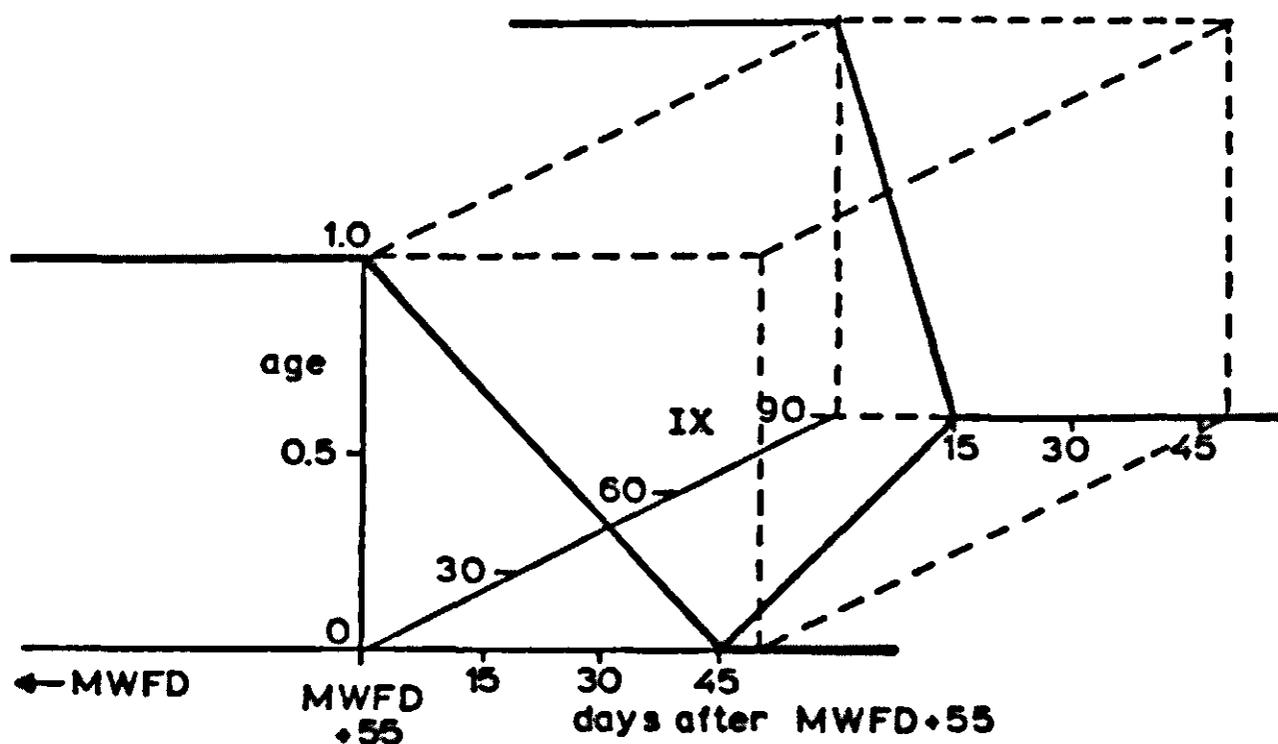


Fig. 6 | LEYFARM: Dependence of ageing factor (AGE) on time of flowering (MWFD) and IX, a function of mean time of seedling emergence (MERGD) where $IX = 0 < (\text{MERGD} - 138) < 90$. (Derived from Arnold et al., 1974b).

$$IX = \text{MERGD} - 138 (\equiv 1 \text{ April S.H.} \equiv 1 \text{ October, N.H.})$$

$$0 < IX < 90.$$

Till the 55th day after flowering, AGE = 1. When MERGD < 138, then AGE = 0 on the 100th day after flowering; when MERGD > (138 + 90) then AGE = 0 on the 70th day after flowering.

Again, the construction is a three-dimensional surface based on direct interpretation of available data. It is, however, a rather cumber-

some and arbitrary method. Ageing is certainly a complex process, but when more complete information is lacking it would seem that a temperature accumulating treatment would be more appropriate (de Wit & Goudriaan, 1974, Chap. 6).

The temperature factor is composed of a set of curves, the choice of which is dependent on GRNMAT and RAD (Fig. 7). When $\text{GRNMAT} > 1000 \text{ kg ha}^{-1}$, temperature ceases to influence growth.

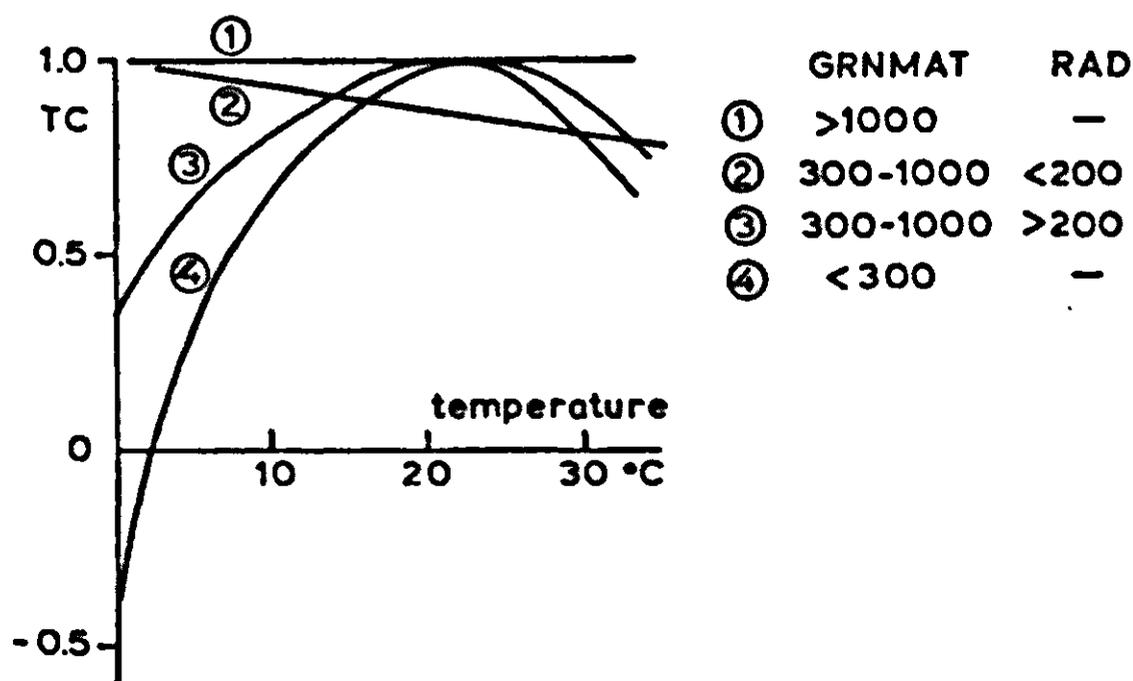


Fig. 7 | LEYFARM: Functions used for temperature factor (TC). Derived from Arnold et al., 1974b).

The daily death rate (DDR) of the vegetation is calculated as a basic death rate dependent on the amount of live biomass (LOSS). This is increased as the plant matures (PHEN) and as the soil dries out (DSF):

$$\text{DDR} = \text{GRNMAT} \times (\text{LOSS} + \text{PHEN} + \text{DSF})$$

$$\text{LOSS} = \begin{cases} .003, & \text{GRNMAT} < 3584 \text{ kg ha}^{-1} \\ 0.019, & \text{otherwise} \end{cases}$$

PHEN is determined by IX and number of days after MWFD on a three-dimensional surface bounded by 0 and 0.5 (Fig. 8).

$$\text{DSF} = \begin{cases} .242, & R < 0.1 \\ 0, & \text{otherwise} \end{cases}$$

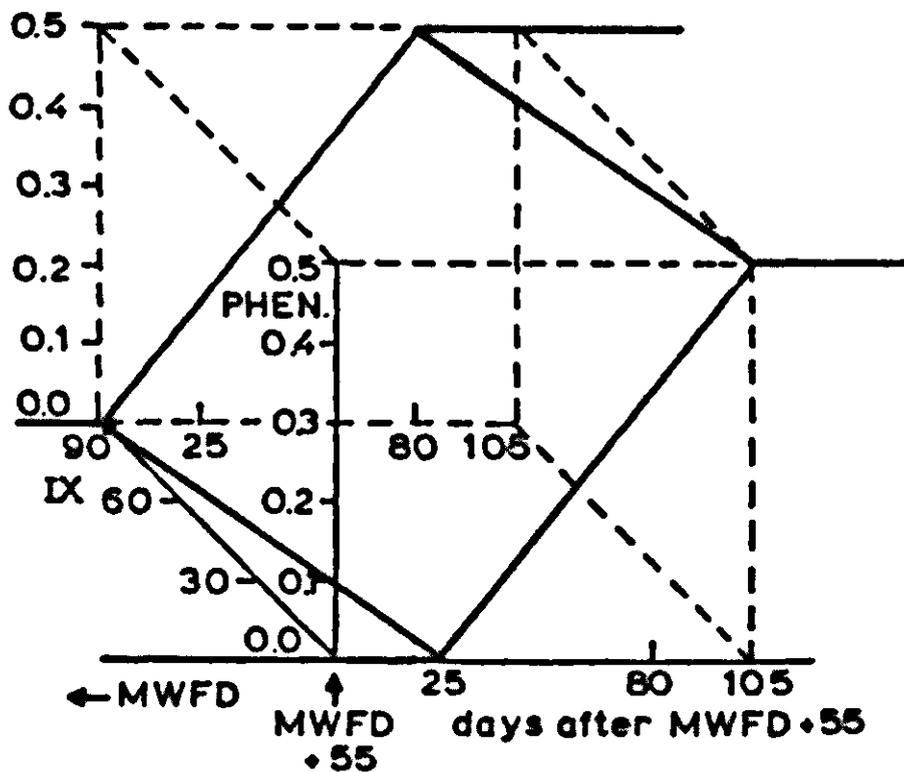


Fig. 8 | LEYFARM: Dependence of herbage death due to maturity (PHEN) on time after flowering (MWFD) and on IX, a function of mean time of seedling emergence (MERGD) where $IX = 0 < (MERGD - 138) < 90$. (Derived from Arnold et al., 1974b).

The effect of the grazing animal on the growth rate of the pasture is assumed to operate solely through the reduction of GRNMAT caused by forage consumption. This assumption is substantiated by experimental data which indicate that potential growth rate is very closely related to the amount of green pasture whether it is being grazed or not (Arnold, 1975; Greenwood et al., 1974). In fact Arnold shows that when $GRNMAT > 100 \text{ kg ha}^{-1}$ the amount of herbage removed by the sheep per day at normal stocking densities is generally much less than 10% of what is available. The effect on the canopy is thus quantitatively weak. However, at the beginning of the season when there is very little herbage available, then as much as 30% of what is available can be removed in one day. Arnold maintains that even at such intensities of defoliation the major quantitative effect on growth is directly due to the reduced biomass. Although this is qualitatively a gross over-simplification, much of the data presented supports this view. The matter should be more thoroughly investigated especially for intensive defoliation as it is important to know the limitations of this assumption if it is to become an important means of representing the growth-grazing relationship in a simple and meaningful way. The model produces satisfactory results (Fig. 9), despite the arbitrary

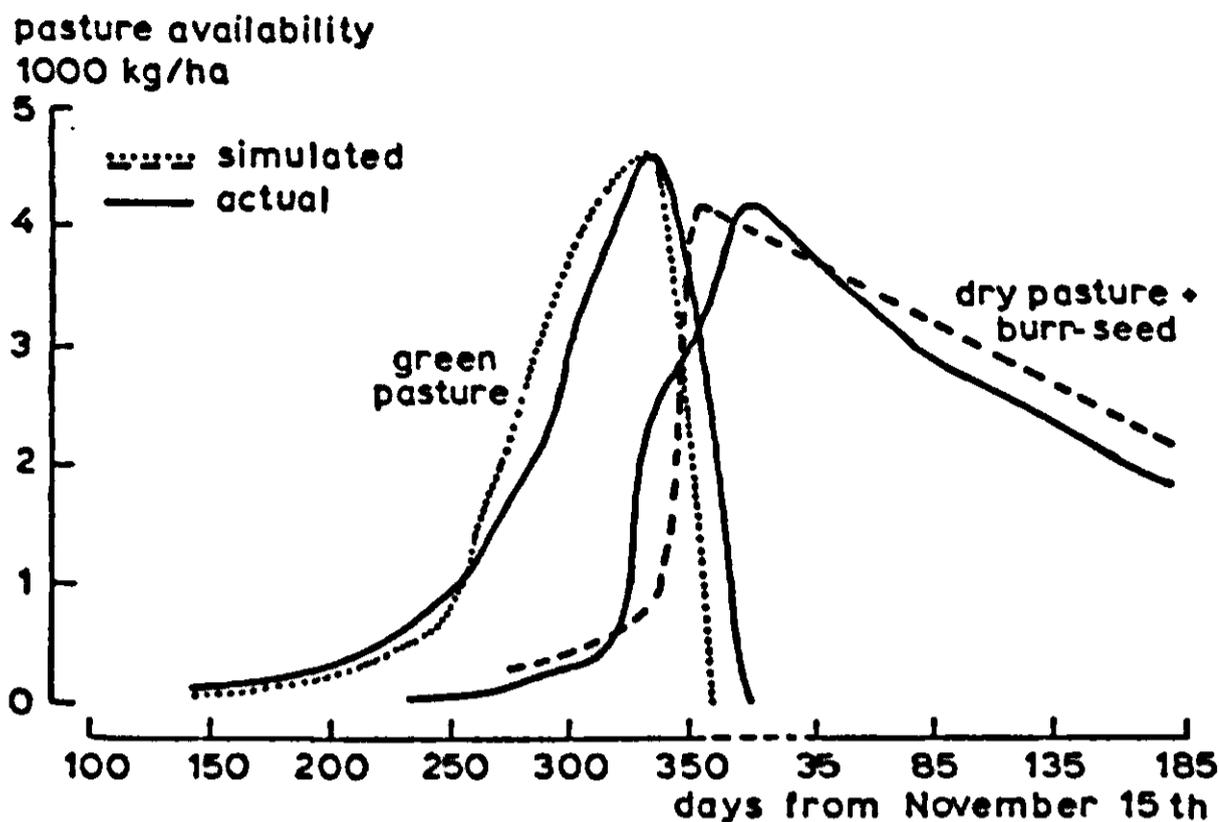


Fig. 9 | LEYFARM: Measured and simulated values for pasture availability when stocking rate is 10 sheep ha⁻¹. (Derived from Arnold et al 1974b).

functions and awkward constructions (or it is because of them!). This proves again that although there are many ways of reaching the top of the hill, some are more devious than others. In the context of LEYFARM a more concise and conceptually sound formulation could be a useful improvement. When so many empirical relationships are employed, a degree of elegance does become important if only to limit the unpredictable and unintended consequences of loose and conceptually weak structures in complex models.

The Armidale Model

The Armidale model (Vickery & Hedges, 1972a, b) is of an improved *Phalaris tuberosa* – *Trifolium repens* pasture grazed by merino sheep at different stocking densities. The emphasis in the vegetation section is on the growth, forage value and consumption of the pasture. As it is a perennial pasture, germination and seed-formation are neglected. The soil moisture balance is also treated simply: a 75 mm soil moisture capacity is filled by rain and emptied by transpiration which is $0.8 \times (\text{pan evaporation}) \times \text{SLMR}$. The latter term is a reduction factor dependent on soil moisture (Fig. 10). Root distribution is assumed to be always adequate for moisture extraction, – probably a reasonable assumption for the specific conditions, but a possible

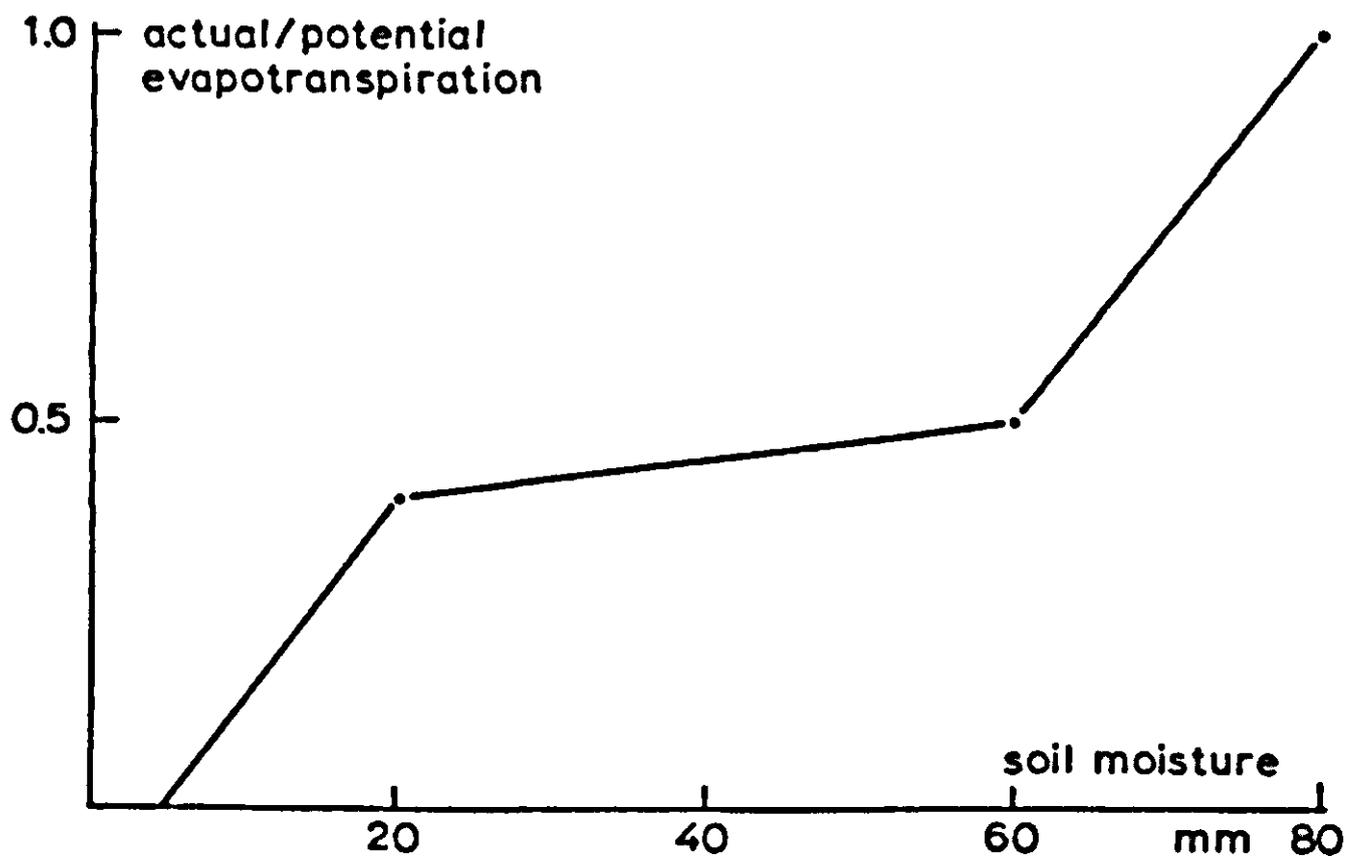


Fig. 10 | Armidale: Dependence of evapotranspiration on soil moisture. (From Vickery & Hedges, 1972a).

source of error. The time unit is one week as is the time step. The relative growth rate (RGR) of the herbage is calculated as a potential rate dependent on soil temperature at a depth of 4 cm. This is adjusted by a series of reduction factors for soil moisture, leaf area, age and a dry soil factor (DRYSOL).

$$RGR = RGRT \times SMGR \times PLAI \times AGE \times DRYSOL$$

RGRT is the temperature dependent potential growth curve (Fig. 11), whereby there is no growth below 4°C and a maximum relative growth rate of 0.5 kg kg⁻¹ week⁻¹. The soil moisture growth reduction factor (SMGR) given in Fig. 12 is nearly linear between 20 mm and 75 mm soil moisture. Below 20 mm growth almost ceases.

The leaf area reduction factor (PLAI) starts to operate when the green herbage exceeds 2500 kg ha⁻¹ (dry weight) and reduces growth to 0.1 of potential when it exceeds 5000 kg ha⁻¹.

The ageing factor (AGE) is dependent on stocking density and time of the year and takes values of 0.75 to 1.5. It is entered as a table and is based on data by Hutchinson (1969). Thus the growth can be raised above the temperature dependent 'potential' rate. DRYSOL has a value 0.2 and operates for higher stocking densities only during weeks

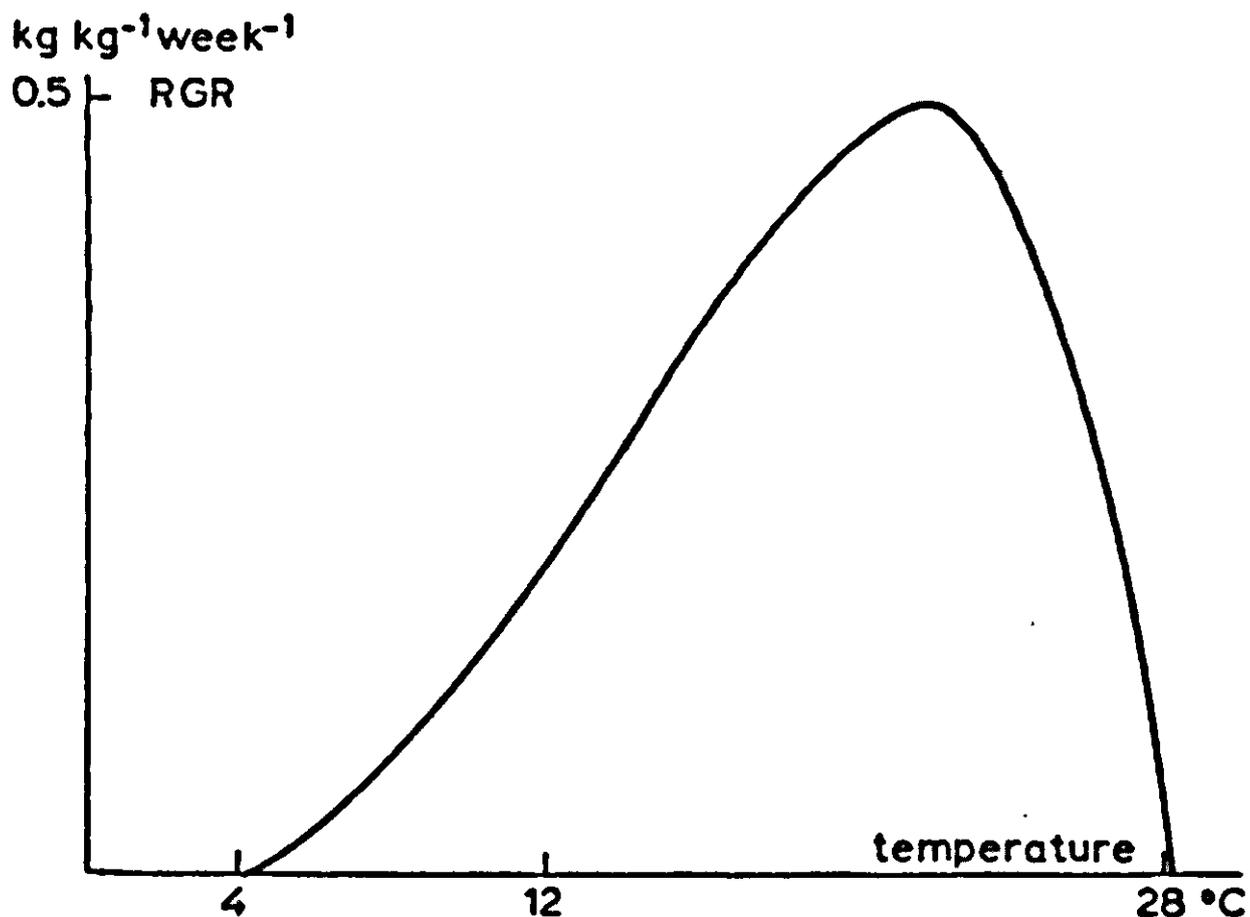


Fig. 11 | Armidale: Dependence of relative growth rate on soil temperature measured at 4 cm depth. (From Vickery & Hedges, 1972a).

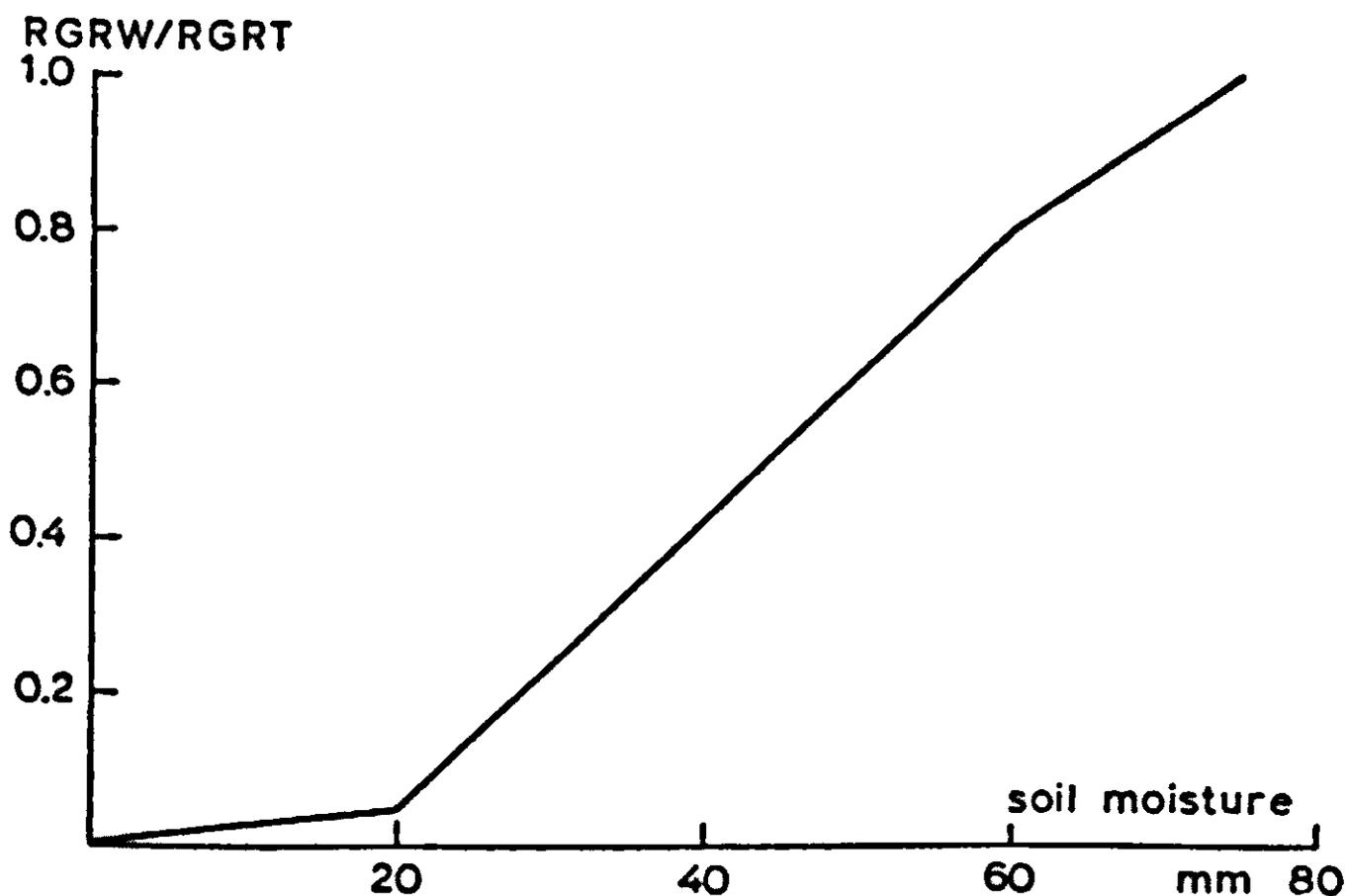


Fig. 12 | Armidale: Relationship between soil moisture balance and the ratio RGRW/RGRT where RGRT is the weekly relative growth rate at soil temperature T with soil moisture unlimiting, and RGRW is the relative growth rate at a particular level of soil moisture and the same soil temperature. (From Vickery & Hedges, 1972a).

4 and 5 (end January/beginning February). It represents dormancy in *Phalaris tuberosa* induced by low soil moisture conditions in mid-summer. Total weekly growth is then calculated by multiplying RGR with the live shoot biomass plus a fraction of the root biomass. The fraction is a table, dependent on time of the year and has a range from 0.25 to 0.65. The total growth is limited to a maximum of $1500 \text{ kg ha}^{-1} \text{ week}^{-1}$ and is partitioned between roots and tops according to a function dependent on stocking density and time of year. This function is also entered as a table.

The shoot biomass dies according to a rate dependent on time of year which ranges from 0.001 to 0.75 week^{-1} . The current value is increased by a factor of 3.5 when soil moisture is less than 20 mm and concurrently soil temperature is above 19.5°C . In addition to removal of biomass by grazing there is also consumption by insects. Root biomass dies with a time dependent mortality factor and some of it is consumed by soil fauna.

The growth and death of the pasture vegetation is thus a highly site specific process, fairly rigidly determined by empirical time-dependent functions. Here, as in LEYFARM, grazing affects the pasture only by reducing the live and dead biomass by consumption.

The most distinctive part of this model is probably the approach to determining the forage value of the pasture and the herbage consumption by the sheep. The emphasis is on the ageing of the live and dead biomass. Both are divided into 13 4-week age classes. New growth enters the youngest age class and progresses through the classes, residing in each class for 4 weeks. Live biomass that dies is decremented from the oldest classes and entered into the youngest dead biomass class. This procedure is adopted so as to determine the forage value of the pasture which is here age dependent according to the functions in Fig. 13. It is also used to determine the forage value of the herbage actually consumed by the sheep, as the method allows for selection of young green herbage in preference to old. This is done by accumulating the amount of herbage in the successive age classes and reading off the proportion consumed from each successive class from a curve that relates the proportion of green herbage in the diet to the total amount of green herbage available (Fig. 14). This is admittedly an arbitrary approximation but is used for want of better data on herbage selection.

Despite the fact that herbage is divided into 4-weekly age classes, it

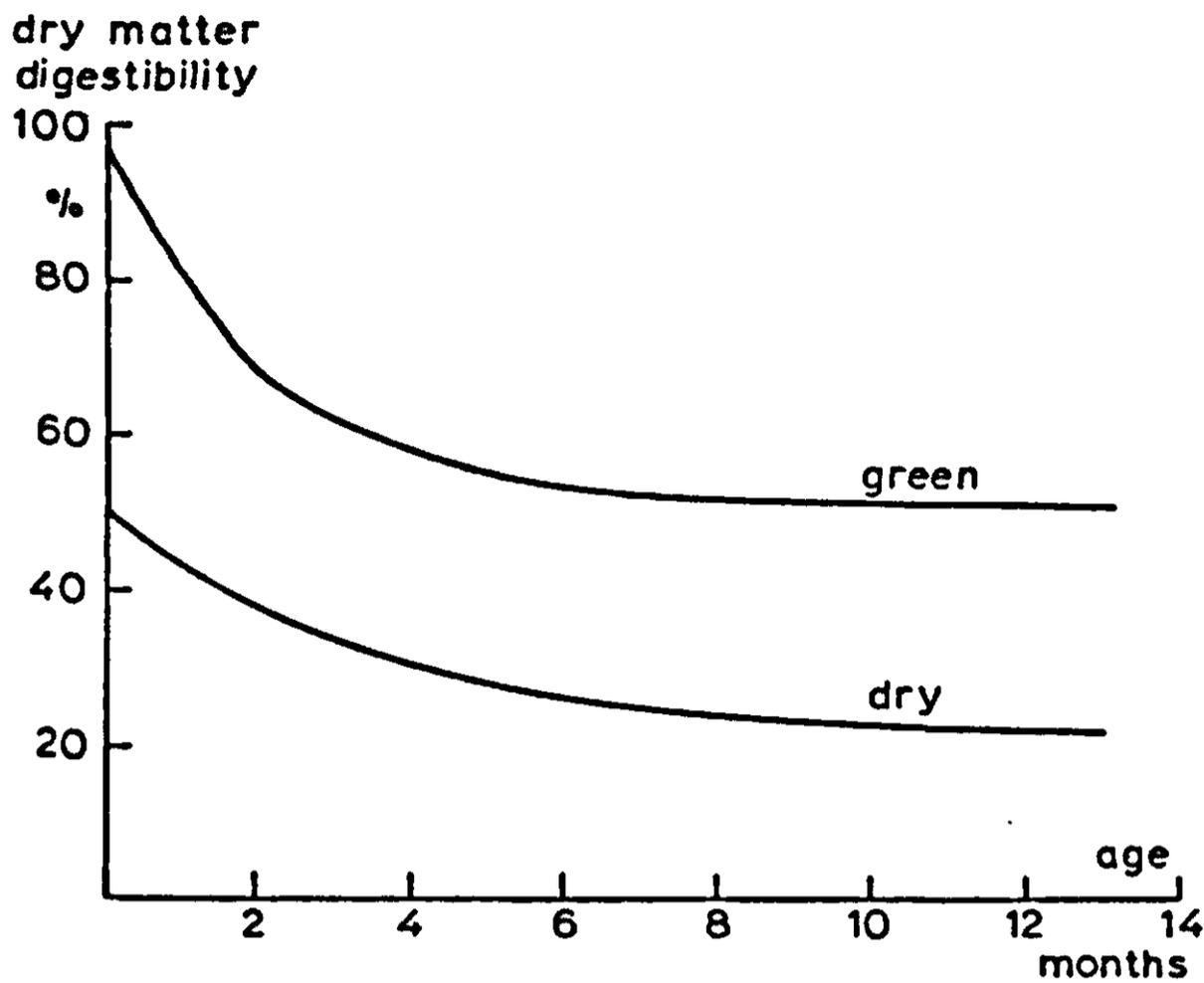


Fig. 13 | Armidale: Relationship between age and digestibility of green and dead herbage. (From Vickery & Hedges, 1972a).

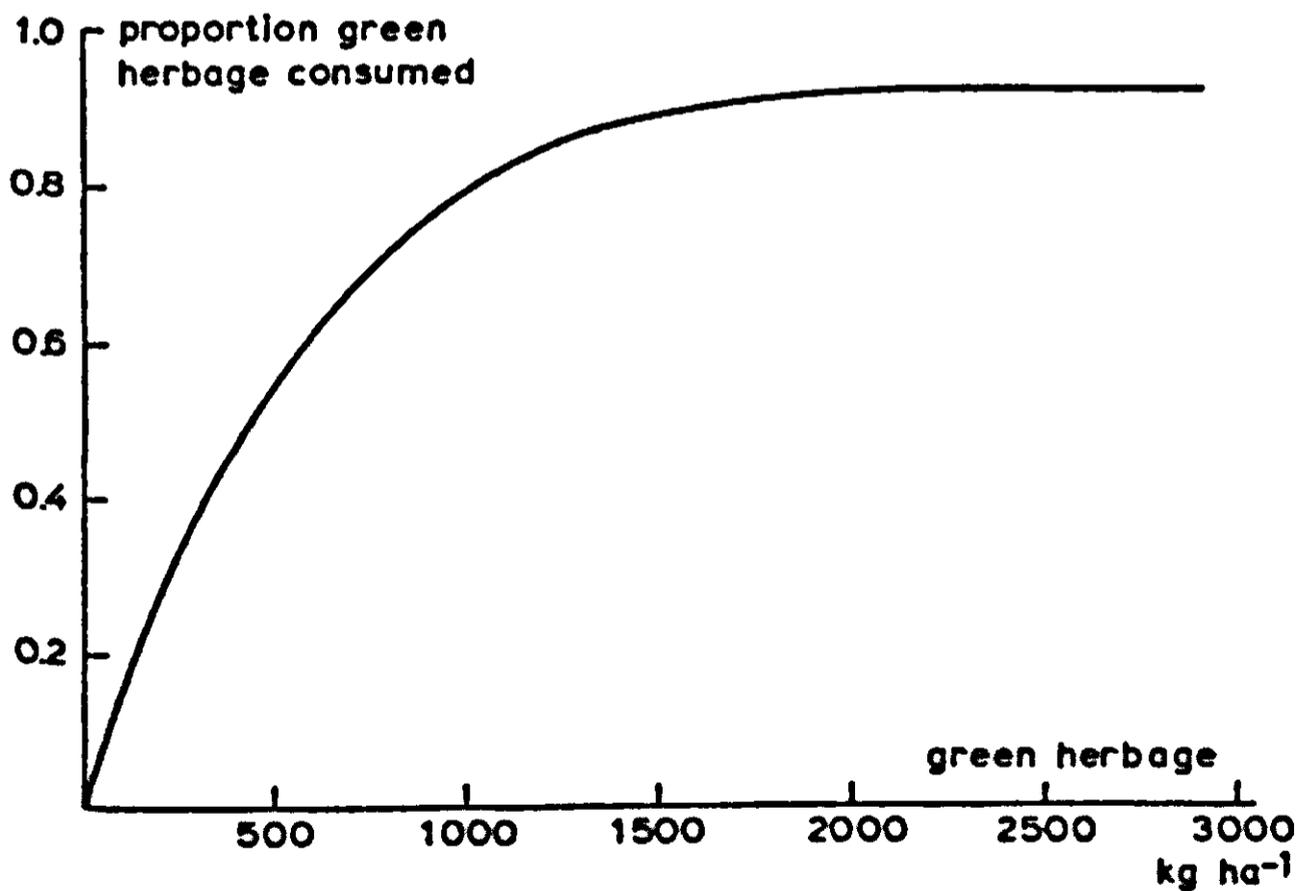


Fig. 14 | Armidale: Relationship between green herbage availability and the proportion of green herbage in the diet. (From Vickery & Hedges, 1972a).

ages continuously, i.e. in weekly steps. Thus some herbage is moved from the one class to the next every week. The actual amount is determined by the proportion grazed in the current week. It is assumed that the same proportion was grazed in the previous 3 weeks. The amount of 4-week old herbage left over to be moved to the next class is calculated as an approximation of:

$$P_i = e^{-k_i t/t}$$

where

P_i = proportion of herbage in class i that is transferred to the next age class;

k_i = proportion of herbage in class i that is currently being grazed;

t = 4 (weeks).

This again is a simplification but this time not because of lack of data: it is implied that in fact these are not 13 4-week age classes but 52 1-week age classes. If the herbage had been so divided, then the actual content of each class could have been aged every week and the digestibility and consumption calculations could then be made on the basis of 4-weekly classes by linking the 4 consecutive 1-weekly classes. However, the treatment as used results in a dispersion with a standard deviation of

$$\sqrt{\frac{1-F}{N}} \approx 0.24$$

where

F = time step/residence time = $\frac{1}{4}$

N = number of classes = 13.

If no dispersion at all was intended, then 52 1-week age classes would have been necessary (Goudriaan, 1973). It could be questioned whether in fact such detailed ageing was justified, or compatible with the detail of the digestibility and consumption calculations. Moving the total content of each 4-week class once every four weeks may have been sufficient for the purpose. This method and its application to ageing processes is discussed by de Wit & Goudriaan, 1974, Chap. 6.

The output of the model was checked against field observations and

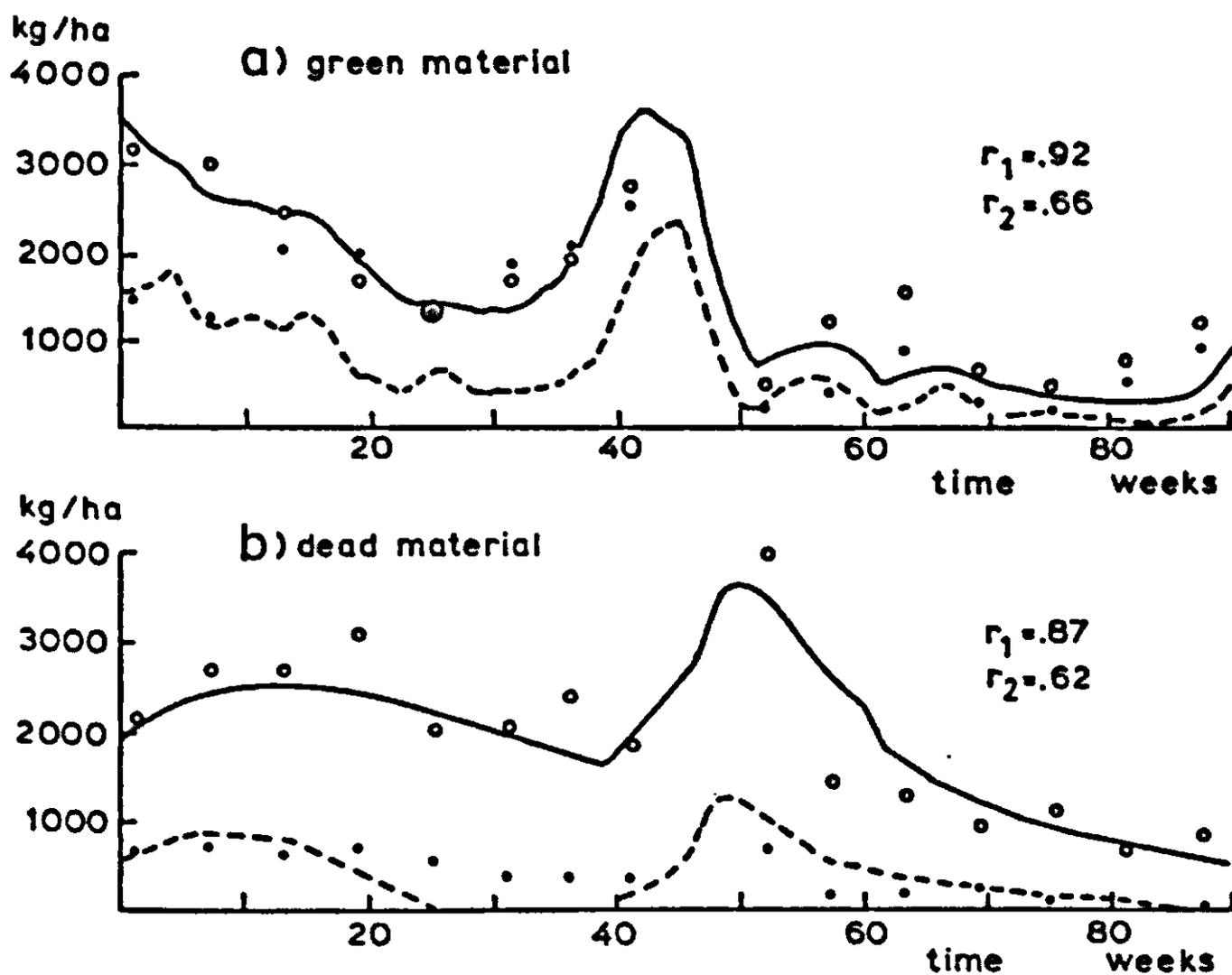


Fig. 15 | Armidale: Comparisons of predicted values obtained from the sheep production model with actual data of Hutchinson (1969): (a) green herbage kg ha^{-1} ; (b) dead material kg ha^{-1} . Stocking densities 9.9 (—) and 29.7 (---) wethers ha^{-1} . (From Vickery & Hedges, 1972).

some of the results for herbage growth are given in Fig. 15 for two stocking densities, 9.9 and 29.7 wethers ha^{-1} . The model results for the lower stocking density are much better than those for the higher stocking density. This would indicate that the interaction between the grazing animal and the growing pasture is not represented well enough to account for the actual growth of the pasture under conditions where this interaction is important, as it is at high stocking densities. The source of the discrepancy could be in the way that grazing is represented as influencing growth as well as in the way the forage consumption by the sheep is calculated.

The Armidale model is not a class exercise (Seligman et al., 1971) or a strenuous two week workshop effort (Wielgolaski, 1972). It is, like LEYFARM, a serious attempt to model a well defined situation in fair detail and is based on a wealth of experimental data. It has been carefully formulated and clearly represented (Vickery & Hedges,

1972a, b). Yet its performance is somewhat less than satisfactory. This is an indication that either the best information available or the conceptual basis (or both) are not yet good enough to allow construction of a reliable model in such detail. This is a useful result because it not only indicates that there is a dearth of knowledge on important aspects of pasture growth and grazing, but it provides a meaningful criterion by which to judge the contribution of new information and new concepts.

A Simple Analytical Model

Noy-Meir (1975a, b, c) has used a deliberately simplified model as the basis for an analytical approach to the problem of pasture stability under different stocking densities and different grazing systems. His model consists essentially of a vegetative growth rate function dependent only on 'quantity' of vegetation in the pasture and a family of consumption functions dependent on stocking density and on the quantity of pasture on offer. He shows that many properties of such a system under continuous grazing can be determined by simple graphic means (Noy-Meir, 1975a, b). However, to analyse the system for rotational grazing it is necessary to define an explicit mathematical model (Noy-Meir, 1975c). The model simulates net change in vegetative biomass, V ,

$$\frac{dV}{dt} = G - C$$

where G is the growth rate of the pasture and C the rate of consumption by the grazing animal.

$$G = gV \left(1 - \frac{V}{V_m} \right), \text{ a logistic growth function;}$$

$$C = c_m H \frac{V - V_r}{(V - V_r) + (V_k - V_r)} \text{ if } (V < V_r, C = 0), \text{ a Michaelis satura-}$$

tion function,

where

g = maximum relative growth rate;

V_m = maximum plant biomass;

c_m = maximum consumption rate per animal

H = stocking density

V_r = 'residual' ungrazable plant biomass

V_k = plant biomass at which consumption is half that at satiation (Michaelis constant). Serves as a measure of 'grazing efficiency'.

When

$$\frac{dV}{dt} = 0,$$

the system is in equilibrium and stability conditions can then be defined.

"The rotational scheme was defined by two parameters: n = the number of sub-plots (degree of subdivision) and t_r = length of the whole rotation period or cycle. For continuous grazing ($n=1$) animal density in the pasture H was set equal to the average throughout the simulation. For rotational grazing, it was set to $H=n\bar{H}$ for the part $t_r/n=t_g$ days (grazing period) and to $H=0$ for the part $t_r-t_r/n=t_d$ (rest period)". The model was written in CSMP-II and run for 100-250 day periods. In addition to V , cumulative animal consumption, $\int C dt$, was calculated as a relative estimate of gross animal productivity (assuming $P=eC-m$, where e is a utilisation efficiency coefficient and m is the amount of intake used for animal maintenance).

The behaviour of the model was studied for different management options by varying mainly n , t_r , H and V_0 , the initial biomass at the start of the growing period. The effects of changing V_r , the ungrazeable plant residual and V_k , an expression of the grazing efficiency of the animals, were also tested. V_m , g and c_m were held constant throughout the study as $500 \text{ kg dunam}^{-1}$, 0.1 day^{-1} and 3.0 kg respectively (1 dunam=0.1 ha).

An example of the graphic stability analysis of continuous grazing is given in Fig. 16 and an example of the effects on vegetative biomass of a given rotation scheme in Fig. 17. The graphic representation (and the analytical treatment) define five different stability situations: 1 under-

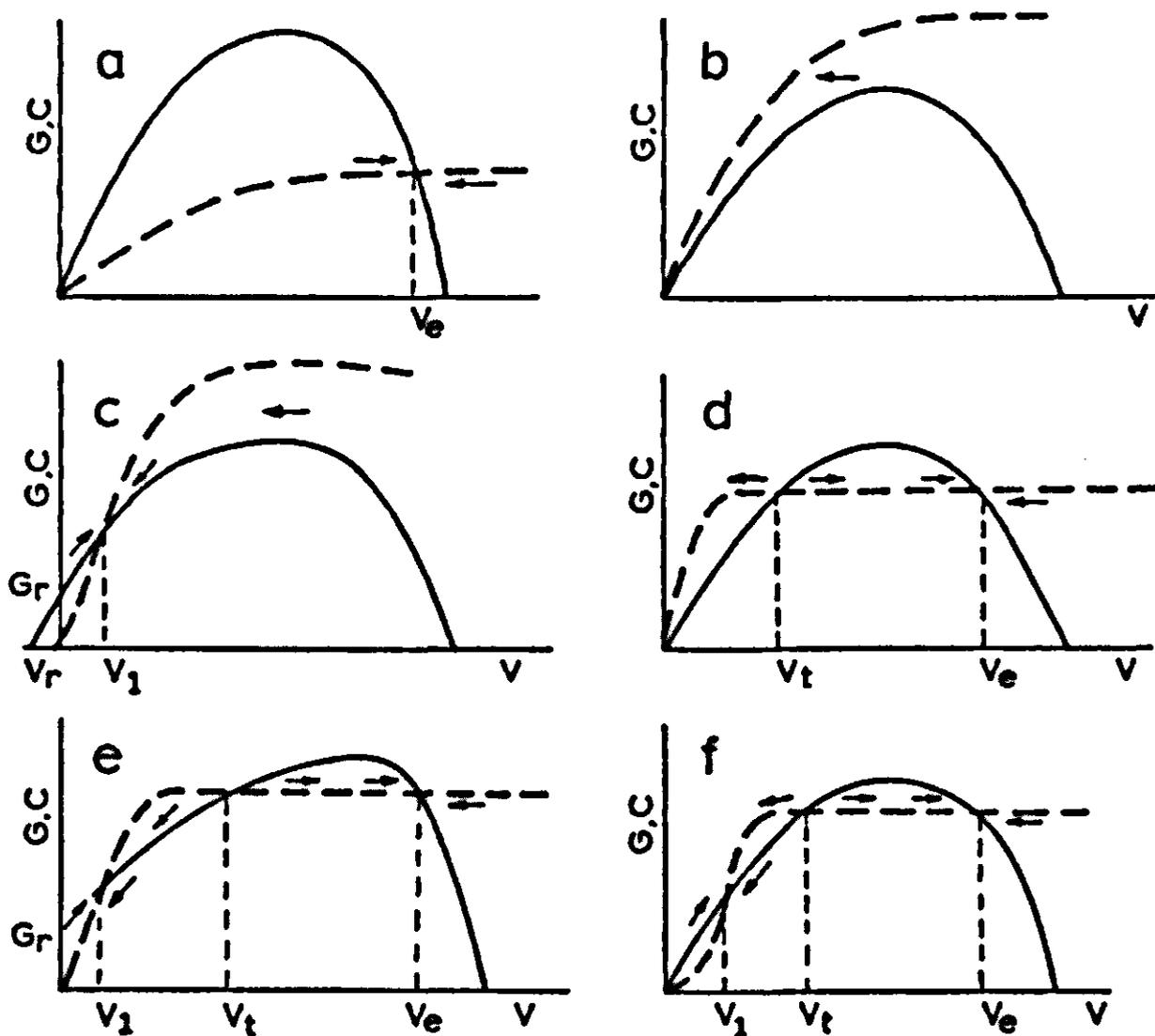


Fig. 16 | Stability of grazing systems: application of predator prey graphs. Possible stability conditions of G and C curves at given H .

- a. undergrazed, stable steady state (V_e).
- b. overgrazed to extinction.
- c. overgrazed to a low biomass steady-state (V_1); V_r – reserve (ungrazable) biomass; G_r – residual growth potential.
- d. steady state (V_e) and unstable turning point (V_t) to extinction.
- e. two steady states (V_e, V_1) separated by a turning point (V_t).
- f. as e, but caused by a sigmoid C – curve, not by ungrazable plant reserve. (From Noy-Meir, 1975b).

grazed steady state; 2 overgrazing to extinction; 3 overgrazing to a low biomass steady state; 4 steady state and turning point to extinction; 5 two steady states (Fig. 16).

Noy-Meir concludes that ‘applied to a simple plant herbivore model this approach has yielded a series of general conclusions, about stability and productivity of the system. These appear to be relevant at least to some classes of real-world pastoral systems and to some problems in their practical management’ (Noy-Meir, 1975b). It can be added that this approach allows for the stepwise development of a

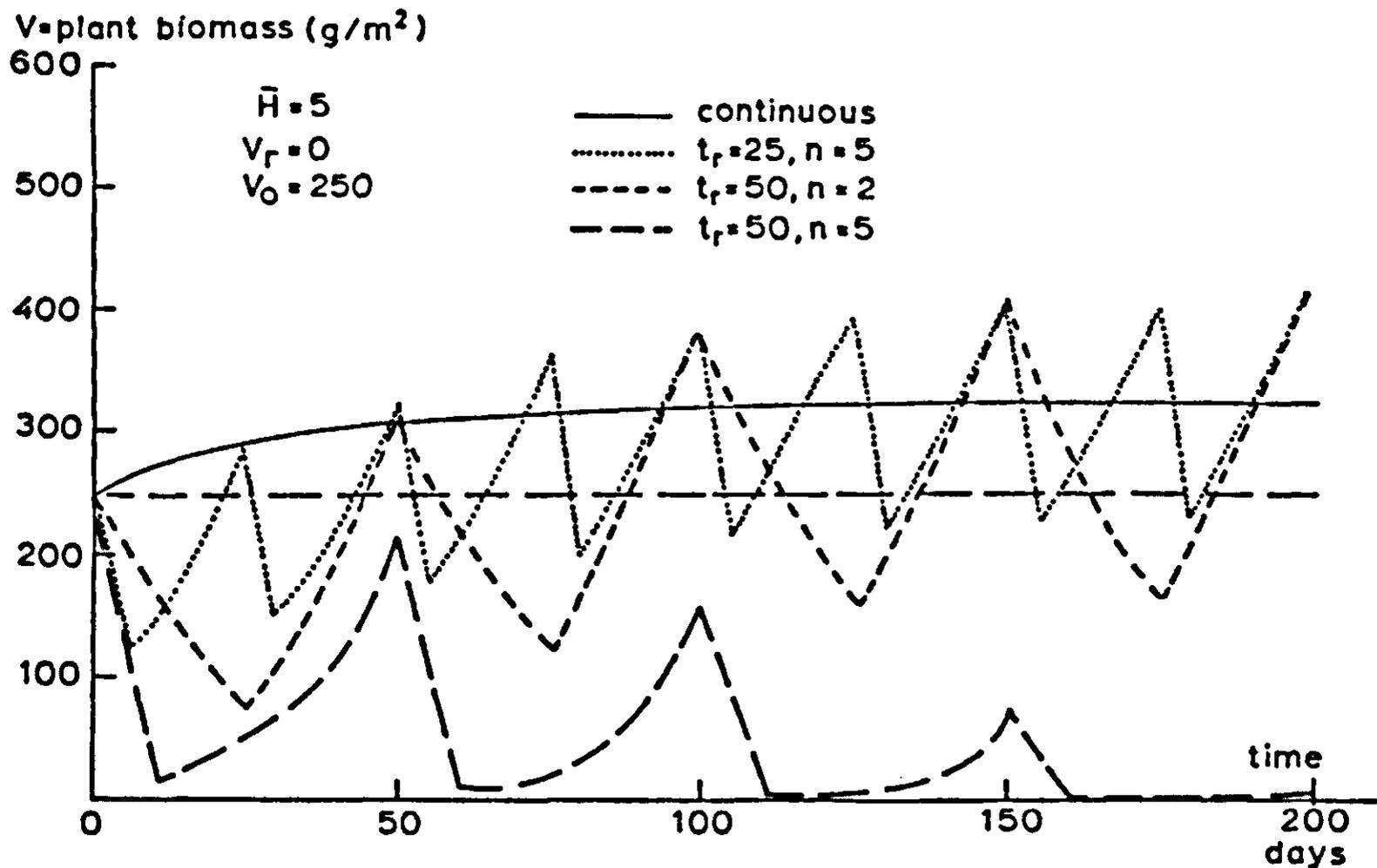


Fig. 17 | Sample output of simple grazing model of pasture rotation. H = mean stocking density in sheep dunam⁻¹ (= 0.1 ha); V_r = residual ungrazable reserve in kg dunam⁻¹; V_0 = initial biomass in pasture in kg dunam⁻¹; t_r = length of rotation cycle in days; n = number of subdivisions of paddock.

The rotation scheme $t_r = 50, n = 5$ results in fluctuations to extinction; the other rotations fluctuate around an equilibrium value. (From Noy-Meir, 1974c).

comprehensive theory of grassland dynamics. It also links grazing problems to existing theory of prey-predator systems thus increasing, hopefully, the fruitful contact between grassland management and ecological theory. It is certainly refreshingly fundamental and whatever the shortcomings of such generalized grassland systems, their analysis does contribute significantly to a clear and exact statement of the problems.

The PASTOR Model

PASTOR (Goodall, 1967) is probably the first pasture management model to have been published and was meant to be an example of how such models could be constructed. It is a simulation study of the effect

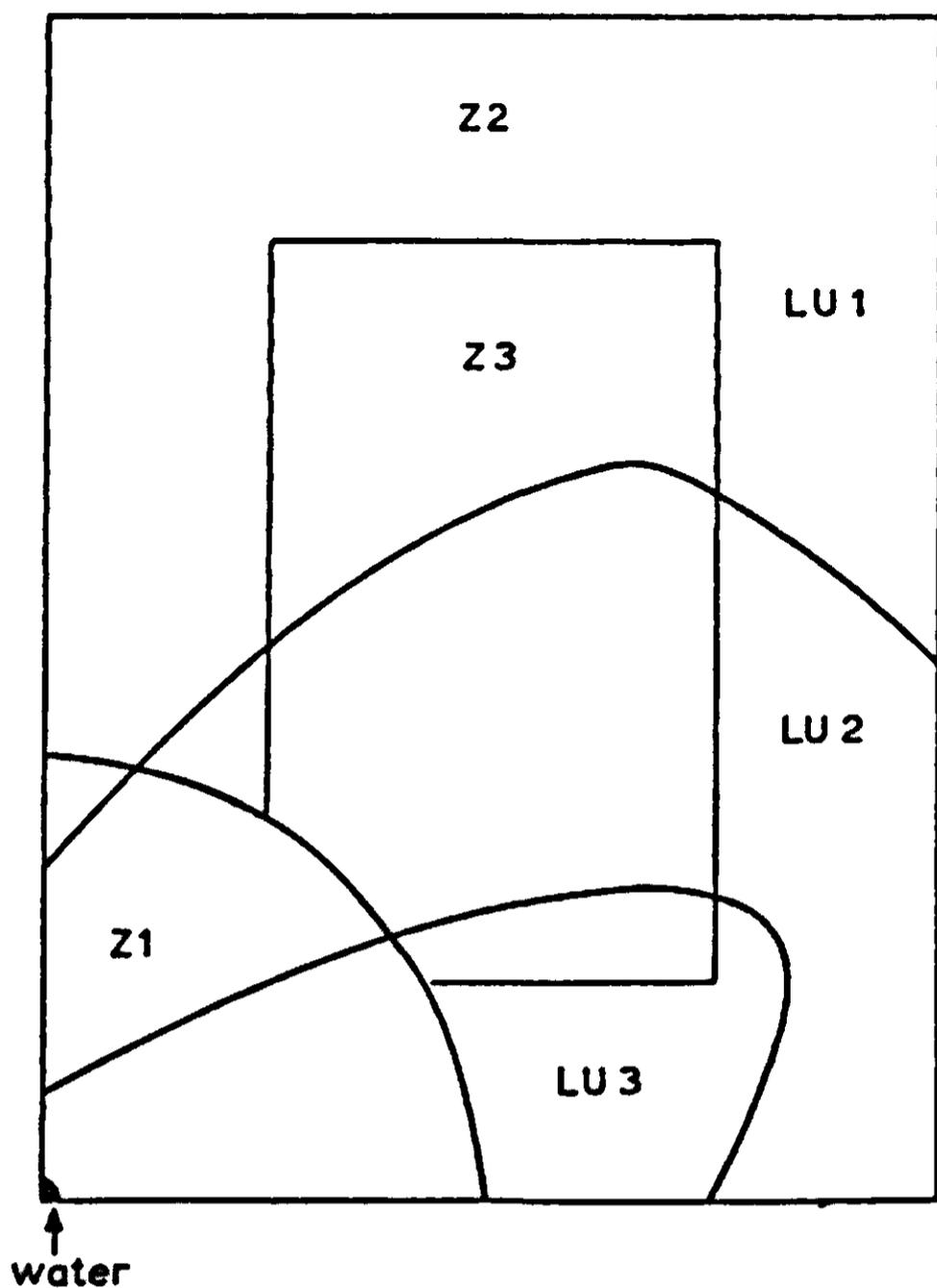


Fig. 18 | PASTOR: Map of hypothetical paddock. Z_i = preference zones for sheep grazing, LU_i – land units (From Goodall, 1967).

of fencing and the placement of watering points on the vegetation usage and livestock performance (Fig. 18). It considers five different plant species as forage sources with five different (forage?) growth parameters for each species and three land-unit types (LU_{1-3}) with different soil characteristics. The modelled paddock is subdivided into three preference zones (Z_{1-3}). The sheep that graze the paddock choose their forage according to the availability of the different species in the different preference zones and the species palatability.

The model results are presented for what they are worth without comparison with observed data. They are judged reasonable, the implication being that with suitable species and land parameters it could be used for actual management studies. However, this remains to be proved and considering the problems encountered in the less complex situations envisioned by LEYFARM and the Armidale model

(herbage in one species class; one land type) there are grounds for doubting over-confidence in reasonable, unverified model results obtained from situations where many, if not most, of the critical growth and preference parameters would have to be guessed. A trial run of a recent version of PASTOR without grazing animals resulted in annual growth increases of 6.8-25.0% for the five hypothetical species. When growth curves are based mainly on statistical parameters, it is difficult to judge whether such small growth increases of available forage over a whole season intentionally mimic a real situation or are simply errors in parameterisation. The latter possibility is clearly a major hazard in all large and complex programs but especially when the model components contain many statistically fitted functions, often with parameters that do not represent a recognisable characteristic of the reality being represented. PASTOR, which is carefully and professionally programmed, contains at least another example of what appears to be an inadvertent error. The runoff function is intended to have the general shape shown in Fig. 19. The

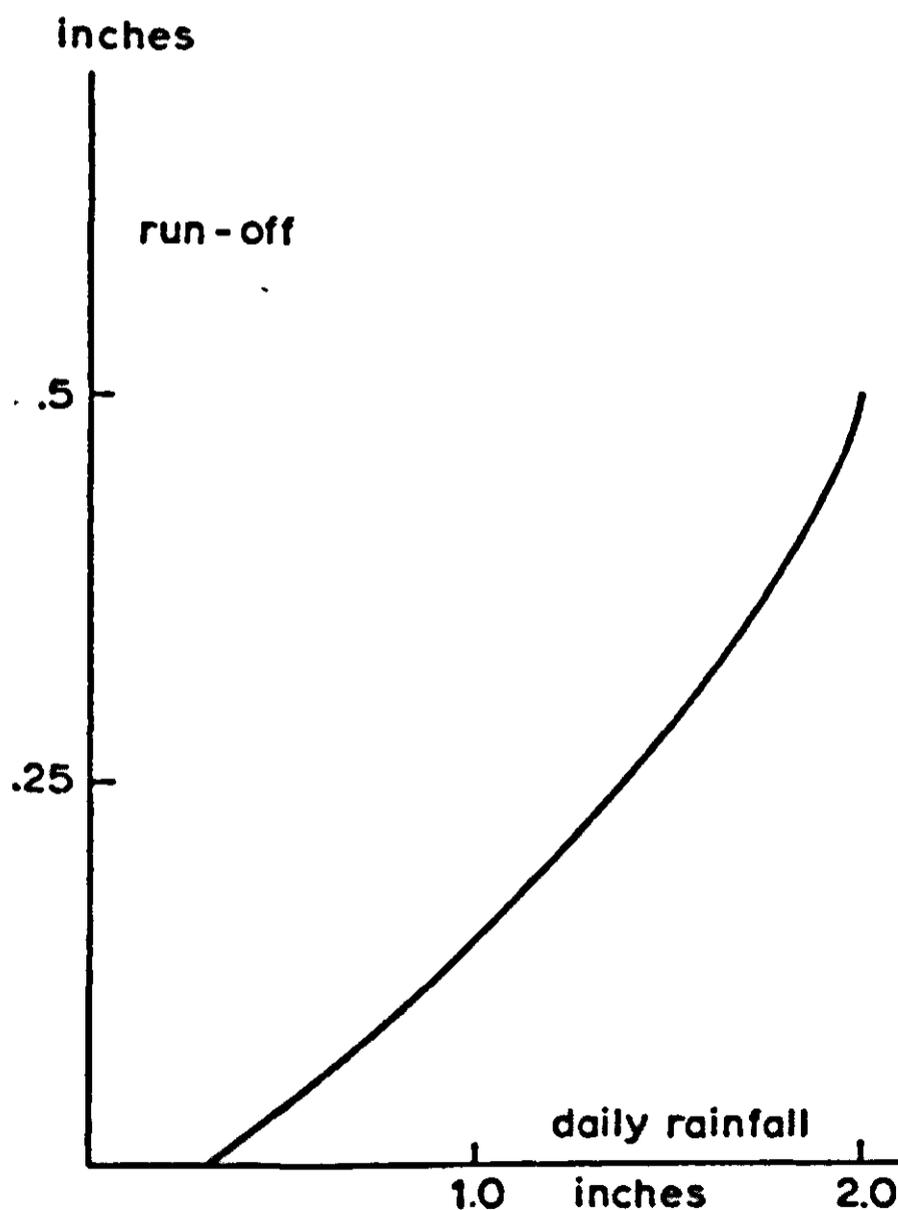


Fig. 19 | PASTOR: Intended form of runoff-rainfall relationship. (From Goodall, 1967).

curves generated by the program for the three land-unit types are given in Fig. 20. These could be intentional representations of special rainfall runoff relationships (e.g. runoff in land unit 3 related to runoff from land unit 1) or unintentional error. It is often possible that misrepresentation of a function can be incorporated in a model and yet remain undetected.

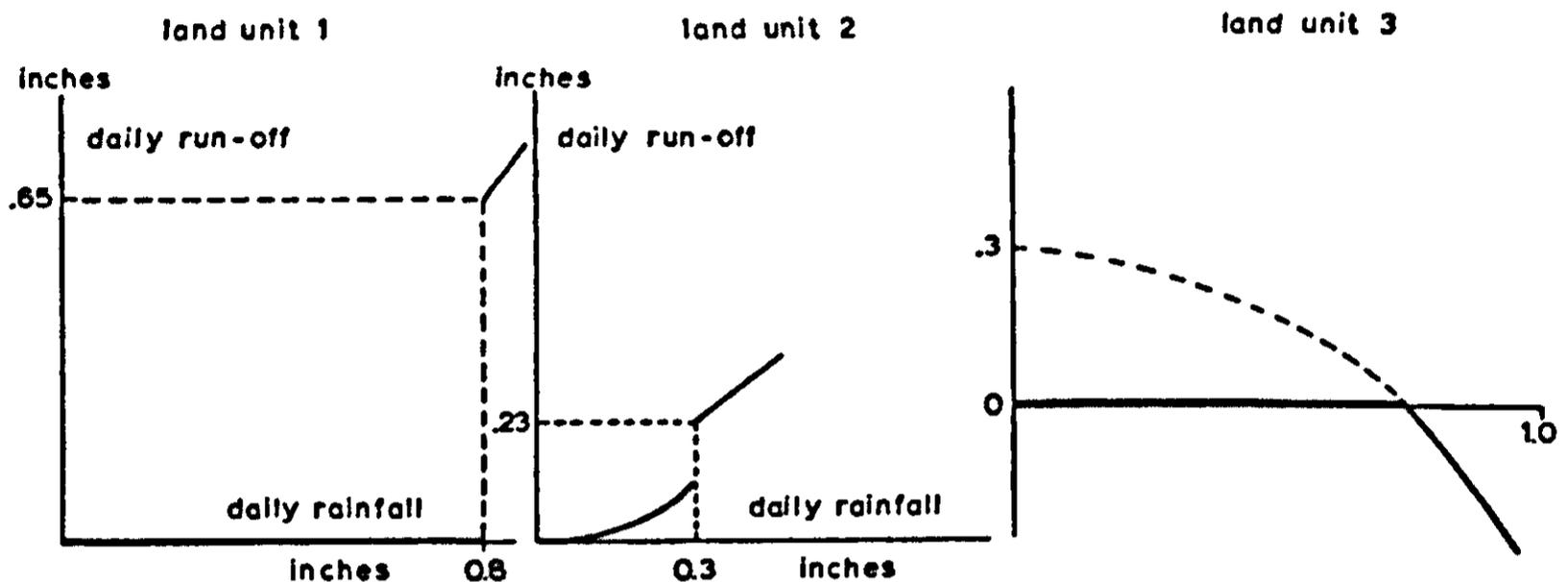


Fig. 20 | PASTOR: Runoff-rainfall relationships used in a recent version. (Derived from Goodall, 1973).

When this will become practically important will depend on whether this function becomes critical under certain legitimate conditions. As one would hardly intentionally incorporate functions that are never important, it is self-evident that the aim must be to remove all conceptual and parameter errors from a model. Even then it will take a major intellectual effort to determine whether a complex model is really doing what it was intended to do. Of course, even if it does do all that it was intended to do, it may still be an unsatisfactory model because of deficiencies in the definition of the system and in the aim of the simulation.

The Negev Model

NEGEV (Seligman et al., 1972) is a model of a semi-arid winter-rainfall grassland grazed by sheep. It was developed during and after a course in ecosystem modelling given in Jerusalem by Prof. G. M. Van Dyne of the U.S. Grassland Biome programme. It is of moderate complexity having four types of state variable (soil moisture, plant biomass, animal weight, animal numbers) which were subdivided

by land-form, species or age into about 50 actual state variables. About 200 parameters were used in defining the system, most of which were estimates or 'intelligent guesses'; some had to be changed in order to 'tune' the model. Pasture growth depended on existing biomass, soil moisture and temperature. Regrowth was restarted each growing season from a fixed residual reproductive biomass (seeds, buds) as soon as moisture and temperature conditions were suitable.

The results were 'reasonable' in that they were qualitatively in keeping with what was known of pasture growth and animal production in the region. The model was then used to test the stability and productivity of the system. The main conclusion was that without management of the livestock, the system would always crash in severe drought years. In addition, the exercise was thought to be 'useful in inducing interdisciplinary cooperation and in improving our general understanding of the semi-arid ecosystem' (Noy-Meir, 1975a). It was also proved that even when very little data are available, a fairly complex grassland model can, after some adjustment, give reasonable results. The catch, of course, is that such a model cannot add very much to what is already known because its reliability for prediction is low: if an unusual result is obtained it is generally impossible to know without further experimentation whether it is valid or an error. The validity of a model depends on sound conceptualization and good experimental data. NEGEV does show that a grassland model can produce presentable results with neither. It also shows that the usefulness of such models is rather limited.

The PWNEE Model

PASTOR and NEGEV are in a way relatively simple ecosystem models. Whatever criticism holds for them, holds even more for the large, complex ecosystem models like PWNEE or ELM (Patten, 1972; Anway et al., 1972). Here a considerable concerted effort has been made to collect as much of the necessary information as was necessary to construct a reliable model. The program involves many trophic levels, many species at each of the trophic levels, and many processes, not a few of which are poorly understood quantitatively, like some of the soil microbiological processes for which quantitative data are particularly difficult to obtain. It needs only a good programmer to make such a program run, but it takes a super-biologist to comprehend

the implications of some of the statistical constructions and most of the interactions and feedback mechanisms that are implicitly built into the model. It may be argued that the whole point of computer simulation is that the incomprehensible can be managed; that systems of analytically intractable differential equations are by nature incomprehensible, but that does not make the numerical solution less valid. That of course would be true whenever the formulation of the system of differential equations is both conceptually and parameterically sound. Can this be said of even the best of the ecosystem models?

The ISLE ROYALE Model

The Isle Royale biome model is quoted here as an example of a highly simplified ecosystem model run as a stochastic system (Beyer et al., 1973). The vegetation is entered as an initial amount that increases at a fixed relative rate due to growth in the growing season and decreases at a fixed relative rate due to death during the dormant part of the season. The vegetation is consumed by moose which reproduce and die at rates determined by the availability of the forage. The moose are also killed by wolves who do so at a rate dependent on a moose density: wolf density relationship. The data on which the parameters are based come mainly from Isle Royale itself. The programming approach for the stochastic processes of predation, birth and death is event dependent, which is apparently rather efficient in the use of computer time when the model simulates many discrete events with much 'dead time' between them. Even this relatively simple model contains some conceptual and parametric errors, at least in the version released for publication. Most of these could be corrected without adding significant complexity. The model is used to predict the population dynamics of Isle Royale and is said to be applicable to other situations too.

This model raises the question whether such gross simplifications of an ecosystem can be justified. The answer would depend on the objective of the simulation. If it was intended to predict what was going to happen to all the state variables in a given year, it would probably be unreliable. However, if it was intended to gain some insight into the effect of initial conditions, parameter values and function forms on the long term trends and population stability of the system, it could probably help to clear up some implications of the variables studied.

These simplified simulation models, which are much less restricted than some of the classical formulations in population dynamics, can be useful as aids to reasoning in complex situations. Concepts can be worked out in simplified models (Noy-Meir, 1975a, b, c). They may even make further development unnecessary either due to the problem being solved satisfactorily or, as is more likely, due to the now obvious lack of quantitative understanding at even a relatively coarse level. The conclusion could be quite useful as it would then be possible to define fairly clearly what need be done to improve understanding of the system.

The limits of an ecosystem can be set arbitrarily; but once defined, every ecosystem is unique in the sense that there is no other exactly like it. It has been maintained that because every ecosystem is unique, it cannot be simulated (de Wit, 1973). This is because once it has been studied and used for obtaining initiation and validation data, it will have changed and the model would not apply anymore (de Wit, 1973). However, it is also true of agricultural research that most field experiments are done in specific situations which are not identical in all respects anywhere else. Yet agricultural field research is still conducted on a wide scale and many believe that some of it is useful partly because the uniqueness of the experimental situation is judged to be a minor source of variation compared to the effects that are being studied. In the same way it would have to be shown that general aspects of an ecosystem are being investigated and that they are more important to the study situation than the specific or unique aspects. The problem of recognising what is unique and what is general appears difficult to solve purely objectively and may depend on the intuition of an experienced ecologist. These considerations do restrict the validity of 'realistic' ecosystem models drastically and force attention towards the highly simplified but more general type of models cited above.

Conclusion

It has been said that even if a biological model is of necessity an approximation of reality, it should always be an exact representation of what one thinks about the system (de Wit, 1973). This may not be good enough to be useful but it at least allows one to test one's thoughts. With inspiration, luck and perseverance, these may bloom into veri-

fied concepts capable of contributing to greater understanding of the worlds around us. Grassland models have a more immediate and practical objective: to optimize the management of the animal, herbage system and possibly some related systems too. Till now fairly complex grassland models have generally done little more, at best, than to confirm what has been known previously. Whereas this may not be a highly marketable result it should be seen in terms of the age of grassland modelling. What is being done is a start and a learning process which needs to be constantly checked with reality until the technique becomes really productive. The model development itself can be heuristically useful but the purpose of the exercise will always be to test ideas. This test, however, can generally only be a preliminary test. The crucial test in biological systems will be the experimental verification. If experiment and modelling go hand in hand, even some of the less convincing models that have been discussed here may yet become at least useful integrators of available research results and at best reliable extrapolators to significant management problems.

Acknowledgements

This essay reflects, albeit with some inevitable distortion, some of the views and prejudices held by members of the Department of Theoretical Production Ecology, headed by Prof. dr ir C. T. de Wit. He encouraged me to write it up after a seminar on grassland models given in his department. Jan Goudriaan, Herman van Keulen as well as Graham Arnold and Immanuel Noy-Meir read the draft and most of their suggestions have been incorporated. If any *faux pas* still shows I must take the blame.

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