

TOWARDS AN UNDERSTANDING OF THE CONCEPT OF GENOTYPE–DIETARY INTERACTION

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OPSOMMING: 'N BESPREKING VAN DIE PROBLEMATIEK VAN DIE BEGRIP: GENOTIPE–VOERINTERAKSIE

Die begrip genotipe-voerinteraksie is van besondere belang by veral twee fasette van die vleisbeesbedryf: prestasietoetsing van bulle en die seleksie- of ontwikkeling van geskikte genotipes vir bepaalde produksiestelsels. Ten opsigte van prestasietoetsing het die resultate getoon dat genotipe-voerinteraksie die meriterangorde van bulle kan wysig. Gevolglik is dit wenslik dat bulle verkieslik binne die voedingsmilieu waarin hulle aangehou word, getoets moet word. Ten opsigte van die begrip soos moontlik van belang in produksiestelsels blyk 'n herevaluasie van sommige resultate in die literatuur aangewese te wees. Wat moontlik as genotipe-voerinteraksie geïnterpreteer is kon bloot die gevolg gewees het van onvoldoende begrip van die invloed van skaling vir grootte, die multiplikatiewe (kromlynige) aard van groei en die differensiële grootte van metingsfout by verskillende voere of voedingspeile.

SUMMARY:

The concept of genotype-dietary interaction has considerable bearing on especially two aspects of the beef industry: performance testing of bulls and the matching of most suitable genotypes to particular production systems. With regard to performance testing the results imply that the order of merit between bulls could be altered due to genotype-dietary interaction. Therefore, it is preferable that bulls should be tested within the nutritional environment in which they are kept. With regard to the concept as possibly applicable to production systems, it would appear that some results in the literature need re-evaluation. What is possibly being interpreted as genotype-dietary interaction could be a function of inadequate apprehension of the impact of the effects of scaling for size, the multiplicative (curvilinear) nature of growth and the differential size of measurement error with different feeds and feeding levels.

As in many other countries, performance testing of young beef bulls in South Africa is done under standardized conditions using a well-balanced concentrate diet. Some (indigenous) breeds have been subjected to natural grazing for generations. The question therefore arises whether bulls from such breeds could be effectively tested on concentrate diets. The question therefore poses the possibility of genotype-dietary interaction in growth and efficiency.

Genotype-dietary interaction, both in the context of feeding level and energy concentration effects, has been reported by a number of authors (Béranger, 1976; Langholz, 1976; Andersen, 1978; Byers & Rompala, 1979; Byers, 1980), but not by others (Skjervold & Gravir, 1961 as cited by Langholz, 1976; Ferrell, Kohlmeier, Crouse & Hudson Glimp, 1978), or else, have been considered negligible sources of variation for highly heritable traits (Harwin, Brinks & Stonaker, 1966; Kress, Hauser & Chapman, 1971).

Theoretical Considerations

The disagreement in the literature may have different causes. One is undoubtedly inadequate genetic or nutritional variation in some experiments (Langholz,

1976), or related to this, that measurement error has not been effectively controlled in some cases (Meissner & Rouz, 1979).

The combined effect of small between animal or genotypic variation and relatively large measurement error very often obscures biological reality. A second cause relates to the problem of finding comparable criteria between genotypes (Taylor, 1965; 1968; 1971; Meissner, 1977). Interpretation of genotypic merit or interaction effects very often depend on the method of comparison, e.g. at equal body masses, fat percentages or metabolic age scales.

A third cause of disagreement between authors results from a failure to follow the full implications of the multiplicative nature of growth. The multiplicative nature of growth derives from the importance of relative growth rates in time relationships as well as interrelationships between body parts, as is convincingly demonstrated by e.g. Brody (1945). Since relative growth per time unit translates to absolute growth on the logarithmic scale, it follows that additivity can be expected to hold

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only on this scale of measurement. The multiplicative nature of growth might even extend to the error structure of data, which would indicate a logarithmic transformation for valid statistical analyses.

Flowing from the multiplicative nature of growth it follows that even if no significant interaction is found on the additive (log) scale interaction could be significant on the arithmetic scale due to multiplicative effects.

Let

$$w = cv^b \quad (1)$$

be the allometric equation relating two components of growth, thus

$$dw/dv = cbv^{b-1} \quad (2)$$

Assume, for instance, that b differs between diets and c between genotypes. Then it follows by definition that there will be genotype-dietary interaction in w or dw/dv . On the other hand, if

$$x_1 = a + b x_2 \quad (3)$$

where $x_1 = \ln w$, $a = \ln c$ and $x_2 = \ln v$, it follows by definition that there can be no interaction in $dx_1/dx_2 = b$ or in x_1 for a given x_2 .

In the growth model of Roux (Roux, 1976; 1981; Meissner, 1977) the allometric equation describes growth of one component relative to another and the Gompertz equation describes growth with time

$$w(t) = \alpha_w \exp [\ln (w(0)/\alpha_w) \exp - \gamma t] \quad (4)$$

where

$w(t)$ = value of the growth component under consideration at time t

α_w = $w(t)$ as $t \rightarrow \infty$

$w(0)$ = $w(t)$ at the beginning of the experiment $t = 0$, arbitrarily

γ = the rate constant for the relative growth rate of $w(t)$.

The growth rate of $w(t)$ is given by

$$dw/dt = -\gamma w(t) \ln (w(0)/\alpha_w) \exp (-\gamma t) \quad (5)$$

Also, by substitution from (4) in (5)

$$dw/dt = -\gamma w(t) \ln (w(t)/\alpha_w) \quad (6)$$

It follows from (5) that there will be interaction in dw/dt if there are both genotypic and dietary differences in γ , $w(t)$ and $w(0)/\alpha_w$. Genotype – time interaction in dw/dt would be significant for some differences between genotypes in the parameters or variables on the right hand side of (5).

If $w(t) \rightarrow \infty_w$, $\ln (w(t)/\alpha_w) \rightarrow (w(t) - \alpha_w)/w(t)$,

then (6) becomes

$$dw/dt = \gamma (\alpha_w - w(t)) \quad (7)$$

Equation (7) is the differential equation used by Brody (1945) to describe postpubertal growth, and is the basis of the criterium of interbreed comparisons suggested by Taylor (1965, 1968, 1971). It is clear from (7) that when breeds are compared at similar values of $(\alpha_w - w(t))$ there can only be genotype-dietary interaction in dw/dt if γ shows such interaction. For equation (6) this statement will, of course, only be approximately true.

In the log form (4) becomes

$$x(t) = \alpha_x + (x(0) - \alpha_x) \exp (-\gamma t) \quad (8)$$

and likewise (5) becomes

$$dx/dt = -\gamma (x(0) - \alpha_x) \exp (-\gamma t) \quad (9)$$

For purposes of estimation the equivalent of (8) is

$$x(t) = \rho x(t-1) + (1 - \rho) \alpha_x + \varepsilon(t) \quad (10)$$

the so-called autoregressive equation (see Roux, 1976; 1981) with $\rho = \exp -\gamma$.

Materials and Methods

Details of the experiment are given in the paper by Meissner, van Staden & Pretorius in this edition.

Afrikaner, Hereford and Simmentaler bull calves were hand reared on cow's milk and a creep feed from 48 h *post partum* until 11 weeks of age.

At weaning they were introduced to either a pelleted concentrate diet or a roughage diet which was not pelleted. The calves were allocated to their respective diets at 48 h after birth in the order that they were born. Total intake of calculated DE until weaning was recorded. From weaning voluntary intake of DM and body mass were measured every week until approximately 27 months of age. Body composition was estimated in terms of moisture, protein, fat, lean and energy of combustion by tritium dilution at 3 to 4 week intervals

from 12 weeks of age onwards. The apparent DE of the two diets was determined *in vivo* at *ad lib* intake on a number of occasions throughout the experimental period.

Cumulative DE intake of every individual was then calculated between 12 and 80 weeks, the total DE intake before weaning plus a calculated amount of *prenatal* energy uptake added, and related on a weekly basis to body mass and its components on the log scale by ordinary least squares procedures. Time relationships were compiled using the autoregressive equation as previously mentioned.

Results

Concept of parameter analysis

The growth of one component relative to another or with time may be summarized by the parameters in the relevant equations, i.e. slope (b) and intercept (a) in the log form of the allometric equation and ρ , α and x (o) as described previously, in the autoregressive equation. In statistical terms these parameters are sufficient to describe the pattern of any number of measurements on an animal in a particular growth phase because under 'regularity assumptions' all information from the data is contained in them. Consequently, it is a valid procedure to substitute the parameters for the data and to do the required statistical analyses on them.

Analyses on the parameters of the log form of the allometric equation

Roux (1976) and Meissner (1977) showed that \ln (cumulative feed intake) and \ln (body mass) or \ln (component of body mass) describe a straight line within a particular growth phase when measured in temporal sequence on the same animal or group of animals. The fit of these lines is usually extremely accurate with

r^2 in excess of 0,97 and the lines in this experiment were no exception (see Meissner, van Staden & Pretorius, this edition).

In the relationships reported on here, DE intake was used as the measure of feed intake and tritium space was used as the measure of the components of body mass, i.e. protein, lean and fat. It was considered a more valid procedure to do statistical analyses directly on tritium space which was the actually measured variable in stead of on protein, lean etc. which would be derived variables. As the different growth phases (see Fig. 2 & 3 in Meissner, van Staden & Pretorius – this edition) could not be effectively identified for tritium space relationships, they were ignored in this analysis.

For the purpose of the questions considered here covariance analysis or a variance analysis procedure are effective tests. One should however realize that if differences between the b's (slopes) are significant, the test on the a's is invalid, because a depends geometrically on b. In this analysis where a two-way analysis of variance procedure with genotype and diet as variables were used, the b's genotypes were not significantly different. The b's between diets however, differed highly significantly ($p < 0,01$). Hence, common b's for diets could be calculated. These were 0,634 and 0,583 for the \ln (cumulative DE intake) – \ln (live mass) relationship on the concentrate and roughage diets respectively. The corresponding b's for the \ln (cumulative DE intake) – \ln (tritium space) relationships were 0,583 and 0,553. The a's were then adjusted according to the common b's and the two-way analysis of variance procedure used to test for differences. The results are shown in Tables 1 and 2.

The adjusted a's in both cases (Tables 1 and 2) differed highly significantly between diets and genotypes but not significantly in the analyses for genotype-dietary interaction. This implies that the proportional difference in

Table 1

Adjusted a's in the relationship \ln (cumulative DE intake) and \ln (live mass) and the F-tests for differences between diets, genotypes and genotype-dietary interaction

Genotype	Diet		F-values for differences between		
	Concentrate	Roughage	Diets	Genotypes	Interaction
Afrikaner	-0,510 ± 0,041	-0,147 ± 0,031			
Hereford	-0,340 ± 0,041	-0,019 ± 0,051	409***	78,6***	1,27 NS
Simmentaler	-0,242 ± 0,062	0,087 ± 0,051			

*** $\rho < 0,001$

NS not significant

d.f. diets: 1,27

genotypes and interaction: 2,27

Table 2

Adjusted a 's in the relationship \ln (cumulative DE intake) and \ln (tritium space) and the F-tests for differences between diets, genotypes and genotype-dietary interaction

Genotype	Diet		F-values for differences between		
	Concentrate	Roughage	Diets	Genotypes	Interaction
Afrikaner	-0,609 ± 0,046	-0,448 ± 0,034			
Hereford	-0,470 ± 0,044	-0,338 ± 0,051	403***	73,5***	0,85 NS
Simmentaler	-0,330 ± 0,048	-0,178 ± 0,067			

exponent a between genotypes was the same on the two diets for the total period of study. In the context of units of mass produced per unit of cumulative DE intake for example, the Afrikaners produced 100, the Herefords 116 and the Simmentalers 129.

Analyses on the parameters of the autoregressive equation

In the growth-with-time relationships γ , $x(o)$ and α_x are the determining parameters as was discussed in the Introduction. Only the growth-with-time relationships of \ln (cumulative DE intake) is considered here. The parameters of the corresponding relationships of \ln (live mass) and \ln (tritium space) are derived by algebraic substitution from the \ln (cumulative DE intake) relationships as indicated by Meissner (1977). Therefore, these parameters are not shown since tests for significance

on them would be merely reproductions of those on the parameters of \ln (cumulative DE intake) with time.

A two-way analysis of variance procedure was conducted on γ , $x(o)$ and α_x and the results are shown in Table 3.

As shown in Table 3 the parameter γ differed highly significantly between diets and genotypes, but the result for genotype-dietary interaction was not significant. The parameter $x(o)$ was not significantly different between diets, highly significantly different between genotypes and there was no significant genotype-dietary interaction. Because $x(o)$ is the initial value of \ln (cumulative DE intake), and in this case, the value at 12 weeks of age which in actual fact reflects the cumulative DE intake of milk, it follows that differences between diets should not have been significant. Genotypic

Table 3

Parameters γ , $x(o)$ and α_x in the relationship \ln (cumulative DE intake) with time and the F-tests for differences between diets, genotypes and genotype-dietary interaction

Genotype	Diet		F-values for differences between		
	Concentrate	Roughage	Diets	Genotypes	Interaction
γ					
Afrikaner	0,027 ± 0,005	0,015 ± 0,001			
Hereford	0,032 ± 0,002	0,018 ± 0,001	150***	4,16**	0,10 NS
Simmentaler	0,030 ± 0,003	0,017 ± 0,001			
$x(o)$					
Afrikaner	7,282 ± 0,085	7,302 ± 0,084			
Hereford	7,509 ± 0,133	7,438 ± 0,071	2,46 NS	33,5***	1,31 NS
Simmentaler	7,755 ± 0,185	7,620 ± 0,067			
α_x					
Afrikaner	10,73 ± 0,246	11,59 ± 0,199			
Hereford	10,88 ± 0,163	11,29 ± 0,142	92,4***	2,75 NS	4,93**
Simmentaler	11,01 ± 0,136	11,51 ± 0,083			

** $p < 0,01$

differences on the other hand resulted because the milk schedules were calculated relative to metabolic live mass as described in the paper by Meissner, van Staden & Pretorius (this edition) and mass for age differed between genotypes. The parameter α_X was highly significantly different between diets, not significantly different between genotypes and showed a highly significant genotype-dietary interaction.

Thus, in the time relationship of \ln (cumulative DE intake) one of three parameters showed significant interaction. Furthermore, two of the three parameters differed significantly between genotypes and diets, indicating genotype-dietary interaction in the differential of the growth with time relationship of \ln (cumulative DE intake), i.e. rate of DE intake (e.g. intake per day), and consequently also the growth rate of live mass (gain) and those of the components of body mass such as protein or fat deposition. The conclusions follow from Equation 5 as discussed in the Introduction.

As a consequence of the results in Table 3 genotype-dietary interaction would be expected in the case of Equation 7. However, if $\alpha_W - w(t)$ is kept constant between genotypes the influence of the interaction in α_X is eliminated so that a smaller effect would be expected due to the approximation of Equation 6 by 7. This is demonstrated in Figures 1 and 2 where in the one case $\alpha_W - w(t)$ was kept constant and in the other not. In Equation 6 the arithmetic scale gives the distance between $w(t)$ and α_W as a proportion. This has the advantage that differences in α_W is eliminated by taking proportions. In Fig. 1 DE intake per day is plotted against different proportions of α_W . In Fig. 2 DE intake per day is plotted against live mass, i.e. $\alpha_W - w(t)$ was not kept constant and the effects of interaction are evidently more substantial.

Discussion

Genotype-dietary interaction in performance testing

The results showed that the influence of genotype-dietary interaction might have bearing on the validity of interpretation of performance testing data. Depending on the genotypes under consideration interpretation of merit of different genotypes might be biased, i.e. if one of the goals in performance testing is to evaluate genotypes. In this particular case the voluntary DE intake of the Afrikaner on the concentrate diet was proportionally lower than on the roughage diet, while that of the other two genotypes was similar as can be deduced from Figures 1 and 2. This effect is also evident for live mass gain as depicted in Fig. 3.

From the results of Rogerson, Ledger & Freeman (1968) and Ledger, Rogerson & Freeman (1970) in Kenya low intakes of concentrates appear to apply to most indigenous genotypes on the African continent with a history of only being exposed to low quality diets.

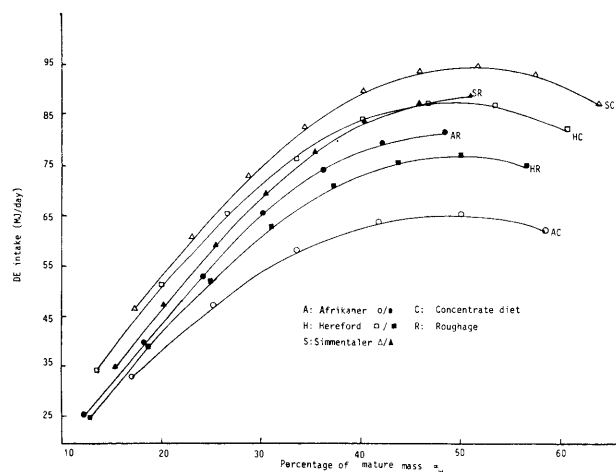


Fig. 1 DE-intakes at different proportions of α_W

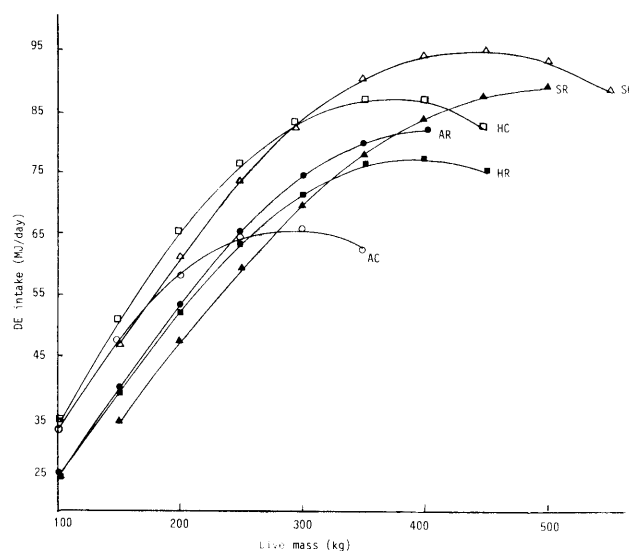


Fig. 2 DE-intakes at different live masses (same notation as in Fig. 1)

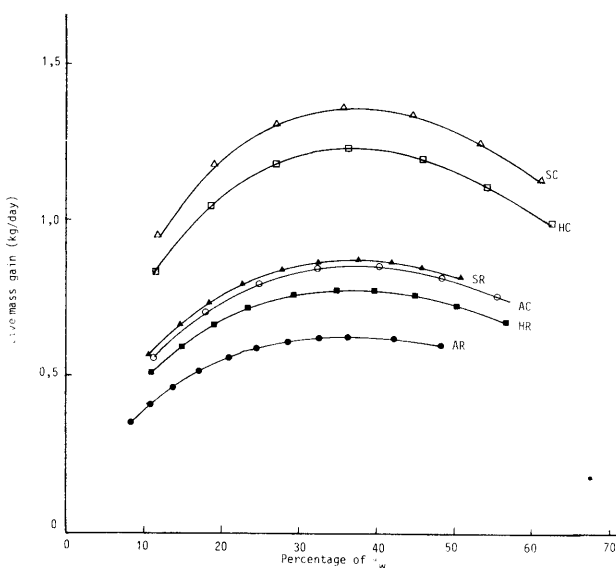


Fig. 3 Live mass gain at different proportions of α_W mass (same notation as previously)

The implication further is that the order of merit of some bulls when fed a concentrate diet will not necessarily hold on a roughage diet. Again, this may only apply to indigenous types since the results on the Hereford and Simmentaler did not show extensive interaction, and presumably they are reasonably representative of exotic types.

The above statements apply when standardized diets are used and one should not extrapolate to the natural grazing situation. Under such conditions the animal is confronted with palatable and less palatable plant species and individuals or genotypes may differ in their selection preferences which may cause differences in energy intake and consequently differences in relative performance.

Consequences and relative impact of interaction effects

The results in Tables 1 and 2 and Figs. 1 to 3 are cases in point of the theoretical arguments put forward in the Introduction. Consequently, it was shown that the concept of genotype-dietary interaction is a function of a number of influences. It is considerably influenced by method of comparison as discussed by Taylor (1965; 1968; 1971) and Meissner (1977) and as effectively demonstrated in Fig. 1 vs Fig. 2. The implication here is that the effects of genotype-time and genotype-dietary interactions can be reduced by certain methods of comparison.

The correct basis of comparison might be called 'physiological age' (Brody, 1945) and it would appear that in practice the metabolic age scale of Taylor (1965) based on observed mature mass, approach this rather recondite basis of comparison. So does comparison relative to α_w of course.

Cognisance should however be taken of the fact that the work of Blaxter (1976) showed that rams fed a moderate diet kept on growing, even past their generally accepted mature mass. This implies first of all that α_w and Taylor's mature mass are not synonymous and secondly that mature mass as a practical guide in scaling for size may sometimes not be an effective substitute for α_w .

In the growth model proposed by Roux (Roux, 1976; Meissner, 1977) breakpoints occur in the lines, with a first linear relationship describing the data in the log scale before such a breakpoint and a second one thereafter. These breakpoints appear to have biological meaning (Scholtz & Roux, 1981 (a)), one of which, for example, is apparently the onset of sexual maturation (von Bertalanffy, 1960). The corresponding distance between one breakpoint and the next of different genotypes appears to reflect a particular growth phase or the same physiological age. Similar to proportions of mature mass as a basis of comparison, comparison within growth phases decrease interaction effects substantially as were indicated with the deliberations on and analysis of $dw/dt = \gamma(\alpha_w - w(t))$.

A further substantial influence which may affect the validity of interpretation of interaction effects is measurement error. The variance of an observation comprises of two components, that due to biological variation (σ_x^2) and that due to measurement error (σ_e^2) (Meissner & Roux, 1979). The error variance can be reduced by replicatory measurement to σ_e^2/n , where n denotes the number of measurements, thereby also minimizing the total variance. It can in the case of growth with time or growth of one component relative to another be further reduced to almost negligible magnitude by fitting a suitable function to the data such as the log allometric or autoregressive equation. The effects of negligible measurement error are illustrated in Table 4. Tests of significance for the mean growth rate calculated for the live mass interval 20 - 50% of α_w are depicted. In the one instance, denoted 'uncorrected', observed gain from 20 to 50% α_w was merely divided by the observed number of days required to grow from 20 to 50% of α_w .

In the other instance, denoted 'corrected', the autoregressive equation was fitted to the growth data as discussed, the number of days required to grow from 20 to 50% α_w accurately calculated from the parameters of the function and then divided into the mass interval. The F-values in the case of the corrected growth data are noteworthy higher.

In this particular experiment genotypic and dietary differences were large. In many other experiments this may not be the case. This implies that in such experiments uncorrected growth data as defined for the example in Table 4 may not show significant differences or interaction. Furthermore, differences between genotypes in growth data on one diet or feeding level may be significant while not on the other. If measurement error is not reduced differences on a high feeding level or dietary energy concentration could be significant while they might not be on a low feeding level or dietary energy concentration (roughage). This follows as measurement error would not result in constant coefficients of variance, while genotypic variation might result in constant coefficients of variance for different treatments. Therefore, the effect of measurement error could be relatively more substantial on a low feeding level or dietary energy concentration and consequently the tests for significance would be less sensitive. It is conceivable that this could lead to serious misinterpretation.

Table 4

F-values on corrected and uncorrected mean growth rate

	F-values for differences between		
	Diets	Genotypes	Interaction
Uncorrected	192	69,3	17,9
Corrected	388	104,0	25,4

One of the major goals in genotypic evaluation or cross breeding programs is to match natural resources to genetic potential, i.e. to find the most suitable genotypes or combinations of genotypes for particular production systems. Most reports indicate large frame types to be superior in gain on feeding systems with high concentrate levels but that the differences between types on feeding systems involving silage or pasture appear to be small - thus implying genotype-dietary interaction (Andersen & Andersen, 1974; Béranger, 1976; Langholz, 1976; Andersen, 1978; Byers & Rompala, 1979; Byers, 1980). The discussion above implies that even if the method of comparison is reasonably above board (most authors use mature mass as basis), the apparent interaction could be an artifact of measurement error. The situation may be further influenced if multiplicative growth is linearised on the arithmetic scale as is discussed below.

The effects of linearisation of a multiplicative process on for example, gain, are shown in Fig. 4. The data of the Simmentalers were used for illustration purposes.

The curves in Fig. 4 show gain on the concentrate and roughage diets as calculated from the differential of the growth-with-time equations at specific percentages of α_w . The straight lines indicate the situation if mean gain is calculated according to ordinary procedures, i.e. total gain interval divided by the number of days. To avoid complication of the issue by measurement error the latter procedure was also calculated from the growth-with-time equations. The crosses on the lines show the gain at the mean percentage of α_w .

Gain at different percentages of α_w is over- or underestimated by the linearised procedure on both diets. What is more pertinent to the discussion on genotype-dietary interaction though, is that the error introduced by the linearised procedure is more pronounced on the concentrate than on the roughage diet as can be seen e.g. from the values (crosses) at the mean percentage of α_w . On the concentrate diet the value of the linearised procedure is 91% of the value of the multiplicative procedure and on the roughage diet 94%. Therefore the proportionally greater effects of linearising multiplicative growth and the fact that these proportions might be different for different genotypes, indicate the need for a re-evaluation of some of the results on genotype-dietary interaction as reported in the literature.

The intricacy of the question of genotype-dietary interaction is further exemplified by some apparently contradicting results such as those experienced with intake and gain vs efficiency. The ratio of gain to intake

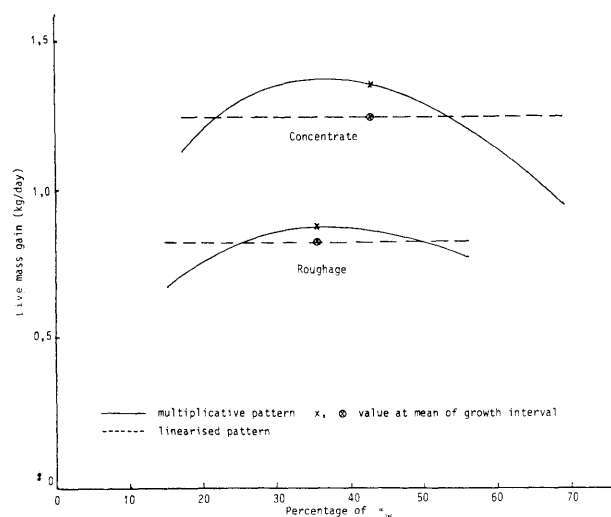


Fig. 4 *Multiplicative vs linearised pattern of live mass gain of Simmentaler on the concentrate and roughage diets*

(efficiency) is described by Equation 2 in the Introduction, which by definition in statistical terms, implies interaction if b differs between diets and c between genotypes, as were the case in Tables 1 and 2. Gain or intake as derived from Equation 6 show significant interaction because γ_w and α_w either differed between genotypes and diets or showed significant interaction.

It is, perhaps, of some interest to try to examine the reason for the difference in interactive behaviour of dw/dv and dw/dt or dv/dt . Perhaps part of the explanation lies with the possibility of standardizing the allometric equation to

$$w/\alpha_w = (v/\alpha_v)^b,$$

which implies some implicit scaling relative to α_w .

This explanation tallies with Fig. 1, in which the interaction as illustrated in Fig. 2, is considerably reduced. Another reason might revolve around the fact that b is a parameter by which an animal is scaled from infancy to adulthood according to the principle of allometry. In the light of present understanding such a biologically important characteristic should be canalized. The discussion by Scholtz & Roux (1981) is perhaps pertinent here, although according to their results the canalization of b cannot be very narrow, since it had a significant heritability.

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