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SOME ASPECTS OF GRAZING ECOSYSTEMS

A thesis  
presented in partial fulfilment of the requirements  
for the degree  
of  
MASTER OF AGRICULTURAL SCIENCE  
at  
MASSEY UNIVERSITY

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1970

## ACKNOWLEDGEMENTS

I should like to record my appreciation to the following people for their contributions to the work presented in this thesis:

To Professor B.R. Watkin, my supervisor, who provided stimulation, guidance and, above all, encouragement.

To Dr G.A. Wickham for many useful suggestions and helpful discussions; to Dr W.G. Healy of the Soil Bureau who gave advice on aspects of soil ingestion and made available the X-Ray fluorescence unit used for this part of the work.

To Mr R. Battersby who assisted with all the field work; to Mr B. Thatcher and Miss K. Nikolaison who helped with much of the practical work, and in particular in the collection of wool growth data; to Mr N.A. Thompson who advised on laboratory procedures; to Messrs. R.G. Keogh, P. Vlieg and A.S.D. King, who prepared the oesophageal fistulae in the sheep and to the many other members of the Agriculture Faculty who contributed to this thesis both by discussion and material assistance.

To Mrs D. Hoskins, who typed the final copy of the text and to Mr W.B. Currie, who assisted with the final compilation of the thesis.

Lastly I wish to thank my wife Rosemary, who made an important contribution to this thesis, by assisting with the practical work and by preparing both the draft copy and figures of the text.

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## INTRODUCTION

The conversion of plant material to meat and milk by ruminants is one of the main ways in which the demand for energy and more especially protein for human consumption is met.

While research in soil, plant and animal sciences is all more or less relevant to this conversion process a considerable amount of the agricultural research effort in Australasia has been directed more specifically to the grazing situation.

Much of this work has been concerned with specific components of the grazing ecosystem such as the factors limiting pasture production (Brougham 1968), the definition of those plant factors contributing to nutritive value (Butler et al. 1968; Minson 1968), animal nutrition (Moir 1968) and pasture establishment (Swain 1968). While such research is basic to the understanding of the processes operating within a grazing system it must be complimented by a recognition of the interactions which exist within such grazing ecosystems and the way in which such interactions can affect interpretation of evidence from isolated parts of the grazing ecosystem. For example, the adoption of defoliation systems based on evidence from experiments of which grazing animals are not an integral part is often difficult to reconcile with the reality of having to graze a more or less fixed number of animals on a fixed area of land over a long period of time (Campbell 1969).

In an effort to take account of the interactions which may invalidate conclusions based on evidence from component parts of the grazing ecosystem, the "whole-farm" approach to experimentation has been evolved. However in many cases such experiments have been designed to study the importance of different management factors on animal production from a given area of land (McMeekan 1961; Willoughby 1968) rather than to study the inter-relationships occurring between the soil, plant and animal components of the ecosystem. For example there is little information available on these inter-relationships from over 150 experiments of this kind carried out in Australia, evaluation of treatments having been carried out almost entirely in terms of animal production (Allden 1968).

The grazing ecosystem comprises soil, plant, animal and climatic components. These components will have varying levels of interdependence at any one time depending on the pattern and level of input of each component up to that time. For example the way in which the grazing animal

defoliates, excretes and treads will, both by its indirect and direct effects on the plant community, affect future pasture productivity. This will have reciprocal effects on animal production and soil characteristics which in turn will affect pasture productivity and so on. However since plant productivity will also depend on climatic inputs the extent to which it is effected by the animal and soil components of the ecosystem will vary. Thus in a four month growing season with annual species, the grazing animal may affect future pasture productivity during the growing season but during the senescent eight month period the animal's effect is limited to its effect on the seed supply (Arnold 1968). On the other hand the effects of the soil and animal components on pasture productivity may be expected to operate more continuously in an environment where climate only has slight effects on seasonality of pasture production. In a similar way pasture production at a particular time, and hence feed supply at that time, may have disproportionate effects on animal performance over an entire productive cycle.

In addition the level of interdependence will vary with the extent to which each component of the ecosystem has the capacity to buffer itself against the effects of other components. For example the grazing animal may counteract the effects of fluctuating feed supplies in several ways including recycling of nitrogen, sodium and phosphorus, alteration of grazing behaviour, compensatory growth and mobilisation of body reserves. In the same way changes in the botanical composition, morphology and growth rate of the plant community buffer the effects of other ecosystem components. However such mechanisms will become of limited importance as grazing pressures increase with the result that interactions between components of the ecosystem increase with increasing grazing pressure (Morley 1966; Arnold 1968).

Thus the grazing ecosystem involves many components each affected by several more or less continuous but variable inputs as well as by its variable interactions with the other components of the ecosystem. It is not surprising that such dynamic systems have been subject to so little research given their complex nature, the lack of suitable measuring techniques, the costs involved and their lack of "publication value" (Willoughby 1968).

The work presented in this thesis was designed to introduce the author to some of the techniques available for, and problems in, studying grazing ecosystems. It was also designed to provide information on some of the basic parameters of the grazing situation in one particular environment.

## CHAPTER I

### REVIEW OF LITERATURE

The aim of this review is to provide a basis from which the results of the present experiment can be discussed. Section A deals with the effects of the grazing animal on pasture production with special reference to increasing stocking rates.

Section B considers the behavioural response of grazing animals to different pasture conditions while Section C covers the changes in animal productivity which occur as stocking rates increase.

In Section D body growth and wool growth of sheep are considered and in Section E the use of oesophageal fistulated sheep and methods of measuring herbage intake are discussed.

## SECTION A

The grazing animal exerts its influence on plant communities by the actions of defoliation, excretion and treading. Apart from their direct effects, these activities may also influence the plant community by modifying its micro-environment.

Grazing may affect the botanical composition (Jones 1933), the rates of tiller and leaf production (Brougham 1959) and the rates of senescence and decay (Hunt and Brougham 1967) of a pasture as well as the extent to which regeneration and reproduction of pasture species takes place (Rossiter 1966). All these effects may contribute to the seasonality and level of production of a pasture.

This section attempts to summarize current knowledge of the separate effects of defoliation, excretion and treading on pasture productivity. The implications of these effects are then considered in relation to increasing stocking rates.

### (a) Defoliation

The major variables in defoliation which affect the productivity of a particular pasture are the intensity, frequency, timing and pattern of defoliation. Before discussing these it is perhaps useful to make a distinction between short and long term responses to defoliation.

When a pasture is defoliated the immediate or short term response is mainly a function of rate of regrowth. Long term responses reflect the accumulated effects on botanical composition and plant viability.

The effect of defoliation on pasture production has been investigated in numerous experiments giving rise to many conflicting results.

Both increases (Ridgman 1960; Appadurai and Holmes 1964) and decreases (Jacques and Edmond 1952; Langer and Steinke 1965; Auda et al. 1966) in yield have been noted with increasing intensity of defoliation while in some cases yield may be unaffected by intensity of defoliation (Bryan and Sharpe 1965; Bernardon et al. 1967).

Similarly increasing the frequency of defoliation may result in a decrease (Woodman and Norman 1932; Burger et al. 1958), an increase (Burton et al. 1963; Clapp et al. 1965) or little change (Brougham 1959; Holt and McDaniel 1963) in pasture yield.

Interpretation of experimental results may be complicated by specific and varietal differences in morphology. For example, defoliation to a constant

height will remove a greater percentage of the above ground parts of erect than prostrate varieties (Jones 1959) possibly causing a difference in response. Since intensive grazing may induce normally erect varieties to assume prostrate habits of growth (Kydd 1966a) similar effects may occur on a within variety basis.

Moreover the possibility of specific and varietal differences in physiological response to defoliation must not be excluded.

However part of the explanation for these contradictory results lies in the interaction between severity and frequency of defoliation. The regrowth curve of defoliated pasture is broadly sigmoid in shape having consecutive phases of increasing, constant maximum and decreasing growth rates (Brougham 1955; 1956b). Sward productivity, in a particular environment, will therefore be a function of the maximum growth rate, how soon it is reached and for how long it is maintained (Evans *et al.* 1964). Since the intensity of defoliation may influence how soon the phase of maximum growth rate is reached (Brougham 1956a) and the frequency of defoliation may influence whether this growth phase is reached and for how long it is maintained, it follows that variable interactions may occur between the intensity and frequency of defoliation.

For instance, Brougham (1959) has shown that severe but infrequent defoliation of a short-rotation ryegrass/clover sward resulted in higher yields than were obtained with more frequent defoliations irrespective of their severity. However where defoliation was not severe, yields were not affected by frequency of defoliation. Where rates and periods of regrowth differ interactions between intensity and frequency of defoliation may give different results as shown by the work of MacLusky and Morris (1964). The suggestion that effective leaf area duration may be a main determinant of pasture yield (Campbell 1967) warrants further investigation.

Rates of regrowth will depend on environmental conditions as well as on the physiological and morphological properties of the pasture species. Studies of the physiological factors involved have been confined largely to considerations of reserve substances and residual leaf area although the role of root activity has received more attention recently.

Considerable importance was given to the role of reserves, especially "available" carbohydrate reserves, in promoting regrowth (Weinmann 1961) but little critical experimentation occurred until May (1960) emphasised the indirect nature of most of the evidence available up to that time.

Direct evidence obtained by the use of carbon balance (Davidson and Milthorpe 1966b) and autoradiographic (Marshall and Sagar 1965) techniques has

indicated that reserve substances may contribute, in varying degrees, to regrowth over the first few days after defoliation even if only as respiratory substrates (Alberda 1966; Davidson and Milthorpe 1966a; b; Mitchell and Denne 1967). The importance or otherwise of such a transitory effect is still not clear. If, as Davidson and Milthorpe (1966a) suggest, the main factor controlling regrowth is the rapid development of a photosynthetic surface then reserve substances may be important even though their absolute contribution to plant growth is small.

The concept of leaf area index (LAI) and its association with growth rate (Watson 1947) has been extended to the pasture situation in an attempt to explain the control of rate of regrowth (Brougham 1956a; Donald and Black 1958; Black 1963). Although the concept has been oversimplified (Brown and Blaser 1968) rate of regrowth may be largely controlled by residual leaf area following defoliation (Brougham 1956a; Davidson and Donald 1958). However there may be no association with residual leaf area (Anslow 1965), presumably when light is not a major limiting factor for growth.

By comparison with these two facets of regrowth, the extent to which root activity limits regrowth appears to have been overlooked. Root growth is normally affected to a greater degree than shoot growth (Mitchell 1954) the effect being proportional to the frequency and severity of defoliation (Troughton 1957).

The growth of roots into fresh portions of soil may be slowed (Mitchell and Denne 1967) and in some cases the absorptive zone may even be reduced (Oswalt et al. 1959). This can be expected to result in reduced mineral uptake (Mitchell and Denne 1967) and will be accentuated by any reduction in the absorptive capacity of the roots themselves as has been shown to occur for water (Jantii and Kramer 1956) and phosphorus (Davidson and Milthorpe 1966b).

It is to be expected that rate of regrowth will depend at least to some extent on the interaction between the above factors.

Although scarce, what evidence there is (Ward and Blaser 1961; Davidson and Milthorpe 1966a; Humphreys and Robinson 1966) suggests that in regrowth residual leaf area and reserve substances interact to a variable extent depending on their levels immediately after defoliation.

However once the development of a new photosynthetic surface has begun, the rate of regrowth may be limited by the level of root activity despite the fact that nutrients and water may be readily available (Davidson and Milthorpe 1966b).

Rate of regrowth may be affected by factors other than those already discussed.

Thus removal of expanding or meristematic regions of a pasture plant may be important. For instance, if the apical meristem is removed prior to flowering the rapid growth rate of the reproductive tiller is unlikely to be compensated for by the growth rate of the new vegetative tillers formed at the base of the destroyed tiller (Jones 1959). Any such effect will be variable (Jones 1959) since the number of elevated growing points will vary throughout the year both between and within grass varieties (Brougham 1966).

While the intensity of defoliation interacts with frequency of defoliation to influence pasture regrowth in the short term it may also influence long term productivity by its effect on the pasture micro-environment and hence on botanical composition.

Intense defoliation will generally improve the light environment at the bottom of the sward and may therefore encourage clover growth in grass-clover swards (Jones 1933; Donald 1956; Brougham 1959). Such an environment may be expected to enhance tillering (Evans *et al.* 1964) but the death of tillers following frequent, intense defoliation (Brougham 1959) means that the net effect is variable (Langer 1963).

Close defoliation may also reduce the buffering effect of vegetation. This may lead to increased drying out of the soil near the surface and to a rise in its temperature (Mitchell 1957). Both these factors may restrict pasture growth (Brougham 1959) as may the unavailability of nitrogen induced by such conditions (Mitchell 1957). Run-off and liability to erosion may also be increased (Costin 1964).

While the extent of these effects will depend on the climatic and edaphic environments, it is clear that they may affect the competitive relationships between components of a pasture thereby influencing botanical composition.

The importance of the frequency of defoliation was implied when its interaction with intensity was considered. Thus too frequent defoliation may prevent the maximum rate of regrowth being achieved or it may shorten the potential duration of this phase. Also if defoliation is too frequent, recovery of reserves and roots may not occur and if these are important to subsequent regrowth a loss in productivity may occur subsequently.

However if the period between defoliations is too long losses due to death and decay may be considerable (Hunt 1968), although the reconciliation between the avoidance of such losses and maximum productivity is far from clear (Campbell 1964). L.A. Hunt (1965) has suggested that many of the contradictory results obtained in the defoliation experiments noted at the beginning of this section may be due to the changing relationship which occurs between the rates

of dry matter decay and accumulation under different climatic conditions.

Infrequent defoliation may also lead to shading in the lower part of the sward. This will result in the exposure of the photosynthetically inefficient components of the sward on defoliation (Brown and Blaser 1968) quite apart from the possible effects on tiller density (Mitchell and Coles 1955; Langer 1963). If this latter effect occurs in the autumn the peak of spring growth may be lowered because the number of fertile tillers is lowered (Ivins and Drake 1964).

Similarly a policy of infrequent defoliation may preclude changes in the botanical composition of pasture necessary for sustained production in a subsequent period (Brougham 1960).

The timing of defoliation with regard to elevated growing points has already been mentioned, but its implications in terms of botanical composition and hence future pasture productivity need emphasising.

Under veldt conditions Booysen et al. (1963) indicated that the effects of defoliation on the elimination or survival of a particular species would be largely dependent on the timing of defoliation relative to the accessibility of growing points and seed production.

The effects of timing of defoliation on botanical composition were clearly demonstrated by M. Jones in 1933 and the importance of the timing of defoliation in the development of productive hill pastures in Wales has been shown (Jones 1967).

This and related work has recently been reviewed by Charles (1968) who stresses the susceptibility of plants to hard and continuous defoliation during the early stages of growth. Thus where differences in the seasonal growth pattern of pasture components exist and intense grazing occurs during the early growth of particular components, changes in botanical composition are likely to occur.

An interesting example of a case where botanical composition may not be affected to any great extent is that of Phalaris tuberosa - subterranean clover - annual grass pastures. Willoughby (1959) was unable to show any large effect of timing or intensity of defoliation on the botanical composition of such a pasture. This appears to be largely associated with the similar pattern of growth of the components of such pastures as well as the ineffectiveness of selective grazing where growth rates of all components are far in excess of consumption. However such stability may not occur at high stocking rates (Arnold et al. 1964a; Morley et al. 1969).



The pattern of defoliation of the grazing animal may well affect the response of pasture to defoliation and is therefore not only important in its own right but also in the interpretation, to the grazing situation, of defoliation experiments in which mowing has been used.

Where selective grazing occurs in a pasture, the competitive ability of the selected plant may be reduced in comparison to that of non-selected plants (Norman 1960). This may lead to suppression and even elimination of the selected species from a pasture (Wilson et al. 1969) while differences in selectivity between cattle and sheep may also give rise to differences in botanical composition (Norman 1957). Further discussion of the significance of this effect is more conveniently left until later.

Grazing systems themselves may lead to changes in botanical composition. For instance, changes in the genotypic structure of ryegrass populations may result from different grazing systems (Brougham et al. 1960; Brougham and Harris 1967) while botanical composition may differ between continuous and rotationally grazed situations (Jones 1967). Work at Canberra (Morley et al. 1969) has shown that intensity of rotation may affect botanical composition to the extent that any theoretical advantage in terms of animal production is offset by changes in botanical composition. On the other hand, intensity of rotation may have little effect on botanical composition (Campbell 1969).

The above examples indicate the caution necessary in extrapolation from the mowing to the grazing situation. While the absence of excretal returns may be an important factor in misinterpretation and the possible effects of treading cannot be excluded, the pattern of defoliation is likely to be most important.

In this respect mowing and grazing will differ to the extent that grazing management allows defoliation to be incomplete and non-instantaneous.

The integrated nature of the grass plant (Sagar and Marshall 1966; Marshall and Sagar 1968) and the different photosynthetic and export capacities of the different leaves of a tiller (Milthorpe and Davidson 1965) indicate likely different physiological reactions to mowing and grazing. Recent work (Smith 1968) tends to confirm this reasoning. The position is further complicated by the interactions which may occur between grass varieties and methods of defoliation (Jones 1959).

One of the best examples of the difficulties of interpretation of mowing experiments is provided by defoliation of lucerne. Here the very marked preference by sheep for leaf (Arnold 1960a) and new shoots (Peart 1968) emphasises that the period of grazing rather than the period between grazings is

the critical factor in lucerne survival. Such a situation would occur wherever selection for young growing tissue was so marked that regeneration of the plant was seriously affected. Because such a distinction is impossible in mowing trials, its importance cannot be evaluated.

It should be clear from this discussion that useful prediction of the consequences of a particular defoliation system in any one environment is difficult. However maintenance of sward productivity will depend on the maintenance of viable plants and especially viable root systems (Davidson 1968). This may be achieved either by management or by selection, normally natural, towards pasture plants capable of resisting frequent defoliation.

(b) Excretion

The significance of the grazing animal in the nutrition of pastures has been the subject of some research effort since the investigations of Sears and his co-workers in New Zealand (Sears and Goodall 1948; Sears and Thurston 1952). As a result of this, it is now clear that the grazing animal may play a variable role in nutrient cycling in the grazing ecosystem. This occurs for several reasons.

The quantity of nutrients returned to a pasture as excreta will depend on the type and physiological state of the stock grazing that pasture (Sears 1950; Davies et al. 1962) as well as on the amount of pasture ingested and its nutrient content (Barrow and Lambourne 1962).

The availability of returned nutrients for plant growth will depend on the form in which they are excreted. Thus the plant nutrients in urine - a high percentage of the excreted potassium and sodium (Davies et al. 1962) plus variable percentages of nitrogen and sulphur (Barrow and Lambourne 1962) - are readily available (Barrow 1967) as is the inorganic phosphorus in the faeces when mixed with soil (Bromfield 1961). Faecal nitrogen is of low availability requiring prolonged mineralisation before it can be utilised (Sears and Newbold 1942; Walker et al. 1954), but little is known of the availability of the other nutrients excreted in the faeces (Barrow 1967). These differences in availability may mean that for some nutrients pasture responses occur early in the growing season and for others later in the season, thereby causing differences in the effects of grazing on pasture requirements. This question has been discussed in detail by Barrow (1967).

Loss of nutrients from the ecosystem may be caused by volatilisation and/or leaching. For instance, up to about 80% of urine nitrogen (Watson and Lapins 1969) and faecal nitrogen (Gillard 1967) may be lost by volatilisation,

depending on environmental conditions. Losses through leaching will depend on factors such as the reaction of the particular soil type with the ion in question, rainfall and water holding capacity of the soil (Barrow 1967).

The importance of the "bottlenecks" in energy flow of the ecosystem caused by slow decomposition of organic matter has been noted by Macfadyen (1961) and may become a factor nullifying nutrient circulation via the animal where faecal pads decompose slowly (Gillard 1967). The invertebrate fauna may constitute an important part of the ecosystem in such cases (Bornemissza 1960; Stockdill and Cossens 1966; Gillard 1967).

The deposition of returned nutrients at high concentrations (Doak 1952; Davies et al. 1962) and in a non-random fashion (Sears 1950; Hilder 1966) has important implications for the effectiveness of nutrient cycling via the grazing animal.

For example, the high concentrations of returned nutrients may encourage losses from the ecosystem (Barrow 1967) and implies that only a proportion of the pasture being grazed will receive either dung or urine (Foot 1963). Non-random distribution of excreta gives rise to fertility transfer and may reach the extreme situation reported in Australia (Hilder 1966) where rapid depletion of nutrients from most of a grazed area occurs. Fertility transfer will be largely a function of animal behaviour as influenced by type and breed of stock, topography, weather, flock size, vegetation, paddock size, management etc..

Investigations carried out in New Zealand (Sears and Goodall 1948; Sears and Thurston 1952) and Britain (Watkin 1954; Wheeler 1958; Herriott and Wells 1963) using temperate grass/clover swards have indicated further factors affecting the efficiency of nutrient circulation through the animal.

For example, the response to excretal returns may be essentially a response to nitrogen (Watkin 1954; Wheeler 1958) in which case the resultant dry matter yield will reflect the extent to which symbiotic fixation of nitrogen is reduced and the extent to which excretal and more especially urine nitrogen compensates for this reduced fixation (Watkin 1954; Brockman and Wolton 1963). Since many variables (Walker 1956a; Shaw et al. 1966) can affect the degree of clover suppression and hence symbiotic fixation in a mixed sward it is clear that where nitrogen is the main limiting factor to pasture growth, the effects of excreta will be variable in terms of dry matter production.

In other cases other nutrients, for example phosphorus (Sears 1953), may be the main limiting factors to growth in which case responses to excreta may be different to those noted above. It is important to note that response to excreta will be a function of the species present in the pasture (Watkin 1957;

Davidson 1964).

This discussion has indicated that nutrient returns act through their effect on one of the many factors limiting growth. If factors other than nutrients are limiting pasture growth then return of excreta may have little immediate effect although some residual effects may occur. Where nutrients are a major factor limiting growth then return of excreta may enhance production (Sears and Goodall 1948) or merely result in a change in botanical composition (Sears and Thurston 1952; Watkin 1954) depending on factors such as the amount and form of nutrients excreted, percentage recovery of these nutrients, botanical composition of pasture, soil type and fertility transfer.

A further aspect of this question is the way in which soil fertility changes under grazed pasture. This feature and its implications have been discussed for New Zealand (Walker 1956b; Sears 1960) and Australian conditions (Moore and Biddiscombe 1964).

(c) Treading

Investigations into the effects of treading on pasture production have been largely confined to New Zealand conditions.

From a recent review (Edmond 1966) it is clear that the influence of treading on pasture regrowth is likely to depend both on the direct effects on plants and soils as well as on the interaction between them.

Edmond (1966) considers that loss of production is likely to occur in all grazed pastures although its extent will depend on the amount of treading (Edmond 1958), moisture content (Edmond 1962; 1963), soil type and fertility level (Edmond 1966). Apart from the physical effects, the most common effects on pasture appear to be a modification of plant competition (Edmond 1964) and a decrease in tiller and clover node numbers (Edmond 1963).

Interpretation of these results requires caution. The technique used neglects the protective effect of herbage cover noted in other experiments (O'Connor 1956; Brown 1968) and it also appears to accentuate the treading action of sheep (Edmond 1958). Further, the extent to which pastures may adapt to treading so that its detrimental effects are lessened is not known. Finally, by isolating the effect of treading, any interaction - beneficial or detrimental - with defoliation and return of excreta is not measured. As Edmond (1962) points out the technique is likely to maximize treading effects.

Consequently it is not surprising that where conditions and techniques vary inconsistent results are obtained (Scott 1963; Campbell 1966a; Edmond 1966). It is pertinent to note that in a field scale trial treading over the

winter period has had no detrimental effect on animal production (McQueen 1965; pers. comm.) although interpretation of this result requires caution (Edmond 1965; Campbell 1966a).

(d) Stocking rate

It should be clear that this evaluation of the separate effects of defoliation, treading and excretion represent a considerable oversimplification of the influence of the grazing animal on plant communities. In some cases one particular factor may be of overriding importance while in others either positive or negative interactions may occur.

Further discussion of the effect of grazing on plant communities will be confined to the possible effects of increasing stocking rates on sown pastures in Australia, New Zealand and Britain.

When stocking rate is increased not only will the direct effects of, and interactions between, defoliation, treading and excretion be modified but the percentage utilisation of feed produced will also be increased. Further as this percentage increases and the periods of feed shortage increase, practices such as supplementary feeding, conservation and grazing management become more critical in their contribution to the outcome of a particular stocking rate.

Thus it is to be expected that the effects of stocking rate on pasture productivity are complex.

The way in which defoliation of a pasture changes as stocking rates increase is only partially understood. Limited information (Hodgson 1966; Hodgson and Ollerenshaw 1969; McIvor pers. comm.) suggests that in pure grass swards the frequency of tiller defoliation increase with increasing stocking rates while any increase in intensity of defoliation may be offset by modification of the growth form of pasture components (Kydd 1966a) or by an increase in those pasture components capable of resisting grazing (Moore 1966). This adaptation of a pasture to high stocking rates has recently been demonstrated at Hurley (Kydd 1966b) where sheep at a high stocking rate did not, or were unable to, harvest as high a percentage of the available feed as sheep on a low stocking rate despite the fact that less feed was available at the high stocking rate.

Any such effects on the intensity and frequency of defoliation will be modified by the way in which the selective grazing pattern of the animal is altered. For instance, if the selective grazing pattern of lower stocking rates is maintained then at least the frequency of defoliation of the grazed parts of the pasture may be increased. However selectivity is normally reduced

as stocking rates increase (Willoughby 1959; Suckling 1964a; Arnold et al. 1964a), so it is conceivable that, as stocking rates move from low to intermediate levels, intensity and/or frequency of defoliation are not necessarily increased. However it seems reasonable to assume that when stocking rates are increased to very high levels, at least the frequency if not the intensity of defoliation will be increased. This is supported by indirect evidence from the changes which occur in pasture availability as stocking rates rise.

As levels of stocking increase, pasture availability tends to drop (Arnold et al. 1964a; Anon. 1967; Bublath 1969) although the form of the relationship appears to have been defined in only one study. Campbell (1966b) has shown that a point is reached where a sharp drop in availability occurs with only a small increase in stocking rate, leading to abrupt changes in grazing pressure. Differences in the way in which a pasture is defoliated may be expected where such changes take place.

The competitive effects in a sward may be modified by such a changing pattern of defoliation. For instance, the time during which competitive forces act between defoliations may be reduced while plants may modify their growth forms, in response to the pattern of defoliation, so as to become more resistant to grazing (Kydd 1966a).

The reduction in selectivity may alter the subsequent productivity of pasture in both beneficial (Suckling 1964a) and detrimental ways. Such detrimental changes may occur where carry over of feed (Wilson et al. 1969) or seeds (Rossiter 1966) is reduced thereby lowering future productivity.

If selective grazing persists to any great extent as stocking rates increase, then the chances of overgrazing leading to loss of pasture stability and consequent loss of productivity are increased (Morley 1966a).

The effect of stocking rate on nutrient cycling may be variable. For instance if stocking rate is increased in a situation where fertility transfer occurs, then it might be expected to accentuate the loss of fertility, although the data presented by Hilder (1966) are inconclusive on this point. If, on the other hand, no fertility transfer is occurring increases in stocking rate may be beneficial in terms of an increase in pasture production through an increase in the quantity of nutrients returned (McLachlan and Norman 1966) and/or wider distribution of the excreta produced (Petersen et al. 1956).

Any effects of treading will be increased by stocking rate increases both because there are more hooves per unit area (Edmond 1966) and because animals tend to forage for longer periods at high stocking rates (c.f. Section B).

The effect of increasing stocking rates on pastures will depend on the interaction between the above factors. For instance, the effects of high stocking rates on the physiology of pasture plants may limit their response to any increased circulation of nutrients occurring under such conditions (McLachlan 1968). Another example is the positive interaction which may occur between the separate components of grazing to give rise to high producing grass/clover swards in the North Island of New Zealand (Sears 1956).

In a recent review Moore (1966) concluded that in the more mesophytic temperate regions grazing animals improve the quality and quantity of their feed supply. One of the main interests of stocking rate experiments is the extent to which this process can be maintained, as grazing pressure increases. Unfortunately few stocking rate experiments have had more than a cursory interest in pasture production despite the fact that the deficiencies of such an approach have been stressed (Campbell 1961).

At this point it is appropriate to mention some of the basic requirements of stocking rate experiments. The planning of such experiments has recently been reviewed (Morley and Spedding 1968) but the importance of long term rather than short term trials needs stressing. For instance, long and short periods of heavy grazing may have very different effects on pasture growth (Arnold 1964d) while grazing animals may show different responses when subjected to the same stocking rate for different periods of time (Willoughby 1959). It should also be noted that interpretation of unreplicated trials is limited (Arnold et al. 1964a), although even in replicated trials variations in site productivity may limit extrapolation of results (Morley 1966b).

Where components of pasture productivity have been studied under different stocking rates, results have been variable. Changes in botanical composition have been determined in some experiments and those occurring in annual pastures in Southern Australia have been reviewed by Rossiter (1966).

With increasing stocking rates there is a general decrease in the proportion of annual grasses and an increase in plants such as capeweed (Cryptostemma calendulacea R.Br.) and geranium (Erodium spp.) while subterranean clover (Trifolium subterraneum L.) remains largely unaffected. Of the annual grasses, silvergrass (Vulpia myuros L.) is least affected and may even increase. This results in pastures dominated by herbaceous plants in contrast to grossly understocked pastures which are normally dominated by ripgut brome (Bromus rigidus Roth.) and lack clover.

In an experiment at Werribee, Victoria (Sharkey et al. 1964) it was noted that at a high stocking rate Wimmera ryegrass (Lolium rigidum Gaud.) and

subterranean clover (Trifolium subterraneum L.) largely disappeared from a pasture in which those two components had been predominant being replaced mainly by stonecrop (Crassula spp.), silvergrass (Vulpia spp.), loosestrife (Lythrum spp.) and annual poa (Poa annua L.). This disappearance was attributed to several factors including a decrease in seed production, increases in seed consumption, consumption of seedlings and limitation of leaf area of established plants. This was in contrast to the low stocking rate where the ryegrass became dominant, probably due to its competitive advantage for incident light. At the intermediate stocking rate changes in botanical composition occurred but were not progressive.

On the other hand Arnold et al. (1964a) found that as stocking rate increased the percentage of clover in a Phalaris tuberosa - subterranean clover - annual grass pasture increased until it became dominant at the highest rate of stocking. Although the same grass species remained at all stocking rates, annual grasses tended to increase at the expense of Phalaris especially at the highest stocking rate (McManus 1966). At very high stocking rates such differences may not occur (Morley et al. 1969).

In terms of increasing the content of subterranean clover and decreasing the content of grasses, this result has been repeated in stocking rate trials in Victoria (Anon. 1967).

One of the most interesting features of these experiments is the difference in response of subterranean clover to high stocking rates. Such factors as soil nitrogen supply, seed supplies and the degree to which non-legumes can adapt to high grazing pressures may contribute to this variation (Rossiter 1966).

At Hurley (Kydd 1966a) changes in the botanical composition of a perennial ryegrass (Lolium perenne L.)/white clover (Trifolium repens L.) sward stocked at two different rates were followed over a five year period. Nitrogen was applied at the rates of 182 and 142 kg/ha/year to the high and low stocking treatments respectively. Ground cover assessed in spring increased during the experimental period from about 40% to 80% and 70% on the high and low treatments respectively. The clover disappeared after two years while Poa spp. increased throughout to contribute about 57% and 43% of the ground cover in high and low stocked areas. As each season progressed the ground cover of perennial ryegrass increased while that of Poa spp. decreased.

An experiment on hill country in New Zealand (Suckling 1964b) compared four stocking rates - 3, 4, 5 and 6½ ewes per acre - with and without cattle. The cattle were used as required to remove rank growth. At the start of the trial the pasture over the area appears to have been ryegrass dominant and had a



clover dry matter content of about 6%.

Where sheep were grazed without cattle, accumulation of rank growth occurred except at the highest stocking rate but even here coarse weeds tended to increase. Where cattle were used accumulation of rank growth was reduced although rushes tended to increase with stocking rate because cattle could not be grazed on the areas for long enough to reduce their incidence.

Changes in botanical composition with different stocking rates were largely a function of pasture utilisation. Where utilisation was poor, the clover and ryegrass content of the pasture decreased while the content of other grass species such as Chewing's fescue (Festuca rubra L.) and browntop (Agrostis tenuis Sibth.) increased. On the other hand clover and ryegrass content increased with increasing utilisation although clover content was slightly depressed at the highest stocking rate.

There appears to be little data on the growth of pastures under different stocking rates. This may well reflect the difficulties of making such measurements under the continuous grazing conditions which are frequently used in stocking rate experiments.

Using the Australian "difference" method (Lynch 1960), Bublath (1969) showed in a short term trial that, in spring, growth of a particular pasture type was generally higher at a low stocking rate than at a high stocking rate. During winter differences within pasture types were negligible.

Under rotational grazing, Campbell (1969) noted that high stocking rates tended to depress pasture production although the differences did not reach significance in some seasons, notably the autumn. In another experiment the same worker (Campbell 1966c) found that net pasture production was increased by about 600 lbs. D.M./acre/annum at a low compared to a high stocking rate. However this difference was not significant while year x treatment interactions complicated interpretation.

Further evidence of the reduction in pasture growth at high stocking levels comes from studies in which growth rates of pastures, previously stocked at different rates, have been measured over short periods in the absence of stock (Arnold 1964d; McLachlan 1968) although this may not always occur (Spedding et al. 1967).

There is also the possibility that increasing stocking rate from very low levels will result in increased pasture growth. This may occur when the increased stocking rate results in a sward containing less dead and senescent material and being, as a result, more efficient in terms of photosynthesis (Campbell 1964).

The changing distribution of pasture growth throughout the year is an important characteristic of pasture but here again evidence of changes in this characteristic appears to be limited. In an experiment with dairy cows at Ruakura Campbell (1966c) found that within management systems, heavy stocking generally reduced the proportion of annual net production obtained in summer. The significance of such changes will depend on the extent to which they affect synchronisation of herbage production and animal nutrient requirements.

Up to this point pasture production has been considered almost exclusively in terms of dry matter. This represents a considerable oversimplification in terms of nutritive value and hence animal production.

The nutritive value of pasture has been reviewed recently by several workers (Raymond 1963; McDonald 1968; Corbett 1969) so only a few relevant points will be considered here.

Nutritive value has been defined both in biological (Minson 1968) and chemical terms (Tribe et al. 1963) but it is important to recognise the relative nature of the term. For instance, it is conceivable that two different feeds may have similar values for maintenance but dissimilar values for fattening. As well as this, interactions between type of stock and nutritive value may occur as in the case where plant oestrogens may be harmful to breeding stock but beneficial to fattening stock (Johns 1963).

For present purposes it should be noted that nutritive value is not only a function of the proportion of feed made available to the animal by digestion and the suitability of the digested nutrients for the various metabolic processes but also of the extent to which such a feed can be ingested.

Considerable research effort over recent years has aimed at a clearer understanding of those inherent plant properties important in nutritive value but has progressed little beyond establishing animal production differences between different pasture plants.

There is now considerable evidence to indicate the superiority of legumes relative to grass in supporting high growth rates in grazing animals (Jones 1932; Christian and Shaw 1952; Fernando 1961; McLean et al. 1962; 1965; Hight and Sinclair 1965; 1967; Gallagher et al. 1966; Wilson 1966; Butler et al. 1968; Ulyatt 1969) while differences in animal performance have also been noted between ryegrass varieties (Wilson 1967; Alder 1968; Butler et al. 1968), between grass species (Castle et al. 1962; Milford and Minson 1966; Greenhalgh 1966; Gallagher et al. 1966; Alder and Cooper 1967) and between legumes (McLean et al. 1965).

In most cases an attempt has been made to associate animal performance

with chemical constituents of the feed and/or digestibility, volatile fatty acid production and intake. Despite this few satisfactory explanations of nutritive value have been forthcoming and even in the prolonged research programme at Palmerston North (Butler et al. 1968) it is only now that any real progress is being made towards definition of those factors contributing to differences in nutritive value of the pasture species involved (Ulyatt 1969).

Apparent digestibility is perhaps the most useful single measure of nutritive value of pasture (Ivins 1960; Coop 1967; Corbett 1969) although the limitations of such a measure are increasingly understood (Miles et al. 1969). For this reason the seasonal changes in digestibility of pasture plants and their components have been studied, especially since the development of reliable in vitro digestibility techniques.

Thus, the digestibility of the first growth of grasses and clovers decreases with advancing maturity with each variety having a characteristic relationship between its digestibility and stage of growth (Harkess 1963; Minson et al. 1964; Milford and Minson 1964). These digestibility patterns arise from changes in the proportions and digestibilities of the component parts of the various forages (Pritchard et al. 1963; Terry and Tilley 1964). Where grasses have been cut at monthly intervals following removal of first growth, the first monthly regrowth has had a higher digestibility than subsequent regrowths in most cases although the mean digestibility of all regrowths varied between grasses (Minson et al. 1964). Perhaps the most interesting result from these studies is that digestibility of a herbage is not necessarily related to the proportion of leaf it contains especially when stems and flowering heads are immature (Minson et al. 1964).

The relevance to the grazing situation of such differences and changes in nutritive value is difficult to assess for several reasons.

In those studies designed to measure specific and varietal differences in nutritive value the aim has generally been to ensure that intake is not limited by low pasture availability. Because of this interpretation must take into account at least two factors.

In the first case this type of evaluation ignores agronomic properties such as dry matter production and persistence. This may lead to large stocking rate x species interactions in terms of animal performance (Bublath 1969). In the second case, such evaluations take no account of the possibility of grazing pressure x species interactions. Thus grazing pressure may have varying effects on the rate at which different species and varieties mature, possibly being a function of the way in which the different growth components of each variety are affected by different grazing pressures.

Extrapolation from pastures of a single species to the mixed pastures which are normally grazed may be complicated by selective grazing and possible interactions between feeds in terms of nutritive value (Rattray and Joyce 1969).

Changes in digestibility, and by implication in nutritive value, appear to have only been studied in mowing trials. The relevance of these will depend both on the selective grazing habits of animals and on the differences in regrowth which arise as a result of differences between mowing and grazing. Some of these differences have already been discussed but there is no information on the effects of grazing on the proportionate growth of plant components. This may well be of importance in nutritive value (Terry and Tilley 1964).

Where selective grazing occurs, the relevance of changes in nutritive value which occur under cutting regimes is doubtful. Grazing animals tend to select feed of a higher nutritive value than that available especially when grazing pressure is low (c.f. Section B) so that any change in nutritive value with maturation of feed may be of little consequence. This appears to be one of the reasons for the better liveweight gains of sheep on long rather than short pasture despite the fact that the latter may have a higher nutritive value (Clarke 1959; Hight and Sinclair 1965; 1967; Gallagher *et al.* 1966).

However selective grazing may have detrimental effects when pasture growth rates decrease. Thus, when selective grazing occurs the herbage available after grazing will tend to be more mature than that present before grazing. Furthermore this remaining herbage will continue to mature. Thus the regrowth will consist of varying proportions of young and old herbage. This will be subjected to another cycle of selective grazing leading to a greater accumulation of mature herbage and so on. Provided growth of young herbage matches or exceeds animal requirements the increasing maturity of the pasture as a whole may not affect animal performance. However in periods of slow growth grazing pressure will increase and if rejection of the accumulated mature herbage continues intake and hence animal performance may suffer markedly (Arnold *et al.* 1964a).

From this discussion it is clear that nutritive value is as yet ill-defined and factors causing differences between pasture species in nutritive value are not well understood. Further, interpretation of changes in nutritive value due to grazing will require basic knowledge of the way in which grazing affects the growth components of pasture plants.

Only when such knowledge is available will it be possible to take account of nutritive value in grazing management in a more precise way than is done at present.

There is little evidence of the extent to which changes in nutritive value occur with increasing stocking rates.

If defoliation occurs more frequently and/or more intensely as stocking rates increase, then it is to be expected that the time during which maturation of herbage occurs will be reduced. This will result in an increasing proportion of young growth in the pasture and by implication a sward of higher nutritive value.

Changes in botanical composition may also be expected to result in changes in nutritive value. However the importance of such changes may be small where high stocking rates prevent the full expression of specific and varietal differences in rate of change of nutritive value which occur with increasing maturity.

Direct evidence of such effects is scarce and generally unsatisfactory. Thus differences in diet digestibility between stocking rates which are estimated from faecal nitrogen measures (Arnold *et al.* 1964a) are suspect since faecal nitrogen is affected by pasture availability, intake level (Langlands 1969) and soil intake (Lambourne pers. comm.).

Evidence from Hurley (Spedding *et al.* 1967) indicates that the digestibility of herbage available at a low stocking rate was similar to that at a high stocking rate early in the growing season but declined at a greater rate as the season progressed. However the relevance of this to the grazing animal is not clear.

It should be appreciated that the nutrition of the grazing animal is a function of both the quantity as well as the quality of feed. Thus both these factors must be considered together although the linear relationship which often occurs between dry matter and digestible organic matter production per acre may allow some simplification in the definition of objectives for the nutrition of grazing animals (Campbell 1961).

Plant communities respond both to climatic and edaphic factors as well as to grazing and the outcome in any particular case will be due to the interactions between these factors.

The response of plant communities to light, temperature, rainfall and nutrient supplies results in seasonal patterns of growth. Grazing may influence the utilisation of all climatic factors and further may affect the rates of growth, decay and regeneration as well as the competitive relationships between the components of a pasture.

As stocking rates rise, pasture availability tends to decrease and this may have important effects on the micro-environment of the sward. For instance it has been suggested (Moore 1966) that the wide diurnal temperature ranges at the soil surface and the restriction of roots of heavily grazed plants to the top layers of the soil may promote the mineralisation of nutrients and their efficient uptake. It might also be expected that the susceptibility of such swards to climatic factors is increased.

Increased stocking rates may lead to changes in botanical composition of a sward but the importance of such changes is not clear (Carter 1968). Where the legume content of the pasture is affected then the effect on pasture production may depend on factors such as soil type, nitrogen availability and nitrogen circulation. Where grasses are involved then the effect may be a function of the relative productivity of those species which are increasing and decreasing in the sward. However the similarity in production of most of the common pasture species (Vartha 1966; Lynch 1966; Anslow and Green 1967) suggests that this effect may not be very important (Spedding 1966; Ormrod 1966).

The way in which these changes in productivity will be reflected in terms of animal production is dealt with in Section C.