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This paper will consider some of the limitations to efficient beef production arising from deficiencies in performance of individual animals.

Discussion is confined to principles which are particularly pertinent to tropical areas and to one component of productivity, namely, growth, although the principles are also applicable to other environments and to other components of productivity.

Environmental Stresses

In the tropics and subtropics of Australia there are a number of environmental factors which depress growth rate of cattle, the major ones being heat (high temperature and humidity), cattle tick (Boophilus microplus), gastrointestinal helminths, infectious diseases, such as bovine infectious keratoconjunctivitis (BIK or "pink eye"), and seasonal and annual shortages in the quantity and quality of available feed. Furthermore, these stresses differentially affect the growth of different breeds of cattle (Frisch and Vercoe 1978, 1982).

Much of the research at the Tropical Cattle Research Centre, Rockhampton has been devoted to finding genetic means to minimise the effect of these stresses. It has been in the course of this research the following principles and concepts have been developed.

Determinants of Growth in the Absence of Stress

The determinants of growth outlined by Blaxter (1964) are still valid. These are (i) the voluntary food intake (VFI); (ii) the maintenance requirement; (iii) the composition of the gain; (iv) the digestibility and metabolizability of the ration; (v) the efficiency of utilization of the metabolizable energy and (vi) the relative feeding level (i.e. the ratio of food intake to maintenance requirement). Of these determinants of growth the most important ones which define variation between individuals are VFI and maintenance requirements (Vercoe, 1977) and for the purposes of this paper, discussion will be limited mainly to the between genotype differences in VFI, maintenance requirements and relative feeding level.

Breed differences in growth rate in the absence of stress (growth potential) are closely correlated with differences in VFI, which in turn are closely correlated with differences in fasting metabolic rate (FM). However, the ratio of these two (VFI:FM) which is related, is similar for each breed. The results of two experiments are summarised in Table 1.

Expt.	\mathtt{Breed}^\dagger	Wt. Gain kg/day	VFI g/kg/day	FM KJ/kg/day	VFI/FM
	BX	0.81	26.6	93.9	0.28
1	AX	0.85	27.5	98.9	0.28
	HS	0.84	28.5	97.9	0.29
	B	0.68	31.8	88.2	0.36
2	вх	0.75	33.4	93.1	0.36
	hS	0.81	37.4	99.8	0.37

TABLE 1: Growth Rates, Voluntary Food Intake and Fasting Metabolism of Different Breeds in the Absence of Stress

 † B = Brahman

A = Africander

HS = Hereford x Shorthorn

X = HS

Because of the similarity of relative feeding levels between breeds, breeds with the highest VFI will have the fastest gains at ad *libitum* levels of feeding and any differences between breeds in the efficiency of gain will be unrelated to differences in relative feeding level (Frisch and Vercoe 1977). Conversely, breeds with the lowest VFI and the lowest maintenance requirement will have the highest growth rate or maintain higher live weights when fed restricted amounts of feed. That is, the rank order of breeds for growth rate when fed ad *libitum* quantities of a high quality roughage diet will be reversed when they are fed restricted quantities of the same diet (Frisch and Vercoe, 1977).

When a diet is of sufficiently low quality that animals are near maintenance live weight when fed *ad libitum* amounts, HS cattle have higher intakes than BX or Brahman (B) but may lose slightly more weight or maintain lower weights than other breeds (Frisch and Vercoe, 1977 and unpublished data). The reason for this interaction is probably related to the breed differences in maintenance requirements and in the efficiency of utilisation of metabolizable energy for maintenance (Vercoe 1970; Frisch and Vercoe 1977).

The relationships that exist between breeds for VFI and weight gain seem to exist between animals within a breed. Approximately 75 percent of the between animal variation in growth rate on high quality roughage diets in the absence of stress is accounted for by differences in VFI (Vercoe and Frisch, 1982). Growth rates of steers fed *ad libitum* and their growth rates when fed restricted levels of a high quality feed were significantly negatively correlated (r = -0.4) but the correlation between their growth rates when fed a high quality and a low quality diet *ad libitum* was not significant (r = 0.0) despite a high correlation between their VFI and for the two diets (r = +0.7) (Frisch and Vercoe, 1977).

The growth potential of different breeds and animals within a breed is therefore largely a reflection of VFI which is closely related to FM and maintenance requirements.

Determinants of Growth in the Presence of Environmental Stress

Growth rates measured in the absence of stress are unrelated to growth rates measured in the presence of environmental factors, e.g. heat, ticks, helminths, BIK and other diseases which are known to depress growth rates.

The response of different breeds to treatments which control ticks and worms differs according to the number of parasites carried. Thus, response of Brahman and Brahman crossbred animals is less than that of *Bos taurus* animals because they carry fewer ticks. Breeds differ in their resistance to infestation by ticks but they are equally susceptible to the effect of ticks, i.e. the effect per tick on production is similar for both *Bos indicus* and *Bos taurus* animals (Seifert 1971; Turner and Short 1972). The situation with gastrointestinal helminths is not as clear. There is some evidence which suggests that breeds carry similar burdens but removal of worms produces a greater response in *Bos taurus* breeds (Seifert 1971; Turner and Short, 1972). Other evidence suggests that breeds acquire resistance at different rates and relative faecal egg counts may differ depending on age (Frisch, unpublished). Nevertheless *Bos indicus*, *Bos taurus* and their crosses all respond to treatment for helminths, but the response may differ between breeds.

Elevated rectal temperatures also depress growth rate (Turner, 1962). At the same ambient temperatures, Brahman and BX have lower rectal temperatures than HS cattle and growth rates are consequently differentially affected. Between animals within a breed there is a negative correlation between the elevation of rectal temperature and growth rate (Turner 1962; Frisch 1981).

Breeds differ in susceptibility to BIK (pink eye); Bos indicus breeds are rarely infected whereas Bos taurus breeds may have an infection rate of 70 percent or more. Crossbred (BX and Africander x Hereford-Shorthorn) cattle are also relatively resistant with about 7 percent being infected up to 15 months of age (Frisch 1975). Between animals within a breed, growth rate and the severity of BIK infection are negatively correlated (Frisch 1975; 1981).

The effect of these stresses on growth rate is mediated through food intake and utilisation. In the case of ticks (Seebeck, Springell and O'Kelly, 1971) and worms (Dargie, 1980) some 70-80 percent of the difference in growth rate between infected and control animals is due to a reduction in food intake and the remainder is due to the effects on dry matter and nitrogen digestibility and metabolism. High ambient temperatures accompanied by increases in rectal temperatures result in decreased food intake (Ragsdale *et al*, 1951) and increased protein catabolism (Vercoe, 1969). Anecdotal evidence suggests that depression in growth rate associated with BIK infection is also largely caused by reduced food intake (Hughes and Pugh, 1980).

Thus, growth rate in the presence of stress whilst still a function of food intake and utilisation, is a reflection of the resistance of the animal or breed to stress. The potential intake of an animal may be high, but unless the animal is resistant to stress and can therefore realise this intake, its growth rate may be lower than that of animals of lower potential intake, but higher resistance to stress. The ranking

of different breeds and animals grown in different environments will vary and depend on the levels of environmental stresses in which they are grown. This is illustrated in Table 2 which shows the gain/day of three breeds at three different levels of stress. At the 'low' level of stress the animals were fed lucerne hay ad libitum and the stresses were minimal; the 'medium' level of stress animals were grazing but were dipped and drenched at three-weekly intervals to control ticks and gastrointestinal helminths. The animals considered to be under 'high' stress were grazed with the 'medium' stress group but did not have ticks and internal parasites controlled. At the 'low' level of stress gain/day was a reflection of voluntary food intake and HS grew faster than the BX and B. At the 'medium' level of stress the BX grew fastest, not because it had a higher growth potential but because it could express a higher proportion of its growth potential at this level of stress. The HS, the breed with the highest growth potential ranked only second because it was more susceptible to the stresses of BIK and heat. At the 'high' level of stress the B breed grew fastest despite the fact that it had the lowest growth potential because it was most resistant to the environmental stresses. In each of the three environments a different breed grew fastest because of the different determinants of growth. The same argument can be applied to individual animals instead of breeds.

Implications for Selection for Growth Rate

Because growth rate is determined by two different groups of factors, one related to growth potential and the other to the level of resistance to environmental stresses, selection for growth rate will therefore be for different factors in different environments. Across breeds, these two groups of factors are negatively related (Table 2). The evidence is that a similar situation exists for animals within a breed. Frisch (1981) demonstrated that selection in an unadapted breed (HS) for growth rate in a stressful environment increased the resistance of the selected line to the stresses of that environment, but decreased voluntary food intake, growth rate and maintenance requirement in a non-stressful environment relative to an unselected control line.

The implications will be discussed in relation to three broad environmental classifications.

(i) <u>Selection for growth in a non-stressful environment</u> would be expected to increase voluntary food intake, metabolic rate (and maintenance requirement) and mature size, the major factors which determine growth rate in that environment. High voluntary food intake and maintenance requirement are not disadvantageous where food is not limiting, but some effort should be devoted to making gains in efficiency by maximising voluntary food intake and minimising maintenance requirement, i.e. by increasing the relative feeding level. One way of achieving this would be to rank animals on the basis of relative growth rate (i.e. growth as a proportion of initial weight or geometric mean weight) over a comparable growth period. Deviations in relative growth rate can be interpreted as deviations in relative feeding level provided the composition of the weight gain is similar. Mature size will increase as a consequence of selection for growth rate in non-stressful environments unless positive steps are taken to select only for the rate component of growth and exclude the component related to scale or mature size. Ways of achieving this have been proposed based on birth weight adjustments to growth rate in early life (Dickerson *et al*, 1974).

(ii) <u>Selection in an environment of constant stress</u> will eventually develop animals which are a mixture of productive and adaptive attributes appropriate for that environment. For each environment a particular level of production potential will be coupled with a level of resistance to stress which enables that production potential to be realised. If the environment changes or the animal is transferred to a different environment, the mixture will be no longer appropriate for efficient production.

The concepts of non-stressful and constant stress environments are theoretical rather than practical; all natural environments have seasonal and annual variation in the levels of stress.

(iii) <u>Selection in environments of variable stress</u> pose the greatest problems to genetic improvement. Earlier in this paper genotype x environment interactions were demonstrated and how they occur was explained. Similar interactions occur between years and it seems reasonable that they occur for similar reasons and apply to individuals as well as breeds.

Because growth results from two opposing sets of factors operating on food intake and utilization, the animal identified as being the fastest grower in one year may not have been identified in a different year. In years of low stress, animals with higher growth potentials will rank highest but in years of high stress, those with high levels of resistance to stress will rank highest. Depending on the size of the negative correlation between growth potential and resistance to environmental stresses, gains made in one year when production potential is the principal determinant of growth may be partly lost in subsequent years when resistance to stress is the determinant. The genetic gains made in growth rate under these conditions are likely to be small and inefficiently obtained.

Fluctuations in the quantity and quality of nutrition influence weight gain not only directly, but also indirectly because the susceptibility to tick (and probably other parasitic) infestation is increased when the level of nutrition declines (O'Kelly and Seifert, 1969). In order to minimise weight loss during periods of poor nutrition, animals are needed which have a low maintenance requirement. However, low maintenance requirement is associated with a low voluntary food intake and low growth potential. Therefore, ways must be sought to couple a low maintenance requirement when food is scarce with a high voluntary food intake when food is plentiful. This may be possible if animals can be identified which can vary fasting metabolic rate in response to changes in the level of available nutrition. However, between animals the variation in the ratio of voluntary food intake to fasting metabolic rate is small (Frisch and Vercoe, 1977).

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Stress	Breed [†]	Gain/day (kg)	Tick Count (per side)	BIK Score (per animal)	Rectal Temp. (^O C)	Worn EPG	Feed Intake/kg Live Weight	FM/kg LWT
MOT	В	0.81	ο	2.0	38.2	0	27	81
Shaded pens - parasites	ВХ	06.0	0	2.0	38.3	0	30	68
controlled lucerne hay ad lib.	H H H	1.07 		2.0	38.5 		34	101
MEDIUM	£	0.63	D	2.0	39.1	o	I	I
(Grazing - parasites	BX	0.69	0	2.2	39.2	0	I	I
controlled)	HS	0.66		2.4	39.6 		 	
HIGH		0.56	4	2.0	39.1	340	ı	ı
(Grazing - No parasite	BX	0.53	14	2.4	39.2	460	I	I
control)	SH SH	0.38	28	3.9	39.6	750	t 	
Effect of each : gain/day of each	stress on 1 breed		-0.0062* kg/tick	-0.0081* kg/unit	-0.0386* kg/ ⁰ C	-0.0001 kg/egg		
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TABLE 2: Gains and Some Factors Affecting Gains at Three Levels of Stress

(Source - Frisch and Vercoe, unpublished data)

* P < 0.05
† See Table 1 for key</pre>

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Although there may be as yet unknown physiological reasons why production potential will be difficult to combine with high heat tolerance and resistance to some diseases, the correlation between these two determinants of growth is unlikely to be -1.0, in which case there would be scope to improve both determinants independently. This may involve separate assessments of production potential and resistance to the operative environmental stresses to identify those individuals which have high levels of both. More research is needed to determine the optimum and most efficient times in the growth phase to make these assessments, but resistance to environmental stresses needs to be high early in life because it is then that most mortalities and severe restriction of growth occurs.

Where environmental conditions are such that increases in realised growth are possible by improving growth potential, it is necessary to be able to distinguish between the increases that derive from the rate and scale components of growth potential. Increases associated with an increase in mature size (scale component) do not increase biological efficiency (Morris and Wilton, 1976) but increases in drought susceptibility and slaughter weight are likely to occur, which in many environments, are undesirable. Methods will have to be devised which ensure that estimates of growth potential are not confounded with mature size.

Other Components of Productivity

Whilst this discussion has been confined to growth rate, the same concepts can be applied to other components of beef productivity such as fertility and survival. This has been discussed elsewhere (Vercoe and Frisch 1982; Frisch and Vercoe 1982).

CONCLUSIONS

Individual limitations to efficient beef production exist for two main reasons; either there is a lack of production potential (mainly reflected in voluntary food intake measured in the absence of stress) or there is lack of resistance to the stresses operating in the environment in which the beef is to be produced.

In benign environments where feed is unrestricted, selection for growth rate will increase food intake and, unless positive steps are taken, mature size. In environments where stresses are numerous but vary in intensity and/or frequency, e.g. the tropics and subtropics, selection for performance will be for differently negatively correlated factors in different years and the net gain in either of the two major determinants of performance is likely to be small.

Efficiency of selection and gains in production should be greatest if there is separate selection for production potential and resistance to environmental stresses. Animals in which these two determinants are combined in maximum amounts should be as highly productive in any environment as the level of nutrition will allow. The extent to which such an ideal combination is possible in practice is not yet known. REFERENCES

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