STUDIES OF HERBAGE AVAILABILITY AND PLANT DENSITY IN RELATION TO ANIMAL PERFORMANCE

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SUMMARY

Two field experiments were carried out at the Mortlock Experiment Station, Mintaro, South Australia to study animal responses to a wide range of pasture situations and the effects of grazing pressure on plants.

The aim of the first experiment was to examine the influence of competition between ewes and lambs for feed when grazing pastures of different herbage availabilities in order to define biological criteria for the efficient use of pasture in the ewe-lamb unit for prime lamb production. This experiment consisted of three combinations of livestock, namely, lambs alone, ewes and lambs and ewes alone, grazing swards of Wimmera ryegrass (*Lolium rigidum* Gaud.) of five different initial herbage availabilities and tiller lengths at the same time at one stocking rate.

Weaning consistently increased herbage consumption by lambs but consistently decreased the liveweight gain of lambs during the period of study. The only advantage of weaning noted was when lambs were weaned and transferred from very sparse swards (i.e. less than 5 cm in tiller length) to abundant swards (i.e. greater than 10 cm in tiller length). Increased demands on the ewe for milk were reflected in substantially greater liveweight losses of lactating ewes compared to those of dry ewes when the tiller length of swards was less than 15 cm, but on longer swards responses were similar. Milk production of ewes grazing swards of different availabilities was relatively constant at each

period of measurement during the 33 day experimental period. The use of ewe body tissue to sustain milk production in the short term was an important compensatory mechanism under conditions of adverse nutrition. However, the plant pool was rapidly depleted below its initial level when ewes and lambs were grazing together, whereas weaned lambs had little effect on the amount of plant material present in spring.

The second study examined the influence of a fixed number of dry sheep on pastures with a wide range of seeding rates and plant density. Pastures were sown at eleven seeding rates ranging from 1 to 1024 kg ha^{-1} of Wimmera ryegrass seed and were set stocked 51 days after sowing. An ungrazed area was included within each grazed plot.

When the seeding rate of annual ryegrass was increased from 1 to 32 kg ha^{-1}, there was more than a five-fold increase in total pasture, seed and wool production per hectare and in sheep survival. At seeding rates above 32 kg ha^{-1}, there was little increase in plant or animal production. In contrast in ungrazed swards over this same range of seeding rates, total herbage yield was constant and seed yield was decreased by half.

The eleven seeding rate treatments were found to fall into three distinct categories: low, medium and high - based on sheep live weight and survival in time. In low density swards (seeding rates of 1 to 16 kg ha^{-1}) at the end of the experiment the fleece-free live weights of sheep ranged from 25 to 50 kg and were substantially less than those of sheep grazing higher density swards (the latter sheep weighed 63 kg). Sheep mortality occurred at the low seeding rates, ranging from 100 per cent losses at 1 kg ha^{-1} to 40 per cent deaths at 16 kg ha^{-1}. No sheep mortalities were recorded at higher seeding rates. In low density grazed swards any deficiencies in plant numbers were not fully compensated for by increases in plant weight so that herbage availability and total yield were greatly reduced compared to that of higher density swards.

Evidence is presented that herbage intake estimated by a herbage cutting technique over estimated actual intake by a factor of two on the basis of the nutritional requirements of grazing sheep. Whereas intake estimated by a faecal collection method gave acceptable estimates of actual intake.

The results of the present investigations have described situations in which herbage availability and plant density are major determinants of animal performance from annual swards. The implications of these results to grazing management practices in Mediterranean environments are discussed.

DECLARATION

I certify that this thesis contains no material which has been accepted for the award of any other degree or diploma in any university and that, to the best of my knowledge and belief, this thesis contains no material previously published or written by another person, except when due reference is made in the text of the thesis.

C.M.J. Williams

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1. GENERAL INTRODUCTION

Sheep production in Australia is based largely on an extensive management where animals are able to graze outdoors throughout the year. Each grazing property has a fixed land area of pasture and a relatively constant number of livestock.

The sheep raising areas of Australia are divided into three major geographic zones (Bureau of Agricultural Economics 1976). The pastoral zone is the largest in area and includes the arid and semi-arid areas of central Australia which contain about 25 percent of the nation's 145 million sheep. Here grazing by domestic herbivores of native species of grasses and shrubs is the sole agricultural activity, the area per sheep is extensive, rainfall is low and highly variable. Crop production is generally impractical because of inadequate rainfall.

The highest concentration of sheep per unit land area is in the high rainfall zone which is situated adjacent to the coastal strips of all mainland States and includes the whole of Tasmania. This zone is the smallest in terms of land area but contains about 35 percent of the sheep population. Here rainfall is high and sheep usually graze introduced species of grasses and legumes at relatively high stocking rates compared to those used in the pastoral zone.

The remaining 40 percent of sheep are grazed in the wheat-sheep zone. This zone covers portions of all mainland states (except the Northern Territory) and is bounded by the pastoral zone to the centre of the continent and by the high rainfall zone to the coast. Although rainfall is variable in the wheat-sheep zone (i.e. the cereal belt), it is normally sufficient for crop production. Here there is the traditional agriculture of dryland ley farming which consists of cropping and legume-based pasture rotations.

The studies reported in this thesis examined animal responses to feed shortage and the impact of high grazing pressure on plants in annual pastures in the wheat-sheep zone of South Australia. In this region the climate is typically Mediterranean with cold wet winters and hot dry summers (Donald and Allden 1959; Rossiter 1966).

Many stocking rate investigations have shown that temperate pastures in the high rainfall and wheat-sheep zones of southern Australia are often under-utilized and seldom carry sufficient animals (Rossiter 1958; Wheeler 1962; Allden 1969a; Carter and Day 1970; Langlands and Bennett 1973a,b; Brown 1976). Increased stocking rates do, however, increase the probability of animals being under stress due to a feed shortage at certain times of the year (Donald and Allden 1959; Geytenbeek et al. 1962; Carter and Day 1970). In grazing systems feed shortages are not uncommon and may occur in normal seasons when stocking rates are high at a time when pasture growth is low (e.g. in winter; Wheeler 1968). In each of the above situations a fixed number of sheep on a given area of pasture compete with one another for the herbage available. Results from stocking rate experiments have shown:-

(a) The dry sheep (a wool producer only) is most able to survive apparent feed shortages without undue losses (White and McConchie 1978), although high mortalities may occur in drought years.

(b) For prime lamb production where rapid lamb growth is desirable a feed shortage poses special problems because (i) the lamb requires both milk and herbage and (ii) the ewe requires herbage for both maintenance and milk production. Thus competition between animals for herbage exists and is confounded in the above situation by the dual requirements of the lamb.

Accurate knowledge of animal response to feed shortages and to changes in herbage availability and plant density should provide a sounder biological basis to aid management decisions aimed at alleviating feed shortages and achieving stable production systems. The experiments reported in this thesis examined two specific cases in which grazing animals compete for herbage, namely:-

(i) the prime lamb producing flock in the spring period, and

(ii) the wether flock in the winter/spring period.

The experimental techniques used in each study provided a wide range of herbage availabilities (at the one time) which simulated the pasture yields that might be encountered by the grazing animals in different seasons in a Mediterranean environment. The experiments were of relatively short duration and conducted on specially prepared swards in order to reduce the confounding effects, such as changes in botanical composition of swards and in the nutritional history of livestock which are inherent in many long term grazing experiments. Such experiments are unlikely to give a complete answer to any one problem but they have proved valuable in pin-pointing problem areas and in the elucidation of mechanisms in operation in grazing systems (Allden and Whittaker 1970).

Experiment 1 was a study of competition for feed between ewes and lambs grazing pastures of different herbage availabilities. Five grass swards presenting a wide range of available herbage, from 2 to 63 cms in tiller length (as defined by Allden and Whittaker 1970) were prepared in advance of the period of observation for use at the start of the experiment. Each sward was subdivided and one half was grazed by ewes and lambs with the remaining half being further subdivided and grazed by weaned lambs or ewes alone.

Competition between animals for herbage was assessed in terms of changes in sheep live weight, lamb intake and the components of intake. There are other grazing situations when herbage is in short supply and grazing animals compete for feed. Herbage shortages can be accentuated by one or more 'false' breaks to the season (i.e. early winter rains followed by drought). High seedling mortality in newly emerging annual pastures often occurs at such times (Smith 1968c; Greenwood and Arnold 1968; Cocks 1973). Seeding rate and/or the annual carryover of seed reserves and the resultant established plant population has been shown by Donald (1951, 1954) and Smith (1972) to be a major determinant of early season (autumn/winter) pasture production from annual pastures in Mediterranean environments of southern Australia. In such circumstances sheep live weight is lowest soon after the advent of the winter rainfall period (i.e. break of season). For several months after the break of season, the amount of herbage on offer usually limits the liveweight gain of grazing sheep (McKeown and Smith 1970; Smith *et al.* 1972; Smith and Williams 1973; Birrell *et al.* 1978).

Experiment 2 was undertaken to examine the influence of seeding rate and the resultant plant population on animal production and pasture yield from annual pastures. A wide range of seeding rates were used to develop a sequence of eleven grass swards with different plant densities and amounts of herbage present, ranging from sparse to abundant at a given time. Such differences might be encountered over a range of seasons in annual pastures. The response, in terms of changes in sheep live weight, survival, wool growth, intake and components of intake, of a constant animal population to changes in the plant population and herbage availability were measured. A further objective was to define those pasture characteristics (e.g. plant number, plant weight and tillers per plant) associated with stable and unstable grazing systems and to define the situations in which any deficiency in one pasture characteristic (e.g. plant number) could be compensated for by an increase in another (e.g. individual plant weight). A subsidiary experiment was conducted to compare the growth of pasture and changes in plant characteristics in grazed and ungrazed swards over a wide range of plant densities.

2. REVIEW OF THE LITERATURE

2.1 Introduction

Plants and animals are inseparable in the pasture-animal or grazing systems of Australia. The grazing system is one in which each of its many component processes influences and is influenced by other processes within the system. For example, the productivity of grazing animals is influenced by the quantity and quality of herbage available. In turn, herbage availability is a function of the rates of plant growth, decomposition and the removal of herbage by the grazing animal. A knowledge of these interactions is necessary to gain an understanding of animal response to limited feed and for the development of improved grazing management practices in temperate pasture environments where animals are able to graze outdoors throughout the year.

This review discusses firstly, the influence of grazing (i.e. defoliation, treading and nutrient cycling) on plant communities and secondly, the influence of herbage availability and pasture characteristics on herbage intake and animal performance and factors which may affect this. Thirdly, the nutrition of the grazing sheep is examined with special reference to those factors likely to affect herbage intake. Finally, the discussion concentrates on examining the importance of the above factors on the outcome of weaning of lambs and the productivity of dry sheep grazing annual swards.

2.2 The influence of grazing on plant communities

The grazing animal eats, treads and excretes on pastures. This leads to a unique pattern of defoliation, plant crushing, soil compaction and nutrient recycling.

The response of pastures to different frequencies and intensities of defoliation has been reviewed by Humphreys (1966) and Davidson (1969). Davidson (1969) found variable responses of the same plant species to various cutting regimes, as the frequency and severity of defoliation was increased he gave examples to show that yield may be increased, decreased or unaffected. Hence, it is not possible to predict the responses of plants to different cutting regimes. Since such treatments are conducted in the absence of selective grazing, treading and nutrient return, they allow no clear guide as to the magnitude or even direction of the influence of grazing on pasture growth. However, cutting experiments may to some extent simulate the reduction in leaf area that occurs under grazing. Although yields are generally reduced as the frequency of defoliation is increased, there are exceptions (Myers 1972). Responses to different types of defoliation using the grazing animal have been studied mainly in terms of the defoliation of individual grass tillers in grazed swards and have been reported by Hodgson (1966), Morris (1969), Hodgson and Ollerenshaw (1969), and McIvor and Watkin (1973). All demonstrated that the grazing of tillers within the sward, even under continuous grazing is intermittent, and that the frequency of defoliation increased with increasing grazing pressure. For example, McIvor and Watkin (1973) reported that tillers were grazed every 5 or 6 days when swards were grazed by 80 sheep ha^{-1} and every 7 or 8 days when grazed by 36 sheep ha^{-1}. Herbage removal reduces the amount of leaf area, carbohydrate reserves and root growth (White 1973). Many other factors, however, also affect the regrowth rate of a sward following herbage removal (White 1973).

The prime dependence of rate of photosynthesis on leaf area chlorophyll and light interception (Donald and Black 1958; Brougham 1959) as well as nutrient uptake, root area, competition and other factors has led to regrowth rates being explained in the main on the basis of the amount of leaf remaining after defoliation (Pauli and Stickler 1961) with due regard to the influence of other morphological and physiological factors.

Mathematical expressions to describe the growth and regrowth of grazed pastures are needed to predict plant growth in models of grazing systems and to compare plant growth attributes. Several mathematical functions are found to fit the sward dry matter/time relationship. Common functions reported and used in the literature are: (i) quadratics (Silsbury 1969), (ii) 3rd degree polynomials (Williams 1964; Cocks 1973), (iii) von Bertalanffy function, (iv) sigmoidal or logistic function (Brougham 1955; Williams 1964; Morley 1968; Langer 1970; Fukai and Silsbury 1976).

The use of these growth functions in biology has been discussed by Richards (1959, 1969). For each function plant growth rate can be calculated by differentiating the equation with respect to time. Williams (1964) has pointed out that the total dry matter yield/time relation is complex and different equations may be used to approximate the system at different times. However, although the biological meaning of a mathematical function may not be clear, the use of the function is justified if it allows quantitative comparisons of the growth of pasture plants under different treatments (Richards 1969). Langer (1970) has compared the maximum growth rate of different species by differentiation of the logistic growth equation at the point of inflection. Morley (1968) has examined parameters of Brougham's (1955) growth curves with a view to predicting the probable consequence of modifications of rotational grazing.

Herbage availability in grazed pastures is the net outcome of the processes of plant growth, decomposition and ingestion by grazing animals. Hutchinson (1969) found the rate of decay of Phalaris tuberosa pastures at Armidale to be 0.4% per day of standing dead material. The daily loss of dry matter of clovers was found by Brown (1977a) to be two to three times that of perennial grasses with values for annual grasses being intermediate. Tainton (1974) estimated the loss through decomposition to vary from 23 to 31 kg of dry matter ha^{-1} day^{-1} in perennial pastures in New Zealand subjected to different grazing treatments.

Herbage production of temperate grazed pastures has been calculated by different methods in different environments and it has been found to be increased from low to moderate stocking rates and to decrease at very high stocking rates (Hutchinson 1969; Carter and Dat 1970; Vickery 1972). However, Langlands and Bennett (1973a) found herbage production to be insensitive to increases in stocking rate over similar ranges in stocking rate.

In all cases authors have acknowledged that they were unable to check certain assumptions implied in their estimation of pasture production. Reliable techniques for estimating herbage production under continuous grazing systems are not yet available (Allden 1969a; Hutchinson 1969; Langlands and Bennett 1973a). There is a great need for the development of reliable techniques to estimate herbage production under continuous grazing and for a knowledge of the errors inherent with new and present techniques.

Repeated removal of above ground photosynthetic tissue has been shown to lead to a reduction in the rates of plant growth (Davidson 1969) and of root respiration, root growth and nutrient uptake (Davidson and Milthorpe 1966a, b). The impaired root function that results may seriously reduce plant persistence through sensitivity to moisture stress or nutrient deficiency. For example, Smith (1970a) reported reduced persistence of lucerne stands under frequent continuous grazing or defoliation, while intermittent grazing allowed root recovery between successive defoliations and maintained persistence.

Morphological characters, such as the position of the growing points in relation to ground level and the relative proportions of plant tissues inaccessible to the grazing animal, must affect species persistence under frequent close grazing. Davidson (1969) suggested that to remain productive under close, frequent grazing, grasses and legumes need to have the ability to develop a prostrate habit and dense, low canopy to ensure considerable leaf area escapes the grazing animal and provides a continual supply of assimilate to the roots (Kydd 1966a, b). Changes in botanical composition and density of a sward may result from the different ability of species to develop such a growth habit. There is little direct evidence that a decline in animal productivity accompanies botanical change in annual pastures, however, a reduced density of edible plants may be associated with reduced plant and animal productivity (Sharkey et al. 1964; Carter 1965; Carter and Day 1970). Morley (1966a) proposed that high grazing pressure may encourage botanical stability in the long term but desirable components could be lost from the pasture in the process; adaptable, remaining or invading species may be less productive.

The translocation of assimilates between adjacent tillers (Marshall and Sagar 1965) may be an important buffering mechanism under continuous grazing where some tillers escape defoliation. However, mature tillers of ryegrass have been found to be independent because leaf blades fed labelled carbon dioxide transported labelled assimilates only to the root system of that tiller (Marshall and Sagar 1965).

The amount of tillers and meristematic tissue generated is important in survival and constitutes the regrowth potential of the plant (Langer 1963). The life history, numbers and longevity of tillers may vary with time of origin (Langer 1963; Hill and Watkin 1975), genotype and environment (Mitchell 1953; Langer and Lambert 1959), position on the plant (Langer 1956; Lambert and Jewiss 1970) and depend on genetic factors (Saxby 1956; Langer and Lambert 1959). The number of tillers per plant or per unit area is also influenced by seasonal conditions and nitrogen application (Langer 1957; Silsbury 1965; Wilman et al. 1976). Tillering is reduced by low light intensity (Mitchell 1953), high temperature (Templeton et al. 1961) and low soil moisture (Olmstead 1941).

Under conditions of environmental stress, recently formed tillers tend to die first (Hoen 1968). Once established, however, tillers generally remain alive for longer periods, provided that they remain vegetative. The proportion of these types of tillers determines the habit of the plant (Langer 1963).

Tillers arising at successively later dates have a proportionately smaller chance of developing a seedhead (Langer and Lambert 1959; Ryle 1966; Hill and Watkin 1975).

All these physiological responses may be generated by stocking management and such responses may influence pasture productivity. Silsbury (1966) has shown that dry matter yield of perennial ryegrass and tiller number were positively related at all development stages throughout the growing season. High production in a closely defoliated sward would depend on there being a large number of tillers per unit area to compensate for the relatively small weight of tissue per tiller (Mitchell 1955; Hodgson and Ollerenshaw 1969; Thomas and Steppler 1971). In an annual rainfall environment where the period of pasture growth is limited, conditions which favour the attainment and maintenance of a high tiller population are likely to be associated with high pasture productivity.

Susceptibility of the growing points to removal by the grazing animal will vary with species and physiological stage of growth. In the vegetative state, the shoot apex of grasses is commonly below ground level, well protected from the grazing animal (Wilman et al. 1976), whereas, in the reproductive state the apex or developing seedhead will be higher and more susceptible to removal by grazing (Davidson 1969; Hill 1971). While removal of the shoot apex in the vegetative plant will stop growth of that shoot in the reproductive plant, increased tillering will result during the phase of tiller suppression and if conditions remain favourable for growth more seedheads may be produced (Langer 1957; Hill 1971). However, with spring grazing, when sheep eat maturing seed heads the numbers of seeds produced may be reduced by as much as 70% under heavy grazing (Anon. 1971; Williams and Boyce

1977, 1978). The magnitude of seed production and carryover is critical for the regeneration of annual pasture. Gramshaw and Stern (1977a) found that the intensive summer stocking equivalent to about 3,000 sheep days ha^{-1} reduced seed numbers of annual ryegrass by 20% and concluded that the proportion of head seeds eaten during summer seems to be the principal factor determining the extent of seed losses from the pasture. Losses from ant theft, fire and desiccation may also be large.

Treading by animals can cause a considerable reduction in plant density, pasture yield and soil moisture (Carter and Sivaligham 1977) which is mainly due to bruising of tissues, and to a reduction in tiller numbers (Edmond 1964, 1966; Carter and Sivalingham 1977). Species differ in their sensitivity to treading which may be related to the degree of protection of their growing points and to differences in tillering rate; soil moisture and soil type are also important (Brown and Evans 1974). Treading causes an increase in bulk density in the topsoil and lowers the rate of water infiltration, but adequate plant cover can provide a cushioning effect and can reduce this effect and high stocking rates increase it (Langlands and Bennett 1973a).

The grazing animal retains very little of the minerals or nitrogen of the herbage for its own use (Sears and Newbold 1942; Sears 1956; Barrow 1967). The excretal return of nitrogen, phosphorus and potassium may be important factors influencing sward productivity (Sears 1953; Cuykendall and Marten 1968; Frame 1968), and in particular areas, sulphur return may also be important (Till 1976). The effectiveness of nutrient return by the grazing animal may be reduced by the uneven manner its excreta are distributed. In addition to local heterogeneity caused by random return of excreta (Barrow 1967;

MacDiarmid 1971), there may also be a large scale heterogeneity due to the overall withdrawal of nutrients from the pasture to the camp site (Hilder 1966). Thus, while the mean nutrient level of a paddock may be adequate, it is possible to have suboptimal and superoptimal levels in any one paddock.

2.3 Effects of pasture availability and pasture characteristics on animal performance

The factors likely to affect the herbage intake and productivity of grazing animals can be divided into four main groups; those associated with the animal, the sward, management practice and the environment. This section concentrates on examining the effects of sward variables on intake. Limitations in the quantity or quality of herbage on offer commonly occur in grazing systems and this usually leads to a restriction of the nutrient intakes of grazing animals. At present it is only possible to predict the effects of limited herbage on intake in general terms, partly because of the problems of measuring intake accurately (Langlands 1966, 1975), but also because of the difficulties in describing those characteristics of the sward which affect grazing animals and of dealing with the interactions between them (Hodgson 1977).

Early attempts to estimate herbage consumption were based on differences in pasture availability before and after grazing. Raymond et al.(1956) pointed out that the method was only valid under intensive grazing over a short time interval where herbage growth is small relative to herbage consumption (Leaver 1974). A system of open and closed quadrats, which includes an adjustment for herbage growth, has been used under extensive continuous grazing to estimate consumption (McIntyre 1946; Moore et al. 1946; Carter and Day 1970). McIntyre (1951) examined the effects of estimating intake using open and closed quadrats and suggested that accuracy could be improved using a ranking technique. He found that it was only possible to obtain a reasonably accurate estimate of consumption when near complete consumption of a dense stand of pasture occurs. Such a situation is likely to arise in Australia in only a few favoured areas. McIntyre (1951) also suggested that three weeks is the optimum time period between cuts and that any increase is likely to lead to an increase in the difference between plant canopies in open compared to closed quadrats (Van der Kley 1956).

The reverse use of feeding standards has been used to calculate intake (Hutchinson 1969). Feeding standards which were derived from penned animals have been used in the past and these probably underestimate herbage intake under grazing (Coop and Drew 1963; Corbett and Farrell 1970). With better knowledge of the energy requirements of grazing sheep (e.g. Young and Corbett 1968) and the factors likely to affect this - such as herbage availability (Coop and Drew 1963; Lambourne and Reardon 1963b), this major criticism may not apply. However, much of this information is either not available or of a very specific nature only. It will probably be necessary to derive local relationships, e.g. between liveweight change and body energy, for each class of stock in each environment.

Current methods for estimating herbage intake involve measurements of faecal output and the digestibility of the diet consumed. An alternative method is to administer an inert marker such as chromium sesquioxide and estimate total faeces by rectal sampling and analysis of the marker concentration (Langlands et al. 1963c).

Herbage digestibility has been assessed by a number of methods. Manual methods of herbage sampling do not usually represent adequately the selective behaviour of grazing animals (Van Dyne and Torrell 1964). The use of a regression technique relating to the composition of the diet to the concentration of a naturally occurring faecal indicator in a separate digestibility trial can be effective (Greenhalgh et al. 1960). However, it has been suggested by Young and Corbett (1968) and confirmed by Landlands (1969b) that the use of the faecal nitrogen method for the predication of intakes on heavily grazed pastures may lead to large errors (e.g. Lambourne and Reardon 1963a).

At present the collection of herbage samples by sheep fistulated at the oesophagus coupled with in vitro digestibility methods appears to provide the best estimate of the digestibility of the diet selected by sheep grazing temperate pastures (Langlands 1969b; Ulyatt et al. 1974). The technique is, however, imprecise, and may be subject to certain biases at present undefined (Langlands 1969b).

Thus, large samples of animals are required since between animal variability within a treatment is high and is the major source of variation in the field (Lambourne and Reardon 1963a; Ulyatt 1972). These potential sources of error cannot be ignored, but recent work indicates that it is possible to minimize them. Choice of an even line of sheep and using pre-experimental measured variables as covariates in animal selection should assist in reducing inherent variations between animals.

Since the productivity of animals is controlled largely by the quantity and nutritive value of the herbage eaten (Blaxter 1962), it is important to be able to measure intake accurately and to obtain much more extensive information about the factors affecting herbage intake in the field.

The voluntary intake of herbage by the grazing animal may depend as much on other characteristics of the pasture as on the amount of herbage present (Arnold and Dudzinski 1967b, c; Raymond 1969; Stobbs 1973a, b). The animal may influence the value of pasture availability by selectively grazing pasture components of different acceptabilities. Thus any relation between availability and intake is influenced by interrelated variables. Although the way in which many of these variables interact is not fully understood, studies of pasture availability/animal intake relationships have indicated their importance and much of the variation in experimental results may be attributed to their influence. Different relationships between intake and available herbage have been reported in the literature for sheep grazing temperate pastures.

Allden (1962), Arnold (1963a), Allden and Whittaker (1970) and Gibb and Treacher (1976) recorded an asymptotic relationship between herbage availability and intake. These findings were substantiated by the asymptotic relationship between herbage availability and live weight gain found by Willoughby (1958, 1959) and Arnold (1964b). However, it has not been easy to develop a unifying concept from the evidence available. Since the critical yield of herbage below which intake has declined varied from 670 to 4000 kg of dry matter ha^{-1} for sheep grazing temperate pastures (Willoughby 1959; Scott Young 1960; Arnold 1964a, b; Allden and Whittaker 1970; Langlands and Bennett 1973b). Although differences in methods of measuring sward characteristics and herbage intake undoubtedly contribute to this variation they are unlikely to provide a complete explanation (Hodgson 1977). Differences in intake/availability relationships have been associated with differences in pasture type as reported by Arnold (1964b) and Arnold and Dudzinski (1967c). Maximum intake was attained at a lower level of availability on subclover than on perennial grass swards and part of these differences was attributed to differences in leaf length and digestibility between swards. However, Smith *et al.* (1972) found the level of herbage availability for maintenance of sheep live weight on newly emerging annual swards was 157 and 380 kg of dry matter (DM) ha^{-1}, for Wimmera ryegrass and subclover dominant swards, respectively. They attributed this to the more erect habit of the ryegrass plant in early growth compared to clover and suggested grass dominant swards would be most productive for autumn/winter feed and clover dominant swards in the springtime in Mediterranean environments.

In the face of limited feed, the animal can only maintain daily herbage intake by increasing grazing time (Arnold 1964b; Allden and Whittaker 1970). However, a point is reached after which increases in grazing time became progressively less effective and cannot fully compensate for a reduced rate of intake and total intake declines.

The relationships presumably differ with such factors as animal species, breed, age, weight, physiological status, grazing experience (Willoughby 1958; Hodgson 1975; Curll 1976) and stocking rate and plant factors such as - herbage yield, growth rate, tiller length, digestibility, plant number per unit area, plant weight, species and palatability (Willoughby 1958; Allden 1962; Arnold 1964b, 1970; Allden and Whittaker 1970; Smith *et al.* 1972). Hodgson (1977) has cited several examples, mainly of cattle grazing relatively high availability pastures (ranging from 2880 to 8240 kg DM ha^{-1}), e.g. Corbett *et al.* (1963), Hodgson (1968), Holmes *et al.* (1972) and Rodriguez and Hodgson (1974) and one example for sheep (Arnold and

Dudzinski (1967b), to suggest that with the exception of the results of Allden and Whittaker (1970), different classes of animal within a species appear to respond in a similar manner to variations in the weight or digestibility of the herbage, and in sward structure. Animals grazing annual pastures in southern Australia commonly have access to far lower levels of herbage availability (0-2000 kg DM ha^{-1}) for much of the year (Allden 1968d; Carter and Day 1970; Smith et al. 1972; Brown 1976). It is in situations of such low availabilities in annual swards that Allden and Whittaker (1970) found that smaller animals (lambs, 25 kg) had a higher rate of intake (recorded over one hour's grazing) per unit of live weight than larger animals (yearling wethers, 43 kg), whereas intakes per unit of live weight were similar at high availabilities. This suggests that smaller animals would have a competitive advantage over larger animals at low availabilities. However, the rate of intake measured above was that from a fasted animal in its first hour of grazing (i.e. the 'potential' rate of intake) and such a rate may not be maintained by the animal over the full daily grazing period (Forbes et al. 1972). Also, the larger animal may be more able to compensate for a reduced rate of intake at low herbage availabilities by having a greater ability to increase its grazing time.

Johnstone-Wallace and Kennedy (1944), and Arnold (1964a), found a quadratic relationship between availability and intake, and this result supports the animal production studies of Brown (1977b). Intake increased up to a maximum of about 1350 and 4800 kg DM ha^{-1} for young lambs and dairy cattle, respectively and then declined at higher availabilities. Johnstone-Wallace and Kennedy (1944) related the low intake at high availabilities to a reduction in the digestibility of pasture. Arnold (1964a, b) suggested this decline was due to the lamb's inability to graze and utilize efficiently long, bulky, compared to short, herbage. However, Large and Spedding (1957, 1964) and Lewis and Cullen (1973) have recorded no significant differences in lamb growth on 'long' or 'short' perennial grass swards.

The former authors suggested that lambs by selective grazing were able to achieve similar production on dissimilar swards, whereas, the latter authors proposed that increases in tiller density on short swards fully compensated for the height of pasture. It cannot be determined whether the lack of changes in lamb growth rate were due to the height of pasture *per se*, or different plant species, or to some other effect such as differences in the quality of the herbage.

The digestibility of herbage remains high until the onset of the reproductive phase of growth (generally in spring); thereafter digestibility falls and voluntary intake declines with it (Spahr *et al.* 1961; Radcliffe and Newberry 1968). However, in high availability pastures, the digestibility of the herbage eaten by the grazing animal may be higher than the average for the pasture on offer because of selective grazing (Arnold 1962; Hamilton *et al.* 1973). The potential for selective grazing would be expected to diminish as the quantity of feed diminishes. In very low availability pastures (i.e. less than 500 kg DM ha^{-1}), the digestibility of ingested material was found to be less than the average for the pasture since the grazing animal had little opportunity for selection and ingested much senescent material, relative to green material, presumably because much of the limited green material present cannot be physically prehended by the animal (Allden and Whittaker 1970; Hamilton *et al.* 1973). The grazing animal may cause changes in pasture quality by consuming the more digestible components of the sward and so reducing overall herbage digestibility.

Also continual removal of herbage by the grazing animal is likely to maintain herbage for a longer time, in a more immature stage of growth and thus at higher digestibility than that of a comparable, undefoliated sward.

Low intakes at high availabilities may also vary with pasture structure, especially height and density. For example, on sparse swards, grazing cattle and sheep may experience difficulties in the physical prehension of feed (Johnstone-Wallace and Kennedy 1944; Smith et al. 1972), while on tall dense pasture, grazing sheep (Arnold 1964b) and especially lambs (Arnold 1964a) experience difficulties in feed prehension. The intake of dairy cows has been observed to decline on very tall, open tropical grass pastures (Stobbs 1973a, b). Allden and Whittaker (1970) have suggested that height was much more closely associated with herbage effectively 'available' to the grazing animal (i.e. 'intrinsic' availability) than was DM yield per hectare. Height and yield were found to be closely associated in annual swards less than about 10 cm in height (Smith et al. 1972), but they suggested that on longer swards, height would become less important. Hence, some of the differences in relationships between intake and pasture characteristics may be due not only to differences in the methods of measurements, but to differences in their accuracy as determinants of intake at different levels of herbage yield.

There have also been studies in which workers have been unable to detect any relation between herbage intake and herbage availability (Carter et al. 1960; Wheeler et al. 1963; Hennessey 1973). Carter et al. (1960) attributed this to environmental conditions such as water-logged pastures leading to fouling and rejection of herbage by stock and to errors associated with the techniques of estimating intake.

In addition to the latter problem, Hennessey (1973) attributed the lack of response, in terms of the intake and live weight of cattle to pasture length and availability to the high moisture content (greater than 85 per cent) of irrigated annual pastures. The results of Wheeler et al. (1963) may be misleading because data were pooled for different pasture types and for different seasons and the senescent herbage was omitted in the assessment of herbage yield.

Relationships between intake and herbage availability which have been established apply to specific situations. The many factors which influence such relationships need to be considered when deriving relationships in other pasture situations.

2.4 The nutrition of grazing sheep

A knowledge of the basic needs of the animal as well as of the plant are essential for interpretation and improvement of grazing management practices. Schinckel (1963) has reviewed this subject and stressed the importance of nutritional factors in the various phases of sheep production. McDonald (1968) has emphasized the special nutritional problems of the grazing versus the pen-fed animal. The quantitative aspects of food prehension differ greatly in these later two systems; but the basic biology of ruminants is similar (McDonald 1968). The major emphasis in this section will be on animal factors affecting the intake of energy as it is the main determinant of production of grazing animals (Blaxter 1962). The factors determining the intake of food by grazing animals are complex. Balch and Campling (1962) stressed the importance of the perceptive facilities in the initiation of eating in addition to physical factors which may limit voluntary intake.

Energy balance of the animal body is determined by the differences between energy input (feed) and energy output in the form of faeces, urine, methane gas, heat increment, milk and fibre. Thus, the physiological and productive states of the animal have a considerable influence on herbage intake. Increases have been reported due to cold stress after shearing (Wheeler et al. 1963; Coop and Drew 1963) to the degree of previous undernutrition (Allden and Scott Young 1964; Allden 1970b) and lactation (Young and Newton 1974). Many estimates of the maintenance requirements of grazing sheep have been derived from relationships between herbage intake, live weight and liveweight change (Coop and Hill 1962; Coop and Drew 1963; Langlands et al. 1963a, b; Lambourne and Reardon 1963; Grimes 1966; Young and Corbett 1968; Allden 1969b; Jagusch and Coop 1971; Langlands and Bennett 1973c) and from estimates of heat production (Young and Corbett 1972).

Estimates of the additional energy required for the maintenance of sheep grazing abundant herbage compared to housed sheep ranged from 20-50 per cent. For sheep grazing short pastures, Coop and Drew (1963) recorded an increased maintenance requirement ranging from 50 to 80 per cent. It seems likely that in most grazing situations, the energy costs associated with grazing will not be constant but will vary from 20 to 80 per cent of the maintenance requirements of a penned animal maintained under thermoneutral and minimal stress conditions. The efficiency of utilization of ingested material for animal production is a further factor which influences animal productivity from pasture (Graham and Searle 1970).

Young grazing ruminants often experience a period of adverse nutrition leading to either lowered growth rate or substantial weight loss (Allden and Anderson 1957; Meyer and Clawson 1964). Such animals are known to grow exceptionally fast when feed becomes freely available. This response is commonly called 'compensatory growth' (Allden 1970a). The net energetic efficiency of liveweight gain of compensating animals is probably slightly higher than normal and maintenance requirement lower in the first weeks of recovery, but at other times was the same as for normally grown animals (Allden 1968a, b, c, d). The common observation that grazing time increases on sparse pastures (Allden 1962; Arnold 1964a) may explain in part the higher maintenance requirements of sheep grazing short compared to long pastures (Coop and Drew 1963).

It is common practice to measure liveweight changes of the grazing animal as the criterion of animal production from pasture (Hamilton et al. 1970; Smith et al. 1972). The simplest and perhaps most meaningful example is the measurement of annual liveweight gain of young growing animals as a direct means of comparing methods of grazing management (Jones and Jones 1930), stocking rates (Cannon and Bath 1967) or pasture species (Grimes et al. 1966; Hamilton et al. 1970). When assessed over a prolonged period (several months to years) changes in live weight indicate real changes in energy storage (Searle and Graham 1970), however in the short term (periods of a few weeks) changes in gut fill or in body composition may produce spurious effects (Taylor 1966; Searle and Graham 1970).

Marked season rhythms in wool growth have been reported for sheep at pasture in a number of Australian environments (Hutchinson and Porter 1958). The rhythm in wool production is determined principally by nutrition and by a climatic component postively correlated with temperature and day length (Ferguon et al. 1949; Hutchinson and

Wodzicka-Tomazewska 1961). The fine wool Merino exhibits little annual rhythm when maintained at a uniform level of nutrition in contrast to other strains of Merino such as the South Australian for which Hutchinson (1962) reported a rhythm of 48%. At high stocking rates, seasonal changes in nutrition are much greater and the rhythm at 22 sheep ha^{-1} for fine wool sheep was 62% (Langlands and Bennett 1973c).

Wool production is approximately proportional to intake; liveweight gain is proportional to intake in excess of the maintenance requirements. Langlands and Bennett (1973c) have suggested that wool production per hectare will not be significantly reduced unless the stocking rate imposed is high enough to cause deaths from malnutrition. For the different types of production from the same animals there will be different critical stocking rates at which the depression of individual performance becomes marked (Spedding 1965).

It is necessary to emphasize that however well a simple measurement of animal production may serve to compare gross overall output of a grazing treatment, it gives no indication of the driving forces which determine animal productivity, i.e. of the factors influencing energy flow from autotrophs through to the heterotroph.

2.5 Factors affecting the weaning of lambs and the productivity of dry sheep grazing annual pastures

A greater knowledge of mechanisms in operation in grazing systems will be necessary if greater returns from the management of conventional grassland communities are to be achieved. Underlying mechanisms in operation in the weaning of lambs and in the management of dry sheep at pasture will be examined in order to attempt to define rational bases for management decisions.

The dominant effect of stocking rate in determining the output of prime lamb per hectare has been shown by many workers (Arnold and Bush 1962; Sharkey *et al.* 1962; Arnold *et al.* 1971). However, grazing management practices may have quite different effects on both animal and pasture growth, at different stocking rates (Spedding 1965). Several workers (Wardrop *et al.* 1960; Cannon and Bath 1967) have shown no advantages to weaning at stocking rates where the feed available was evidently adequate. Whereas Corbett (1966, 1968b) found at high stocking rates (20-30 sheep per hectare) early weaning appeared to be obligatory if the lambs were to survive. Geytenbeek *et al.* (1962) found in an environment where a period of pasture deficiency is common in the winter months that weaning at 12 weeks of age had a beneficial effect on the growth rate and wool production of young Merino sheep. Clearly unless a situation of 'stress' arises in which the ewe and lamb are competing for the same pasture substrate, weaning may be a restrictive and unjustifiable practice (Cannon and Bath 1967; Furnival and Corbett 1976). Therefore in certain situations the quantity and quality of pasture available to the ewe-lamb grazing unit may be a basis for predicting an optimum or obligatory time of weaning.

The removal of competition for pasture between ewe and lamb is commonly advocated in grazing management systems (creep grazing, early weaning and artificial rearing). For example, Bakker (1967) has outlined situations in which the adoption of early weaning practices and/or artificial rearing of lambs may be of benefit to lamb growth and survival. They include:

1. increasing the efficiency and flexibility of pasture and flock management (Clark 1954; Spedding 1965),

2. facilitating earlier remating of ewes to increase the frequency of lambing (Munro 1962; Copenhaver and Carter 1964; Hunter 1968).

Other workers have early weaned lambs:

3. in drought conditions to ensure lamb survival (Corbett 1968b),

4. to reduce competition for good quality pasture between ewe and lamb (Clark 1954; Gerring and Scott 1955; Barnicoat *et al.* 1957; Cannon and Bath 1967; Scales *et al.* 1968),

5. to increase ewe wool production (Corbett 1966).

Definition of pasture situations when the adoption of these practices is beneficial to increased lamb growth is not well defined. Spedding (1965) has described systems of creep grazing management commonly used for prime lamb production in the United Kingdom. He has claimed large theoretical advantages to be gained from a system of management involving creep grazing as a means to: (a) control parasites, (b) to increase the quality of forage available to lambs and (c) to increase the carrying capacity of pastures.

However the adoption of such systems has given either small increases in animal production of the order of 5% (Spedding and Large 1959) or little advantage over conventional grazing methods (Arnold and Bush 1962; Fletcher and Geytenbeek 1968; Arnold 1969; Jordan and Marten 1970; Arnold *et al.* 1971). The concept that creep grazing of lambs will reduce competition for herbage between the ewe and lamb grazing unit is sound only if the competition for herbage exists in the non-creep grazing areas, or if there are differences in herbage quality between creep and non-creep areas.

Weaning is theoretically possible when the lamb is physiologically capable of existing on a solid diet; this occurs at about 3 weeks in most breeds (Wardrop and Coombe 1961; Walker and Walker 1961; Langlands 1972). It is unlikely, however, that a solid diet will give maximum rate of growth at such an early age. The reticulo-rumen reaches adult proportions, but not adult capacity, in rapidly growing lambs by 8 weeks of age (Wardrop and Coombe 1961; Hodge 1966a). Most early weaning experiments have shown a decreased rate of gain in the first one to two weeks after weaning. Despite Spedding's (1965) view that early weaning in many situations results in very little if any, reduction in lamb growth, in experiments where the only nutritional variable was the removal of milk, rates of gain were always reduced, but only in the short term (Cannon and Bath 1967; Hodge 1966a; Jagusch et al. 1971). When pasture quality was poor, the effect of removing the milk supply was greater (Watson and Elder 1960; Brown 1964; Spedding 1965). The importance of providing a high quality diet for the young lamb and the superiority of legumes over grasses in promoting lamb growth has been shown by Jagusch et al. (1971) and Reed (1972).

Clearly at the extremes of nutrition it may be that lambs alone and/or ewes (when lambs are weaned) alone may be the most efficient animals in certain environments. The efficiency of food conversion by the ewe may be of much more importance than that of the lamb, since the maintenance requirements of a breeding ewe are the dominant proportions of the ewe-lamb total annual intake requirement (Large 1970). Searle and Graham (1970) have shown the relative inefficiency of producing milk through the ewe for the sustenance of the lamb. On the other hand Hutchinson (1969) and Allden (1970a) have illustrated the significance of tissue storage by the animal during times of plenty to supply energy needs when feed is in short supply. Thus it is not unreasonable to expect that during periods of feed shortage the advantage of utilizing storage depots of the ewe for milk production might outweigh the removal of competition for feed between ewe and lamb with the object of providing the lamb with more favourable pasture feed conditions (Watson and Elder 1960). Furthermore to assess the significance for lamb growth of these different pathways of feed utilization in grazing situations consideration must be given to the relative importance and utilization of milk and pasture in the diet of the unweaned lamb.

The effects of class of animal such as the breed of sire, the breed, age and weight of dam indirectly affect the milk supply and residual pasture available for lamb growth (Barnicoat et al. 1949; McCance and Alexander 1959; Langlands 1972). Langlands (1972, 1973) used a cross-fostering technique to examine the milk and pasture intake and growth of lambs from different breeds of sheep. He confirmed the finding of Allden (1970b) that Merino lambs grew more slowly than crossbred lambs primarily because of their lower voluntary food intake.

Langlands and Donald (1975) considered that the lower milk production of Merino ewes compared to cross-bred ewes was of secondary importance since if herbage was available ad libitum Merino lambs will largely compensate for any lack of milk by consuming more forage. However, in most grazing situations when milk production declines, pasture also is often deficient in quantity and/or quality (Watson and Elder 1960; Corbett 1968b; Furnival and Corbett 1976). Thus, in this situation, weaning practices may be desirable. Thus major factors which influence the relative contribution of milk and pasture to the diet of the lamb may be summarised as:

1. the birth status of the lamb (Doney and Munro 1962),

2. the breed, age and weight of the lamb (Corbett 1966; Joyce and Rattray 1970),

3. level of ewe milk production (Watson and Elder 1960; Hodge 1966a),

4. Stocking rate and quantity and quality of available pasture (Watson and Elder 1960; Corbett 1968b; Jagusch and Coop 1971),

5. the ewe/lamb breed interaction (Langlands 1972, 1973).

The effect of the ewe's presence on the intake of herbage by the lamb is not clearly evident from the literature. Some information from long term stocking rate trials has indicated benefits or a necessity to wean when herbage availability is low, as in droughts (Corbett 1968b). However effects of herbage availability on the partition of nutrients between the ewe/lamb grazing unit cannot be clearly gauged due to the occurrence of interactions inherent in many long term experiments.

The relative contribution of milk and pasture to the lamb has only been studied in pen situations (Hodge 1965) and in grazing conditions where abundant herbage was always available (Langlands 1972, 1973; Langlands and Donald 1975). The question arises, can an increase in herbage availability and consequently herbage intake to the weaned lamb fully compensate for the lack of milk supply brought about by the ewe's absence in different pasture situations. Also there is no direct information on the effect of the ewe's presence on the intake of herbage by the lamb at different levels of pasture availability.

Sheep grazing annual pastures in the Mediterranean environment of southern Australia commonly experience a recurrent cycle of nutrition (Donald and Allden 1959; Carter and Day 1970). In this environment sheep exhibit minimum live weight and wool production in the autumn/winter period (McKeown and Smith 1970; Carter and Day 1970; Smith *et al.* 1973). Also at this time, pasture growth is low and herbage availability falls to a minimum level (Myers 1972).

The autumn and winter growth rates of swards of annual species vary widely (Smith 1970), but the most important single determinant is seedling density (Donald 1951; Smith 1972). With barley grass (*Hordeum leporinum*) dense swards have given autumn growth rates of 25 kg DM ha^{-1} day^{-1} and winter rates of 14 kg DM ha^{-1} day^{-1} (Smith 1972). At an appropriate density, these same rates could be achieved by such species as subterranean clover and Wimmera ryegrass (Smith 1970). Donald (1951) suggested that dense swards give most of the attributes needed if these plants are to be used for animal production, i.e. maximum total yield, maximum winter yield and satisfactory seed production. Smith and Williams (1973) constructed a model relating the early growth of a subterranean clover pasture to the liveweight change of grazing sheep. The live weight of individual sheep was sensitive to stocking rate, length of deferment and initial plant density.

Under favourable growing conditions, Donald (1951) has shown in ungrazed field plot trials that the amount of forage produced by a pasture in the first 80 to 100 days of growth is linearly related to the seeding rate. Over long periods and with the onset of favourable growing conditions the differences in yield caused by differences in the initial seeding rate diminishes (Donald 1951, 1954).

Yet there is little information available on the effects of rate of seeding and plant density on plant and animal production per hectare from continuously grazed pasture communities.

Density affects the growth of individual plants through its effects on the plant's environment (Donald 1951). Thus as density increases from the single, spaced plant situation to the dense sward, competition for light, nutrients and moisture occurs earlier and becomes progressively more critical with time (Donald 1951; Milthorpe and Morley 1974), which ultimately may lead to plant mortality.

The relations between plant yield and number of plants per unit area suggests that two distinct types of response may be obtained (Holliday 1960a, b). The asymptotic relationship is typical where yield is assessed in terms of vegetative growth (e.g. DM). Whereas a parabolic-type yield/plant population relation is typical where yield is assessed in terms of a reproductive component (e.g. seed).

Maximum DM yield and seed yield of ungrazed Wimmera ryegrass swards were produced at a minimum plant density of 400 and 775 plants m^{-2}, respectively (Donald 1951, 1954). Although Donald's work was a very useful preliminary study; the interaction of grazing with plant density in influencing DM yield has not been reported.

Smith (1968c) suggested that the reason for the successful invasion of annual pastures by barley grass (Hordeum leporinum) is in its ability to set seed prolifically in spring and to germinate readily the following autumn. Thomas and Steppler (1971) have provided preliminary evidence that for two species with a knowledge of certain yield components - tiller dry weight and tiller number per unit area, it may be possible to predict yield at any time during the season. Thus seeding rate, fertilizer practice, time of sowing, and, indirectly, yield components could possibly be adjusted to produce a certain amount of herbage at a certain time to meet animal requirements.

Grazing may influence the number of plants which can exist and produce in a unit area of grassland. Harper (1969) noted that grazing of grassland by the rabbit increased the number of plants per unit area compared to ungrazed control areas. However, a decline in numbers in the whole plant population as the growing season progresses and as stocking rate increases has been shown by several workers - Table 1. This may be caused by one or a combination of factors such as:

(i) onset of drought conditions (Rossiter 1966), after the advent of winter rains, i.e. 'false' breaks of season;

(ii) treading damage and uprooting of seedlings by the grazing animal (Greenwood and Arnold 1968).

(iii) competition for light, water or nutrients (Donald 1951).

(iv) overgrazing causing poor root development and poor drought resistance (White 1973).

Whatever its origin, it indicated that plant number and botanical composition in spring may not represent relative germination of the various species.

Hutchinson (1969) at Armidale working on *Phalaris tuberosa* - *Trifolium repens* pastures found a seasonal rhythm in tiller numbers per unit area, with peak values in spring (6000 tillers per square metre). This rhythm was strongly influenced by stocking level

Table 1. The relation between the number of plants m^{-2} during the growing season and stocking rate.

Author	Sheep rate (sheep ha^{-1})	Date of count	Year of experiment	Species: Sub Clover	Species: Rye-Grass	Species: Other	Total
				number of plants m^{-2}			
Carter (unpublished)	7.5 (3)⁄	28.3.66	4	600	10600	300	11500
		10.5.66		1500	5100	100	6700
	15.0 (6)	28.3.66	4	1000	7100	1000	9100
		10.5.66		2400	3800	300	6500
	22.5 (9)	28.3.66	4	900	700	1400	3000
		10.5.66		700	300	200	1200
Sharkey et al. (1964)	2.5 (1)	16.8.62	3	725	9550	250	10525
		1.11.62		450	4575	0	5025
	7.5 (3)	16.8.62	3	1075	2900	1300	5275
		1.11.62		975	2050	525	3550
	15.0 (6)	16.8.62	3	8	8	9050	9066
		1.11.62		0	50	250	*300

⁄ Stocking rate in units of sheep per acre as shown in parentheses.

* Stock were removed from plots from April 1961 to September 1961.

provided rainfall was adequate. This suggests that increased tillering capacity of grasses to a certain extent may compensate for a deficiency in plant numbers. However, the extent of this substitution of tillers for plants in different grazing situations is unknown.

Tillering of grasses was discussed in an earlier section 2.2. Furthermore the size of a plant may affect its survival under stress (Hoen 1968). Accordingly, development of techniques which recognise the integration of tillers in grass plants must provide us with greater insights into processes operating within grass swards.

Few estimates of seed or plant numbers in temperate, grazed pastures are available. Smith (1972) and Gramshaw and Stern (1977a) have measured populations of 20000 to 25000 seeds per square metre (equivalent to sowing 700 kg seed ha^{-1}) in grazed annual pastures in autumn. Data from several authors who measured plant numbers at the beginning of several seasons in continuously grazed annual pastures stocked at various levels is presented in Table 2.

At the beginning of the season if stock numbers were very high during the preceding seasons seed yield is progressively reduced. The range in values recorded by Sharkey et al. (1964) in Victoria (275-5000 plants m^{-2}) is numerically below that of Carter's figures at equivalent stocking pressure (9200-12800 plants m^{-2}). This could be due to many factors, such as site differences in soil moisture, fertility and initial seed reserves. The results of Sharkey et al. (1964) indicate the 'crash point' as defined by Morley (1966b) is reached when plant numbers are between 275 and 2225 m^{-2}. Carter and Day (1970) also associated depressed pasture

Table 2. The relation between autumn plant numbers per m^2 and time and stocking rate on continuously grazed annual pastures.

Author	Stocking rate (sheep ha^{-1})	Year of experiment	Species: Sub Clover	Species: Rye-Grass	Species: Others	Total
Willoughby (1954)	'light'	3	500	6500	N.A.	7000
		10	3250	125	N.A.	3375
Carter (unpublished)	7.5 (3)⸸	2				12800
		4	600	10600	300	11500
	15.0 (6)	2				9900
		4	1000	7100	1000	9100
	22.5 (9)	2				3700
		4	900	700	1400	3000
Sharkey *et al.* (1964)	2.5 (1)	1	1100	1400	75	2575
		3	5000	4500	NIL	5000
	7.5 (3)	1	750	1650	625	3025
		3	1000	2075	600	3675
	15.0 (6)	1	500	1100	625	2225
		3	NIL	200	75	275*

⸸ Sheep numbers per acre are shown in parentheses.

* Stock were removed from plot from April 1961 - September 1961 plus fed hay supplement to maintain 40 kg (90 lbs) minimum live weight.

production at medium and high stocking rates with a reduction of plant density. Waddington and Storgaard (1971) found that reduction in bromegrass seed yield was associated with reductions in tiller density and growth rate. The above data suggest that stability, at least in high rainfall situations, is likely to be promoted by high stand density. However the levels of production achieved by the stable pasture may not always be high (Morley 1966a).

Many experiments have been conducted where stocking rate has been varied on pastures presumably of similar initial plant density (McMeekan 1956; Davies et al. 1966; Brown 1976). Few, if any workers have purposefully varied plant density on pastures continuously grazed at a constant level in order to examine the affects of plant density on animal production.

2.6 Conclusion

The need for a continuous supply of fuel from a dynamic plant community for a relatively stable number of grazing animals poses one major problem in the formulation of grazing management practices. It has to be accepted that the attainment of maximum nutrient intake is a limited objective, and that efficiency in grazing management depends very much upon the balance between maximum intake, maximum herbage production and utilisation. It is still not possible to provide this information for a truly objective decision on the appropriate balance for a particular livestock enterprise (Hodgson 1977).

Accurate knowledge of animal responses to feed shortages and to changes in herbage availability and plant density in annual pastures should provide biological bases to aid management decisions aimed at alleviating feed shortages and achieving stable production systems.

The studies reported in this thesis examined animal responses to feed shortage and the impact of high and low grazing pressure on plants in annual pastures in the wheat/sheep zone in South Australia.

Experiment 1 was a study of competition for feed between ewes and lambs grazing pastures of different herbage availabilities sown at the one seeding rate. Competition between animals for herbage was assessed in terms of changes in sheep live weight, lamb intake and components of intake. The influence of different classes of stock on the tiller length of swards was also assessed.

Experiment 2 was undertaken to study the influence of seeding rate and the resultant plant population on animal performance and herbage yield from annual swards. Here both seeding rate and consequently herbage availability were varied and the animal population held constant. A further objective was to study those sward characteristics (e.g. plant density and weight, tiller length, tiller number per plant, digestibility) and yield associated with stable and unstable grazing systems and to define the situations in which any deficiency in one sward characteristic could be compensated for by an increase in another. A subsidiary experiment was also conducted to compare the growth of pasture and changes in plant components in grazed and ungrazed swards over a wide range of densities.

3. THE ENVIRONMENT

3.1 General description

3.1.1 Location

The experiments were conducted at the Mortlock Experiment Station (latitude 33°55'S, longitude 138°43'E and altitude 440 metres above sea level), Mintaro, South Australia. This station which is 120 kilometres north of Adelaide and 15 kilometres south east of Clare (see Figure 1) is situated in the wheat-sheep zone (as defined by the Bureau of Agricultural Economics 1976) of southern Australia.

3.1.2 Climate

The climate of the region is typical of the southern Mediterranean-type environment described by Donald and Allden (1959). Mean annual rainfall at Mintaro over an 85-year period from 1890 to 1975 was 603 mm of which 72% fell in the 6 months from May to October (Table 3a). The effective rainfall season is 7.5 months (Trumble 1948). Winter rains are of high reliability and usually commence in the April-May period and end between October and December. Pasture growth is closely associated with rainfall although other factors such as low light intensities and low temperatures may restrict plant growth during the winter months (Stern and Donald 1962; Smith 1972; Cocks 1973). Rainfall at Mintaro and at the Mortlock Experiment Station together with monthly temperatures for Clare are summarized in Tables 3a, b and c, respectively.

Summer rainfall in the Mediterranean environment of southern Australia is usually inadequate to support any significant plant growth. Dry herbage carried over from the previous spring declines rapidly

Figure 1. Annual rainfall map of the central districts of South Australia. Average annual rainfall over 100 years, 1866-1966. Rainfall isohyets are shown in millimetres.

ANNUAL RAINFALL MAP OF CENTRAL DISTRICTS OF SOUTH AUSTRALIA
Average over 100 years to 1966

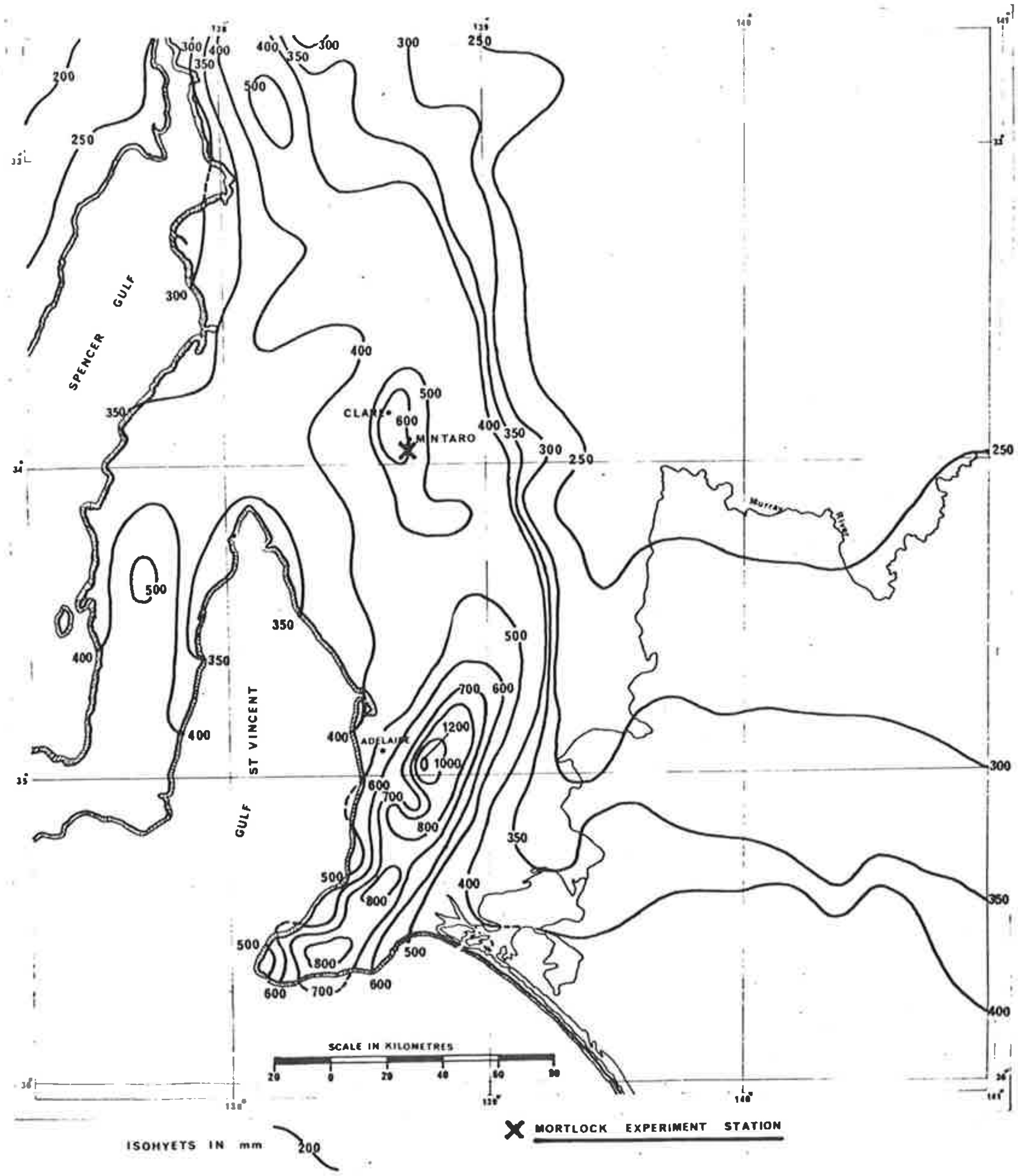


Table 3a. Rainfall (mm) and number of raindays for Mintaro over an 85-year period from 1890-1975.

Variable	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
Rainfall (mm)	21	24	22	39	72	76	79	84	69	55	34	28	603
No. of raindays	3	4	4	6	10	12	15	14	11	8	6	4	97

Table 3b. Rainfall data (mm) for Mortlock Experiment Station for the period 1970-1975.

Year	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
1970	45	-	15	31	68	74	43	116	82	7	35	32	552
1971	4	6	47	68	72	75	30	144	59	23	79	18	623
1972	82	55	-	38	17	33	76	113	20	37	12	4	486
1973	10	140	27	55	51	84	75	81	58	121	51	16	768
1974	79	47	59	69	125	32	140	70	75	104	10	5	816
1975	23	1	41	17	69	6	84	49	97	137	21	22	574

Table 3c. Mean monthly temperature (^{o}C) at Clare over a 52-year period (Bureau of Meteorology 1966).

Temperature	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
Maximum	29	29	26	21	17	14	13	15	17	21	25	28	21
Minimum	13	14	12	8	6	5	3	4	5	8	10	13	8
Mean	20	22	19	15	11	9	8	9	11	14	18	20	15

in quantity and quality during the summer and in general contributes little to the sheep's diet after the advent of the winter rainfall period.

3.1.3 Soils, vegetation and land use

The principal soil of the region is a red-brown earth (Mulcahy 1954). Cultivation and fairly intensive grazing have left little trace of the original vegetation of the area. On the deeper red-brown earths of the rolling to hilly country which comprises most of the property and the region, the dominant tree species is *Eucalyptus leucoxylon* with *Casuarina stricta* on the shallow, stony, well-drained soils of the hill-tops (Mulcahy 1954). The plant community which consists of a few shrubs and a grassy ground flora is a vegetational climax (Wood 1937).

The Experiment Station land was periodically cropped in the late 1800's and early 1900's and thereafter reverted to sheep grazing land carrying unimproved volunteer pastures until 1965. Since that time a cereal-pasture rotation has been practised on most of the area with Wimmera ryegrass (*Lolium rigidum* Gaud.) and subterranean clover (*Trifolium subterraneum* L.) being the two sown pasture species. Superphosphate has been applied at the rate of 210 kg ha^{-1}, every year since 1965 to both improved pastures and cereal crops.

The first experiment reported in this thesis was conducted on an area of shallow, brown soil in the south-western corner of the station. From 1965 to 1969 this paddock received a total of 1050 kg ha^{-1} of superphosphate.

Experiment 2 was conducted on an area of red-brown earth adjacent to experiment 1. From 1965 to 1970 the area had received a total of 1260 kg ha^{-1} of superphosphate.

4. EXPERIMENT 1

4.1 Objectives

The first experiment was designed to examine the influence of herbage availability on the intake and productivity of weaned and sucking lambs, and to study the effects of weaning on the use of pasture and the partition of energy between ewe and lamb. When the lamb is weaned all competition for feed between the dam and her progeny is removed. However, within the confines of any production unit the area normally grazed by both animals must be apportioned between the weaned lamb and its dam, thus removing direct competition for feed. Since the lamb is deprived of its milk supply it presumably needs additional feed to compensate for this loss. Concurrently the ewe, now grazing a smaller area than that occupied by the ewe/lamb unit might place greater grazing pressure on the plant community, influencing intake, the amount of pasture present and plant growth. A study of these changes in the weaned and unweaned ewe/lamb units was undertaken to provide a measure of the influences of early weaning and herbage availability on the factors under study, namely, animal growth, energy retention, the intake of milk and pasture by the lamb, the components of pasture intake, and changes in pasture yield with time. A further objective was to estimate the partition of energy between ewe and lamb under conditions where the supply of herbage and weaning practice varied.

In grazing situations herbage supply is continually influenced by grazing pressure, seasonal growing conditions and botanical composition. Thus when assessing a management practice it is often not possible to separate the influence on the animal of current herbage availability from previous availability. Experiment 1 was designed to reduce the confounding effects of seasonal fluctuations in the quality of pasture by conducting the trial at a time of the year when quality was likely to be uniformly high and by presenting to the animals at the same time pastures which yielded different amounts of herbage per unit area.

4.2 Experimental design

4.2.1 Establishment of swards and herbage availabilities

The aim was to prepare areas of pasture in advance of the period of observation so that at a given time there would be five swards in the vegetative stage of growth each with a different amount of herbage present, ranging from sparse to abundant.

A uniform area of 6.4 ha was sown to Wimmera ryegrass (at 15 kg seed ha^{-1}) on May 21st, 1970. This pasture was heavily grazed in August and subsequently stocked at a level to maintain plant height at approximately 5 cm. The area was then subdivided; half (termed the reserve area) being used by the experimental animals in a period of uniform grazing before the experiment began. Five plots were selected at random from the remaining portion to become the five availability treatments.

The swards of five different availabilities were obtained by removing sheep from the plots at progressively later dates, different periods of regrowth thus being obtained (Allden and Whittaker 1970). Before the regrowth commenced, each plot was mowed with a gang mower to minimize the variation in yield within plots. The interval between closing one plot and the next was based on visual assessment of pasture growth rather than by a predetermined schedule.

Two such areas each containing five 0.2 ha plots were prepared. They were not used concurrently, the time of operations being so arranged that after the first area had been used (phase 1 of the experiment) observations were commenced on the second (phase 2).

4.2.2 Experimental animals and grazing treatments

Eighty-two Border Leicester X Merino ewes were joined with 2 Dorset Horn rams for 6 weeks from March 3rd, 1970. Thereafter the ewes were run on a ryegrass dominant pasture till lambing in August-September 1970.

Each lamb was weighed, ear tagged and tailed at birth. Male lambs were castrated on September 9th. From the flock a group of 40 single wether lambs and their dams was selected for the grazing experiment. They grazed on the reserve area of sown ryegrass pasture from September until the start of the experiment on October 5th, 1970. This flock was divided into 10 groups each of 4 ewes and lambs on the basis of lamb age and live weight data measured in the pre-experimental period. At each herbage availability one ewe/lamb group was allocated to the weaned treatment, one to the unweaned treatment. Lambs allocated to the weaning treatments were weaned on September 28th (at an average age of 5 weeks) one week before the beginning of the experiment. Thus there were two weaning treatments (weaned and unweaned) at five different herbage availabilities. Twenty ewe lambs from the flock were prepared with oesophageal fistula using the method of McManus et al. (1962) on September 14th, 1970. These fistulated ewe lambs were used during the experiment for sampling herbage from the experimental plots (Section 4.3.2).

4.2.3 Treatments

Pastures of five different herbage availabilities were obtained as described in Section 4.2.1. Each of these availability plots was subdivided, with 4 ewes and 4 lambs grazing on half of the area (0.1 ha). The remaining portion was further subdivided with one half (0.05 ha) being grazed by 4 weaned lambs and the remaining portion (0.05 ha) was grazed by 4 dry ewes. Thus the area grazed by each of the latter two treatments was half that grazed by the ewe/lamb combination i.e. the number of animals per unit area was always constant (80 animals ha^{-1}) but the amount of pasture differed.

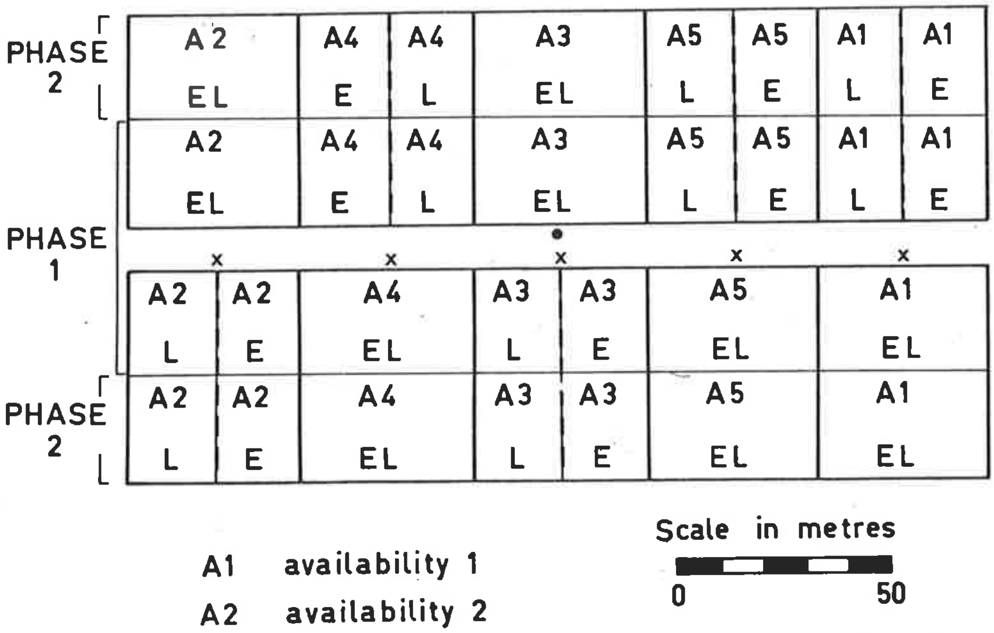
Two areas each with five availabilities were prepared. After the experimental animals had grazed the first area for two weeks (phase 1 of the experiment) they were moved to the second area and observations commenced (phase 2). The aim was to present at each level of herbage availability, a similar initial level of herbage on offer to each grazing flock at the start of each phase. A summary of the treatments is given in Table 4 and a diagram of the arrangement of the treatment groups in the field is shown in Figure 2.

Table 4. Design of Experiment 1.

Five nominal levels of pasture availability		X	Three grazing treatments	X	Two periods of grazing (phases) +
Low	1.		1. Weaned lambs		Phase 1
	2.				October 5th to October 21st
	3.		2. Dry ewes		
	4.				Phase 2
High	5.		3. Lactating ewes and sucking lambs		October 22nd to November 6th

+ Data for each phase were analysed separately

Figure 2. Plan of the experimental area showing the treatments in Experiment 1.



A1 availability 1
A2 availability 2
A3 availability 3
A4 availability 4
A5 availability 5
• shed
x pens

L weaned lambs
E dry ewes
EL lactating ewes + sucking lambs

4.3 Measurements

Pasture components and animal factors were measured concurrently in order to examine relationships between the plant community and the grazing animals within the different management practices. The variables measured in phases 1 and 2 of the experiment are shown in Table 5.

4.3.1 Plant measurements

The availability of pasture to the grazing animal was estimated at weekly intervals by measuring (a) total herbage dry matter yield on offer, (b) tiller length and (c) the relative rate of tiller length change.

(a) Herbage yield

The yield of dry matter (DM) per unit area was estimated using the visual estimation method of Morley *et al.* (1964). Campbell and Arnold (1973) found this method suitable for estimating the yield of pastures differing widely in yield, botanical composition and density. Dry matter yield was also estimated by the electronic capacitance probe method of Bach *et al.* (1969) in order to compare results with those obtained by the visual method.

(b) Tiller length (TL)

A hundred tillers per plot were sampled at random and measured to determine mean tiller length as described by Allden and Whittaker (1970). Tiller length is the length from the base of a tiller to the

Table 5. Variables measured in Experiment 1.

Variables measured[≠]
(i) Plant
(a) Total herbage dry matter yield on offer (availability)
(b) Tiller length (TL)
(c) Relative rate of tiller length change (TLC)
(ii) Animal
(a) Live weight and growth rate of ewes and lambs
(b) Body energy*
(c) Daily intake of herbage and its digestibility
(d) Milk intake of sucking lambs
(e) Digestible energy (DE) intake of grass and milk by lambs
(f) The utilization of dietary energy by lambs
(g) Grazing time and the daily rate of herbage intake*
(h) Potential rate of herbage intake

≠ All variables were measured in both phase 1 and 2 except for TLC and the components of intake (g, h) which were measured in phase 1 only.

* Derived variables.

tip of the longest leaf.

(c) Relative rate of tiller length change

The tiller length measurements taken on two occasions in phase 1 were used to calculate the relative rate of tiller length change with the object of estimating the influence of grazing by ewes and/or lambs on the relative size of the plant pool. The relative rate of tiller length change was defined as the difference between the natural logarithms of tiller length present at day 2 and day 16, divided by time (days).

4.3.2 Animal measurements

(a) Live weight and growth rate of ewes and lambs

Ewes and lambs were weighed at approximately weekly intervals during the experiment after being confined overnight in small pens. The live weight changes of ewes and lambs were estimated over a 33 day period from October 5th to November 7th, 1970.

(b) Body energy

Estimates of body energy were used in order to compare the partition of energy between ewe and lamb in the different treatments. The energy of weight change of ewes and lambs differs by about two-fold (Hutchinson 1969; Allden 1970b) and the values reported by these workers were used in relating body energy (Y, mcal) to weight change (Y, kg) using the equations:

(i) for ewes, $Y = 116.0 + 6.19X \quad r^2 = 0.96$ (Hutchinson 1969),

(ii) for lambs, $Y = 27.95 + 3.12X \quad r^2 = 0.97$ (Allden 1970b).

Body energy estimated in this way was considered to be the most simple method of taking into account the energy differences of weight change in ewes and lambs.

(c) Daily intake of herbage by lambs and its digestibility

The total daily intake of herbage (I) by grazing lambs was estimated from measurements of the faecal output (F) and herbage digestibility (D), being calculated from the expression:

$$I = F \times \frac{100}{100-D}$$

(i) <u>Faecal output of lambs</u>

During the three weeks before they entered the experiment wether lambs were fitted periodically with faecal collection harnesses to accustom the animals to wearing the apparatus. Lambs were then fitted with faecal collection harnesses on day 1 of phase 1 for the duration of the experiment. Collection bags were attached whenever it was required to collect faeces. Faecal collections were made daily from all lambs for a 4 day period in phase 1 and for 3 days in phase 2.

The total output of faeces of each lamb was collected daily, frozen and stored at -4°C. The dry weight for each sample was subsequently determined after drying in a forced draught oven at 85°C for 48 hours. Faecal samples obtained over each collection period were bulked for each lamb, then ground and subsampled. The subsample was analysed for ash by ignition at 550°C overnight in a muffle furnace and the total organic matter (OM) content of the faeces determined. The intake of digestible organic matter (DOMI) was then calculated.

(ii) Digestibility of herbage consumed by lambs

The digestibility of herbage ingested by lambs was estimated by collecting dietary samples using oesophageally fistulated (O.F.) lambs. The *in vitro* digestibility of each sample was determined by the method of Tilley and Terry (1963).

Twenty ewe lambs from the experimental flock were used as diet sampling animals, see Section 4.2.2.

Ten O.F. lambs remained with their dams and were used for obtaining dietary samples on those plots carrying sucking lambs. The remaining 10 O.F. lambs were weaned on September 29th for use on the weaned lamb plots. This procedure was adopted in order to minimize differences in diet selection between weaned and unweaned lambs. The O.F. flock grazed the Wimmera ryegrass pasture in the reserve area adjacent to the experiment plots throughout the experiment, except when samples were being collected on the treatment plots.

In phase 1, a subsidiary experiment was carried out to determine if there were any significant differences in the *in vitro* digestibility of the grass consumed by weaned and sucking lambs. The experiment was of latin square design and comprised 5 diet sampling flocks (each of two O.F. lambs) X 5 days of sampling X 5 availabilities X 2 lamb classes (weaned versus sucking).

In phase 2 of the main experiment a different diet sampling procedure was used. Flocks of 3 O.F. lambs were placed at random on each plot on alternate days of the 4 day collection period. Thus the herbage of each plot was sampled by a total of 6 O.F. lambs over a 3 day period.

The method of collection and processing samples was identical on all occasions. The O.F. lambs were yarded and fasted in the morning preceding each afternoon collection period. Extrusa samples were collected in calico bags secured around the neck by spring clips. On the rare occasions that sheep regurgitated rumen contents the sample was discarded. A sufficient dietary sample was usually obtained in 15-30 minutes grazing. However it was often necessary to prolong the grazing time of O.F. sheep on plots of the lowest availability in order to obtain sufficient extrusa for chemical analysis.

Extrusa samples were kept in cold storage immediately after collections and taken to the laboratory to be oven dried at 80°C in a forced draught oven for 24 hours. The oven dried material was then ground through a 1 mm sieve for *in vitro* digestibility determinations by the method of Tilley and Terry (1963).

The organic matter content of all dietary herbage samples was estimated from the loss in weight of dietary and digested samples when ashed overnight at 550°C in a muffle furnace. Digestibility of the organic matter was then calculated.

Standards of known *in vivo* organic matter digestibility (OMD) were included in each run and regression equations relating *in vitro* to *in vivo* OMD were calculated and used to adjust the digestibility values obtained for each extrusa sample using the method described by Langlands (1966). These standards covered a similar range in digestibility as the fistula samples. The residual standard deviations for the regression equations ranged from 1.3 to 2.0 units of OMD which compare favourably with a range from 1.4 to 2.9 units obtained by Langlands (1966). The *in vitro* digestibility values were then used in conjunction with the faecal output data to determine OM intake.

(d) Milk intake of sucking lambs

Milk production of the ewes was measured over a 4-hour interval on 4 occasions at weekly intervals by the oxytocin technique of McCance (1959). The weight of milk produced in 4 hours was measured and adjusted to a 24 hour basis (grams day^{-1}). An assumption was made that lamb milk intake and ewe milk production came into equilibrium shortly after parturition (Corbett 1968a; Langlands 1972).

(e) Digestibility energy (DE) intake of grass and milk by lambs

The daily organic matter intake of milk and grass by lambs was estimated by methods similar to those of Langlands (1972), except that the OMD of the grass was not reduced by three units.

The energy content of ewe's milk was taken as 6.5 kJ (1.55 kcal) per gram of fresh milk (Perrin 1958). The DE intake of milk was calculated on the basis that the OM content of the dry matter of ewe's milk was 96% and the OMD digestibility 98% (Hodge 1966b; Joyce and Rattray 1970; Jagusch and Mitchell 1971; Langlands 1972). The indigestibility of the milk OM in these experiments was 2% and this value was used to estimate the proportion of faeces OM of milk origin (after Langlands 1972).

Estimation of the herbage DE intake by sucking lambs was based on the following assumptions:-

(1) herbage OMD was independent of the quantity of milk consumed (Gardner *et al.* 1964; Hodge 1966b), and,

(2) the energy content of Wimmera ryegrass was 19.7 kJ (4.7 kcal) per gram of digestible organic matter (Kellaway 1969).

The DE intake of grass by weaned lambs was estimated in a similar way but no correction of the faecal output for milk consumption was necessary.

(f) The utilization of dietary energy by lambs

The objective was to describe and compare the utilization of dietary energy by weaned lambs (grass diet only) and sucking lambs (grass plus milk diet). Adjustments were made for the increased efficiency of utilization of milk DE compared to grass DE for weight gain. The factors used to adjust for the milk intake and the reasons underlying their adoption were as follows:

(1) Ewe's milk is metabolized with an efficiency of 95%; metabolized energy (ME) is used with an efficiency of 70% for both maintenance and gain (ARC 1965; Jagusch and Mitchell 1971).

(2) The DE of a grass diet is metabolized with an efficiency of 82% (Armstrong *et al.* 1964; ARC 1965); the ME is used with a 70% efficiency for maintenance (ARC 1965) and with a 45% efficiency for gain (Allden 1970b).

(3) Milk and grass DE were assumed to be used for maintenance and/or gain in the ratio that they occurred in the diet.

On the basis of the above values the DE intake of milk for maintenance was multiplied by a factor of 1.16 and the DE intake of milk in excess of maintenance by a factor of 1.80 in order to convert the DE intake of milk to DE intake of grass, thus permitting a comparison of the total DE intake of all lambs in relation to liveweight gain.

(g) Grazing time and the daily rate of herbage intake

Measurements were made of the components of intake, namely the time spent grazing and the rate of herbage ocnsumption to examine the influence of weaning on grazing behaviour at different herbage availabilities.

(i) Grazing time

The time spent grazing by each lamb was determined by visual observation over a 36 hour period during phase 1 of the experiment. Observations of each lamb were taken at 10 minute intervals and a record was kept as to whether the lamb was grazing or not. Total grazing time was then determined from the sum of the number of 10 minute intervals in which each sheep grazed during a continuous 24 hour period (after Whittaker 1965).

Observation at night was simplified by the use of coloured fluorescent tapes on the faecal harness of the sheep (as used by Whittaker 1965) - see Plate 1. Four different coloured tapes enabled easy identification by spotlight of each of the four lambs on each plot.

Plate 1. A view of weaned lambs (24 kg live weight) grazing on availability 3 pastures of tiller length 12 cm (plot 4) in phase 1. Note the fluorescent colours on the lamb's back for identifying individual sheep at night when measuring grazing time.

(ii) Daily rate of herbage intake

The rate of herbage intake expressed in g OM per minute was derived by dividing the total herbage OM intake per day by the time spent grazing.

(h) Potential rate of intake by lambs

Allden and Whittaker (1970) measured the rate of intake of herbage by grazing lambs on pastures of different availability. Their method estimates the rate of intake of a hungry sheep in its first hour of grazing, a value which expresses the potential rate of intake which may not be sustained during the full daily grazing period. Therefore the value of the technique was examined in this experiment in relation to the intake and the rate of intake data measured over the full daily grazing period.

The potential rate of herbage intake was then estimated from weight changes of fasted lambs which were recorded during a measured period of approximately one hour (after Allden and Whittaker 1970). Lambs were weighed to the nearest 10 grams before and after grazing by slinging from an Avery balance (capacity 50 kg, chart 500 x 5 g).

4.3.3 Summary of sampling procedures

A schematic outline of the experiment showing the main events during the course of the experiment are shown in Table 6. Sheep were weighed on day 1 and thereafter at approximately weekly intervals. In phase 1, plots were sampled for pasture yield and tiller measurements on days 2 and 3 and this was repeated at weekly intervals. The potential rate of herbage intake, grazing time and the total daily intake of milk and grass by lambs were estimated between pasture harvests. Sheep were weighed on day 17 and moved to new plots for

Table 6. Schematic outline of the sampling programme in Experiment 1.

Day of Experiment	Date			
		PHASE 1		
1	5/10	Weigh sheep and allocate to phase 1 plots		
2	6/10	Pasture		
3	7/10	Sampling (harvest 1)		
4	8/10	Measure potential rate of herbage intake		
5	9/10	Measure milk production		
6	10/10	Measure grazing time		
7	11/10			
8	12/10	Weigh sheep		
9	13/10	Pasture sampling		
10	14/10	(harvest 2)	Collection	Collection of
11	15/10		of faeces	O.F.
12	16/10		from lambs	samples
13	17/10			
14	18/10			
15	19/10	Measure milk production		
16	20/10	Pasture sampling (harvest 3)		
17	21/10	Weigh sheep		
		PHASE 2		
17	21/10	Move to new plots		
18-28	22/10 to 2/11	Initial 10 day period on plots		
29	2/11	Weigh sheep		
30	3/11	Pasture sampling (harvest 4)	Collection of faeces from lambs	Collection of O.F. samples
31	4/11			
32	5/11	Measure milk production		
33	7/11	Weigh sheep		

phase 2 of the experiment. From days 30 to 33 the plots were sampled for pasture yield and tiller measurements, and the daily intake of herbage and milk by lambs was measured.

4.3.4 Statistical analysis of the data

(a) Plant and animal data

Most of the data were analysed in an analysis of variance (Steele and Torrie 1960), the aim being to test for significant differences between the herbage availability and class of stock treatments and for significant interactions.

Least significant difference (LSD) values have been used in preference to Duncan's multiple range test (DMR) for examining differences in treatment values. A computer simulation programme (Atkinson and Chambers pers. comm.) showed that when no differences were significant the LSD classified no more of these as significant than the DMR, but a greater sensitivity was evident when the F test was significant. The values of any variable that are followed by different alphabetic subscripts differ by more than the appropriate LSD at $P \leqslant 0.05$.

(b) Plant/animal interrelationships

Regression analysis was used to relate herbage intake (Y) of lambs and the total intake of milk plus herbage by sucking lambs to tiller length (X). The model used was similar to that of Hamilton et al. (1976):

$$Y = A + BX + C\sqrt{X} + DX^2.$$

where A, B, C and D are constants. The equation was fitted by a stepwise regression technique as described by Draper and Smith (1967). The variables $\sqrt{X}$ and X^2 were force fitted, so that $\sqrt{X}$ or X^2 would not alternate between different equations, according to which happened to be fractionally better. The values fitted were those that applied on the individual plots.

Components of intake, namely the potential and daily rate of herbage intake (Y) were related to tiller length (X) by the model:

$$Y = A + BX + C\sqrt{X}.$$

Where A, B and C are constants these equations were calculated as above.

Grazing time was related to tiller length in a curvilinear fashion. A technique for fitting non linear functions involving iterative methods to minimise the sum of squares (Hill pers. comm.) was used to relate sheep grazing time (Y) to tiller length (X). The model used was:

$$Y = A + \frac{B}{X - C}$$

where A, B and C are constants. Nelder's (1961, 1962) simpler procedure for fitting the non linear regression surface was used.

4.4 Results of Experiment 1

Some comment is needed on the order of presentation of the results. Changes in herbage availability and the levels of animal production resulting from the different treatments are first presented in Section 4.4.1, and the areas in which significant responses were observed to characters of the sward and to weaning practice are defined. These results are discussed in relation to the different management practices. Measurements of lamb intake and its utilization for lamb growth are recorded in Sections 4.4.2, 4.4.3 respectively. The components of herbage intake, namely grazing time and rate of intake are described in Section 4.4.4 and the digestibility of herbage consumed by weaned and sucking lambs grazing swards of different availabilities is given in Section 4.4.5.

4.4.1 Herbage availability and animal production

(a) Herbage availability

The measures taken to produce five swards or markedly different availability at the beginning of the experiment were successful, tiller length values for the different plots being:-

Nominal availability	Tiller length (cm) at harvest 1
1	3.5
2	7.2
3	11.9
4	24.5
5	50.6

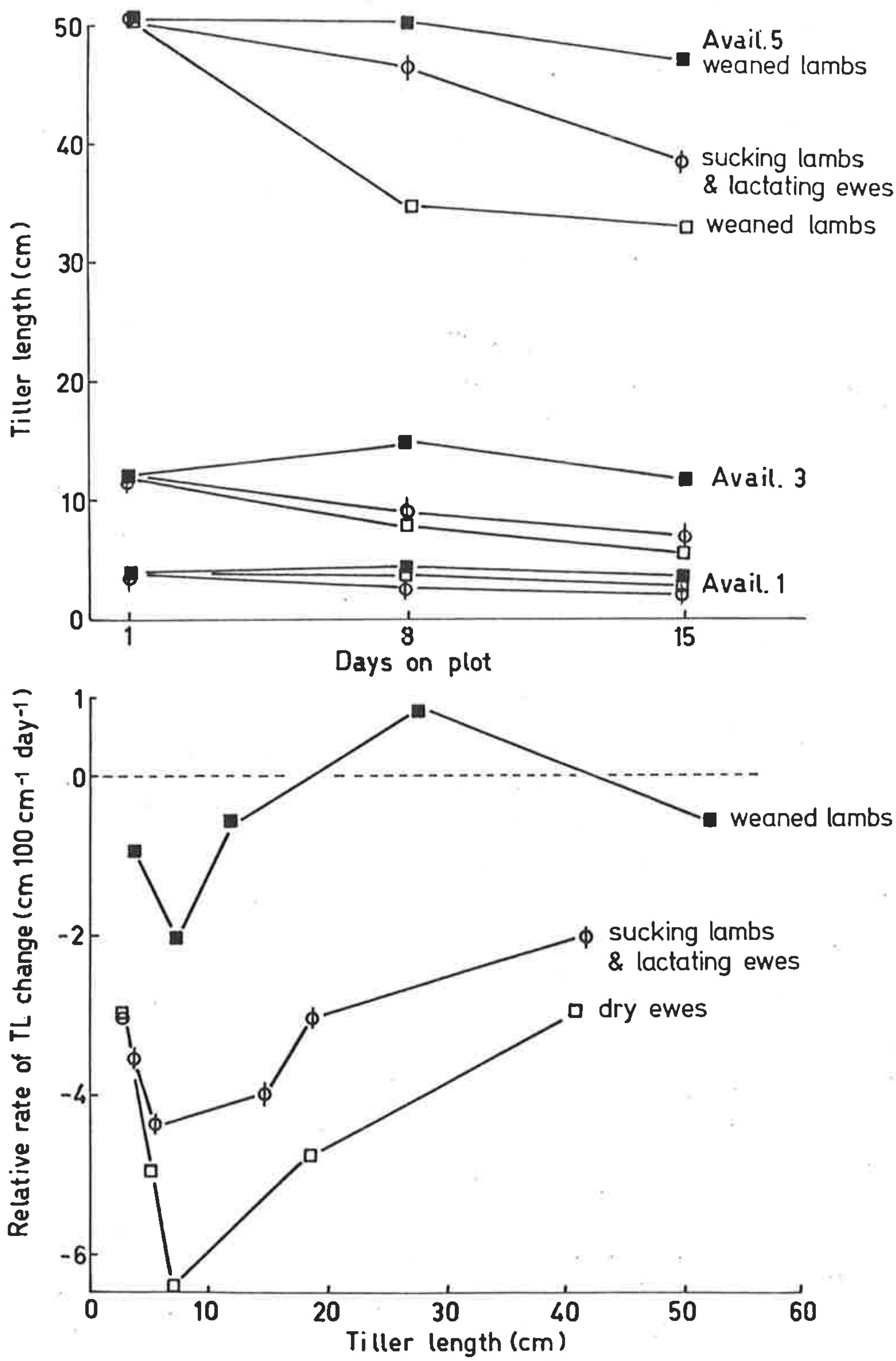
Tiller length (TL) was highly correlated with the total yield of herbage dry matter (DM) present at all harvests (Appendix Table 1) so that the two variables are largely interchangeable. Tiller length will be used as the measure of availability of herbage to the grazing animal. The coefficients of variation of tiller length measurements increased from 8 to 33 percent as the tiller length decreased from 50 to 5 cm (Appendix Figure 1). This suggests that the variability of tiller length is greatest in short swards.

Ewes with or without lambs substantially reduced the pasture available, whereas the weaned lambs had little effect on the amount of herbage present (Figures 3 and 4). This greater reduction of available herbage by the ewe compared to the lamb was highly significant ($P < 0.001$) both in terms of absolute changes in tiller length with time (Table 7) and in terms of the relative rate of tiller length change (Table 8). As time progressed the differences in tiller length diverged as a consequence of differences in grazing pressure by the different classes of stock (Figure 3), consequently a significant interaction between class of stock and occasion (or time) was noted in Table 7. However, the relative rate of tiller length change was not significantly affected by herbage availability (Table 8); the grazing pressure imposed by different classes of stock was the dominant influence (Table 8).

These results show that when an area was divided equally between a ewe and her lamb, the grazing pressure of the ewe was greater and of the lamb less than when the ewe/lamb unit grazed the whole area together.

Figure 3. Time trends in the tiller length of swards of different initial availabilities when grazed by different classes of stock in phase 1. The two extreme treatments (availability 1 and 5) and the intermediate treatment (availability 3) were selected for ease of presentation of data.

Figure 4. The relationship between the relative rate of tiller length change (TLC) and tiller length in swards grazed by different classes of stock in phase 1.



Avail.5
weaned lambs
sucking lambs
& lactating ewes
weaned lambs
Avail. 3
Avail. 1
Tiller length (cm)
Days on plot
Relative rate of TL change (cm 100 cm-1 day-1)
weaned lambs
sucking lambs
& lactating ewes
dry ewes
Tiller length (cm)

Table 7. Analysis of variance and means of the tiller length (cm) of swards on three occasions when grazed by different classes of stock in phase 1.

Source of variation	DF	Mean square	F	Probability
Availability	4	2570.5	431.6	***
Class of stock	2	69.5	11.6	***
Occasion	2	94.8	15.9	***
Availability X class	8	12.0	2.0	n.s.
Availability X occasion	8	12.6	2.1	n.s.
Class X occasion	4	19.6	3.3	*
Residual	16	5.5		

Means

Nominal availability

1	2	3	4	5	LSD
3.1a+	5.8b	9.9c	21.2d	44.8e	2.4

Class of stock

Weaned lambs (L)	Sucking lambs + lactating ewes (EL)	Dry ewes (E)	LSD
19.2a	16.5b	14.9b	1.9

Occasion

Day 1	Day 8	Day 15	LSD
19.5a	16.6b	14.6c	1.9

n.s. = not significant, *P < 0.05, **P < 0.01, ***P < 0.001.

\+ Means with different subscripts within rows are significantly different at P < 0.05.

Table 8. Analysis of variance and means of the relative rate of tiller length change (TLC, cm 100 $cm^{-1} day^{-1}$) during phase 1.

Source of variation	DF	Mean square	F	Probability
Availability	4	2.2	2.2	n.s.
Class of stock	2	18.6	18.6	***
Residual	8	1.0		

Means

Nominal availability

1	2	3	4	5	LSD
-2.5a+	-3.8a	-3.6a	-2.3a	-1.9a	n.s.

Class of stock

Weaned lambs	Sucking lambs + lactating ewes	Dry ewes	LSD
-0.7a+	-3.4b	-4.4b	1.4

n.s. = not significant, *P < 0.05, **P < 0.01, ***P < 0.001.

\+ Means with different subscripts within rows differ significantly at P < 0.05.

(b) Animal production

(i) Liveweight and body energy changes of ewes and lambs

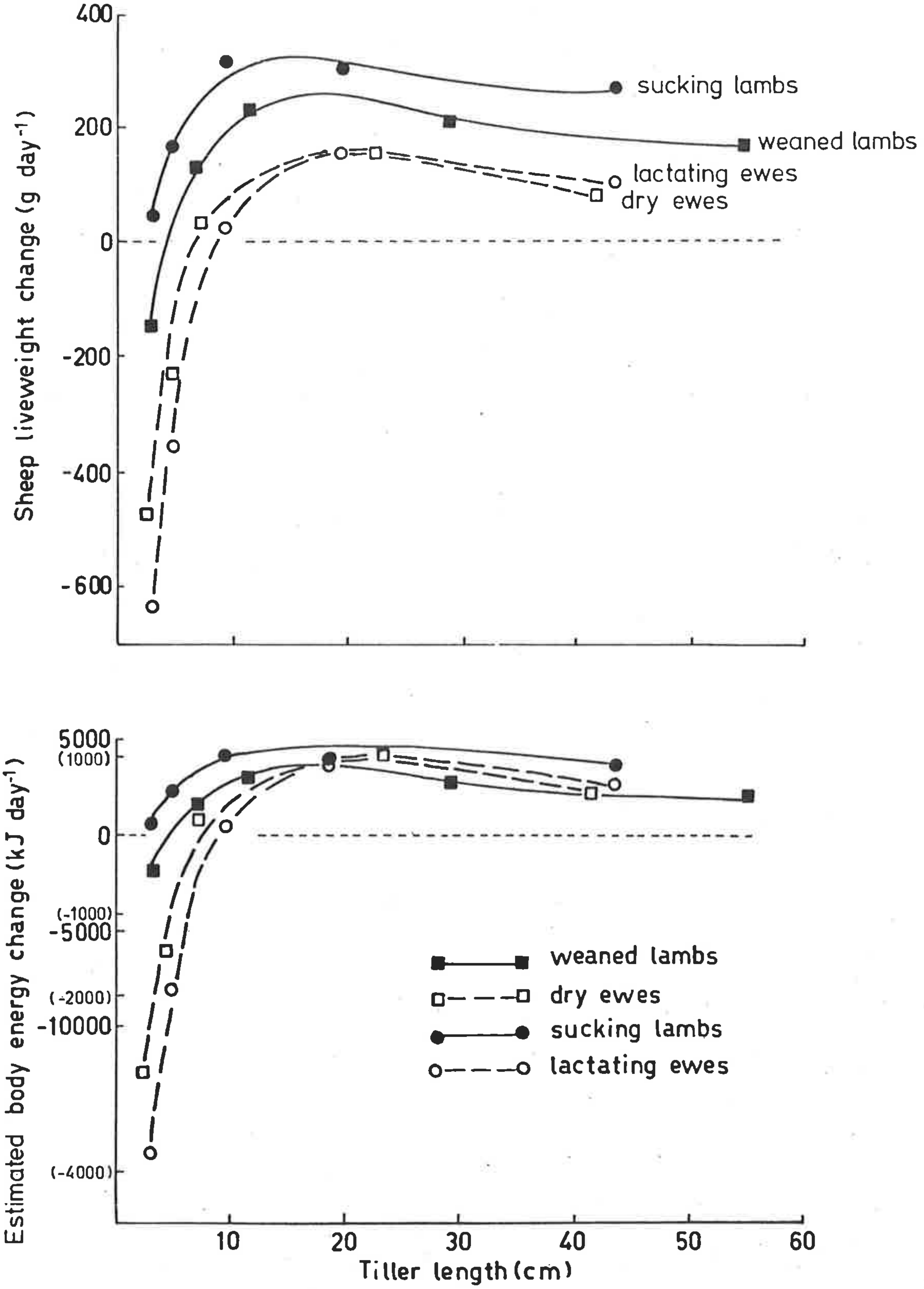
There was a close relation between liveweight change over the whole experimental period and herbage availability for each class of stock. Similar relations were observed for estimated body energy. Figures 5 and 6 illustrate these changes at different tiller lengths for each class of stock. The live weight data are summarized in Appendix Table 2. The curves were fitted by eye. Initially there was a rapid increase in live weight and body energy of all animals as tiller length increased from 3 to 15 cm; thereafter there was little change in these characters. At a tiller length of 15 cm the sucking lambs gained 320 g day^{-1} in live weight, whereas weaned lambs on pastures of similar tiller length grew at 253 g day^{-1}. Corresponding values for dry and lactating ewes were 150 and 133 g day^{-1}, respectively. Similar differences were observed in the body energy values (such values were derived from live weight data as described in Section 4.3.2b).

Sucking lambs had significantly greater growth rates and estimated body energy gains (at least 50 g day^{-1} and 1000 kJ day^{-1} greater, respectively) than did weaned lambs at all pasture availabilities (Figures 5 and 6, and Tables 9 and 10).

However the sucking lamb's grazing partner, the lactating ewe lost more live weight ($P < 0.1$) and body energy ($P < 0.1$) than did the dry ewe at low pasture availabilities (i.e. when TL < 15 cm). Only at high levels of herbage availability did lactating ewes show similar live weight and body energy gains to those of dry ewes (Figures 5 and 6).

Figure 5. Relation of sheep liveweight change to the tiller length of swards grazed by different classes of stock.

Figure 6. Estimated body energy changes (kJ day^{-1}) for ewes and lambs grazing together or separately on swards of different tiller lengths. Figures in parentheses are kilocalories day^{-1}.



400
200
0
-200
-400
-600
Sheep liveweight change (g day⁻¹)
sucking lambs
weaned lambs
lactating ewes
dry ewes
5000
(1000)
0
(-1000)
-5000
(-2000)
-10000
(-4000)
Estimated body energy change (kJ day⁻¹)
weaned lambs
dry ewes
sucking lambs
lactating ewes
10
20
30
40
50
60
Tiller length (cm)

Table 9. Analysis of variance and means of sheep liveweight change (LWC, g day^{-1}), from October 5th to November 7th.

(a) Lambs

Source of variation	DF	Mean square	F	Probability
Availability	4	124.8	24.0	***
Class	1	144.4	27.7	***
Availability X class	4	7.4	1.4	n.s.
Residual	30	5.2		

Means

Nominal availability

1	2	3	4	5	LSD
-53a[+]	151b	232c	251c	219bc	72

Class of lamb

Weaned	Sucking	LSD
116a	223b	46

(b) Ewes

Source of variation	DF	Mean square	F	Probability
Availability	4	711.3	73.4	***
Class	1	21.2	2.2	n.s.
Availability X class	4	11.6	1.2	n.s.
Residual	30	9.7		

Means

Nominal availability

1	2	3	4	5	LSD
-559a[+]	-266b	24c	115d	93cd	98

Class of ewe

Dry	Lactating	LSD
-88a[⌿]	-144a	n.s.

n.s. = not significant, ***P < 0.001

\+ Means with different subscripts within rows differ significantly at P < 0.05.

⌿ Means differ at P < 0.1.

Table 10. Analysis of variance[†] and means of the estimated body energy change (kJ day^{-1}) of weaned and sucking lambs and of dry and lactating ewes.

Source of variation	DF	Mean square	F	Probability
Availability	4	3.5 x 108	76.2	***
Class of stock	3	1.7 x 108	36.6	***
Availability X class	12	55458749	11.9	***
Residual	60	4648898		

***P < 0.001

Means

Nominal availability					
1	2	3	4	5	LSD
-7566a[+]	-2473b	2079c	3643d	2572cd	1337

Class of stock				
Lambs		Ewes*		LSD
Weaned	Sucking	Dry	Lactating	
1439a[+]	2900b	-2271c	-3465c	1196

***P < 0.001

† A complete analysis of variance was possible since differences between classes of stock were taken into account in the estimation of body energy (Section 4.3.2b).

\+ Means with different subscripts within rows differ significantly at P < 0.05.

* Means differ at P < 0.1.

Ewes lost significantly ($P < 0.05$) more body energy than lambs at low availabilities (when TL < 15 cm). It was only on abundant pasture that both ewes and lambs showed similar energy retention (Figure 6 and Table 10). These different responses according to herbage availability produced the significant availability by class of stock interaction shown in Table 10.

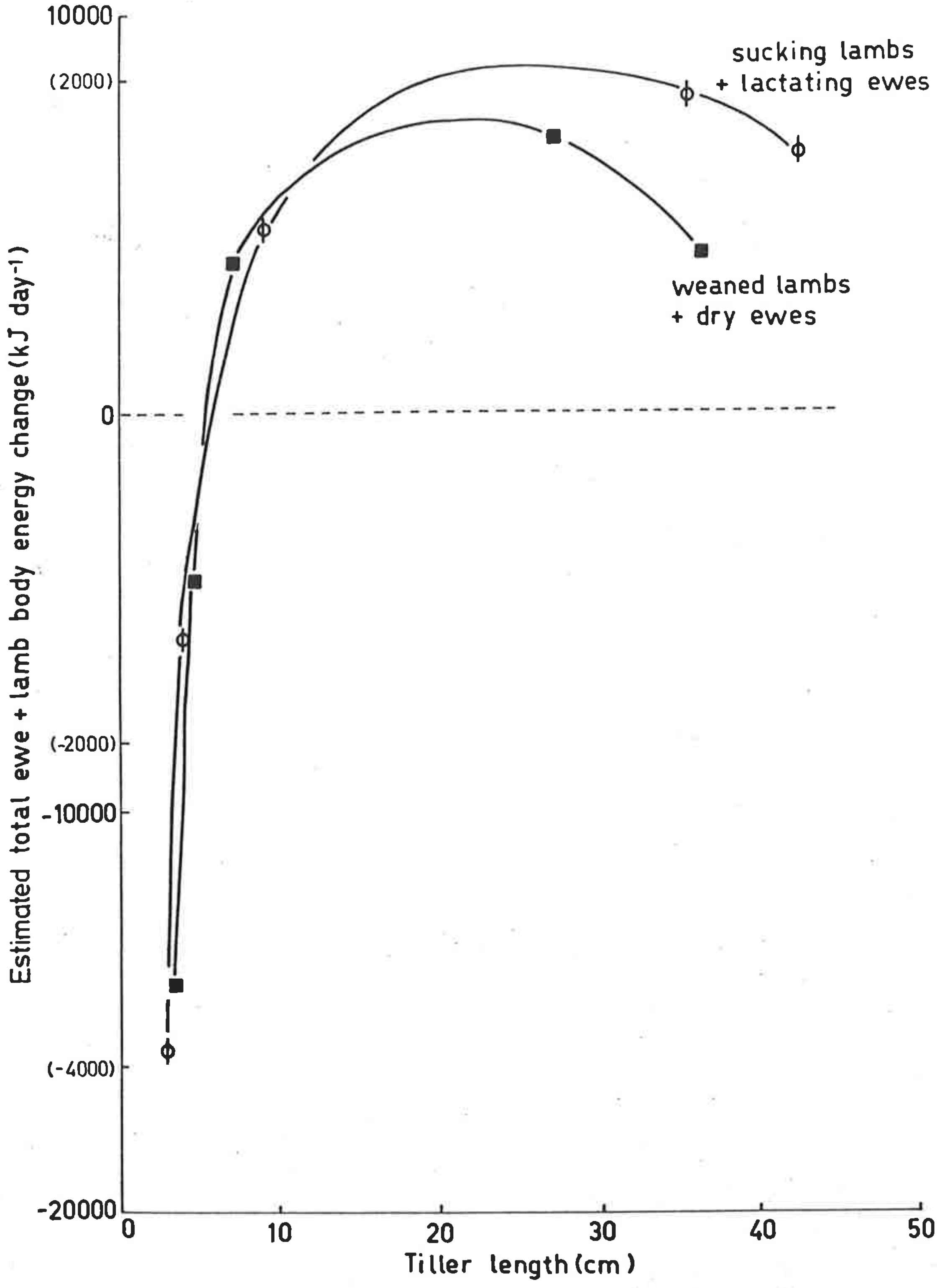
Several points of importance to lamb management are apparent. Firstly when lambs were weaned and transferred to swards of similar or shorter tiller length, lamb growth rate was depressed. Secondly, the only advantage of early weaning was for lambs weaned from swards of less than 10 cm in tiller length to longer swards. This resulted in an increased growth rate from sub-maintenance levels to reasonable gains of about 200 g day^{-1}. Thirdly, at all availabilities the presence of the ewe conferred a benefit to the sucking lamb. Fourthly at low herbage availabilities (where TL < 10 cm) ewes lost appreciable live weight and body energy; however the losses of the early weaned (dry) ewes were less than those of suckling ewes. The significance of such losses will be discussed in a later section.

(ii) Partition of body energy in the ewe/lamb unit

The maximum gain of total body energy by ewes and lambs grazing together and separately was similar and was achieved on pastures of 15 cm in TL or longer (Figure 7 and Table 11). However there were substantial differences in the partitioning of body energy between ewes and lambs and these were dependent on tiller length and on the ewe's presence or absence (Table 12).

Regardless of the rate of ewe body energy change sucking lambs had higher rates of body energy gain compared to weaned lambs at

Figure 7. Estimated total body energy change of the two grazing units (weaned lambs + dry ewes versus sucking lambs + lactating ewes) grazing swards of different tiller lengths. Figures in parentheses are total body energy changes expressed in units of kilocalories day^{-1}.



10000
(2000)
0
(-2000)
-10000
(-4000)
-20000
0
10
20
30
40
50
Tiller length (cm)
Estimated total ewe + lamb body energy change (kJ day^{-1})
sucking lambs + lactating ewes
weaned lambs + dry ewes

Table 11. Analysis of variance and means of estimates of the total body energy change (kJ day^{-1}) of the ewe/lamb grazing units (weaned lambs + dry ewes vs sucking lambs + lactating ewes).

Source of variation	DF	Mean square	F	Probability
Availability	4	7×10^8	75.3	***
Grazing unit	1	2842246	0.3	n.s.
Availability X grazing unit	4	7640251	0.8	n.s.
Residual	30	9411817		

n.s. = not significant, ***P < 0.001

Means

Nominal availability					
1	2	3	4	5	LSD
-15132a*	-4947b	4157c	7286d	5143cd	2681

Grazing unit		
Weaned lamb + dry ewe	Sucking lamb + lactating ewe	LSD
-4100a	-2900a	n.s.

* Means with different subscripts within rows differ significantly at P < 0.05.

Table 12. Estimated body energy changes (MJ day^{-1}) of ewes and lambs when grazing together and alone.

Grazing treatment	Ewe/lamb unit: Separate (weaned) Nominal availability 1	2	3	4	5	Together (sucking) Nominal availability 1	2	3	4	5
Lamb	-2.0	1.7	3.0	2.7	1.9	0.7	2.3	4.1	3.9	3.6
Ewe	-12.4	-5.9	0.8	4.1	2.0	-16.7	-8.0	0.5	3.9	2.8
Total	-14.4	-4.2	3.8	6.8	3.9	-16.0	-5.7	4.6	7.8	6.4

each level of herbage availability (Tables 10 and 12). However lactating ewes tended to lose more body energy compared to dry ewes at low pasture availabilities. Thus the total body energy change of the two ewe/lamb units were similar when the data were meaned over all herbage availabilities (Table 11).

In the ewe/lamb unit the ewe lost her own body tissue when grazing on short swards in order to sustain the growth of her lamb. The weight loss of the ewe when separated from her lamb was substantially less than that of the suckling ewe. However the profitable part of the prime lamb enterprise is the sale of the lamb. Therefore the current advantage of increased weight gain of the ewe through weaning resulted in a decline in marketable lamb. Clearly some residual benefit to the ewe would be needed to offset the loss of lamb growth.

It is recognised that the work presented does not permit a long term estimation of the effects of feed deprivation on the ewe/lamb unit, nor does it measure that amount of feed needed to restore the weight losses of the deprived ewes. Such factors would clearly need to be taken into account in management practices relating to early weaning.

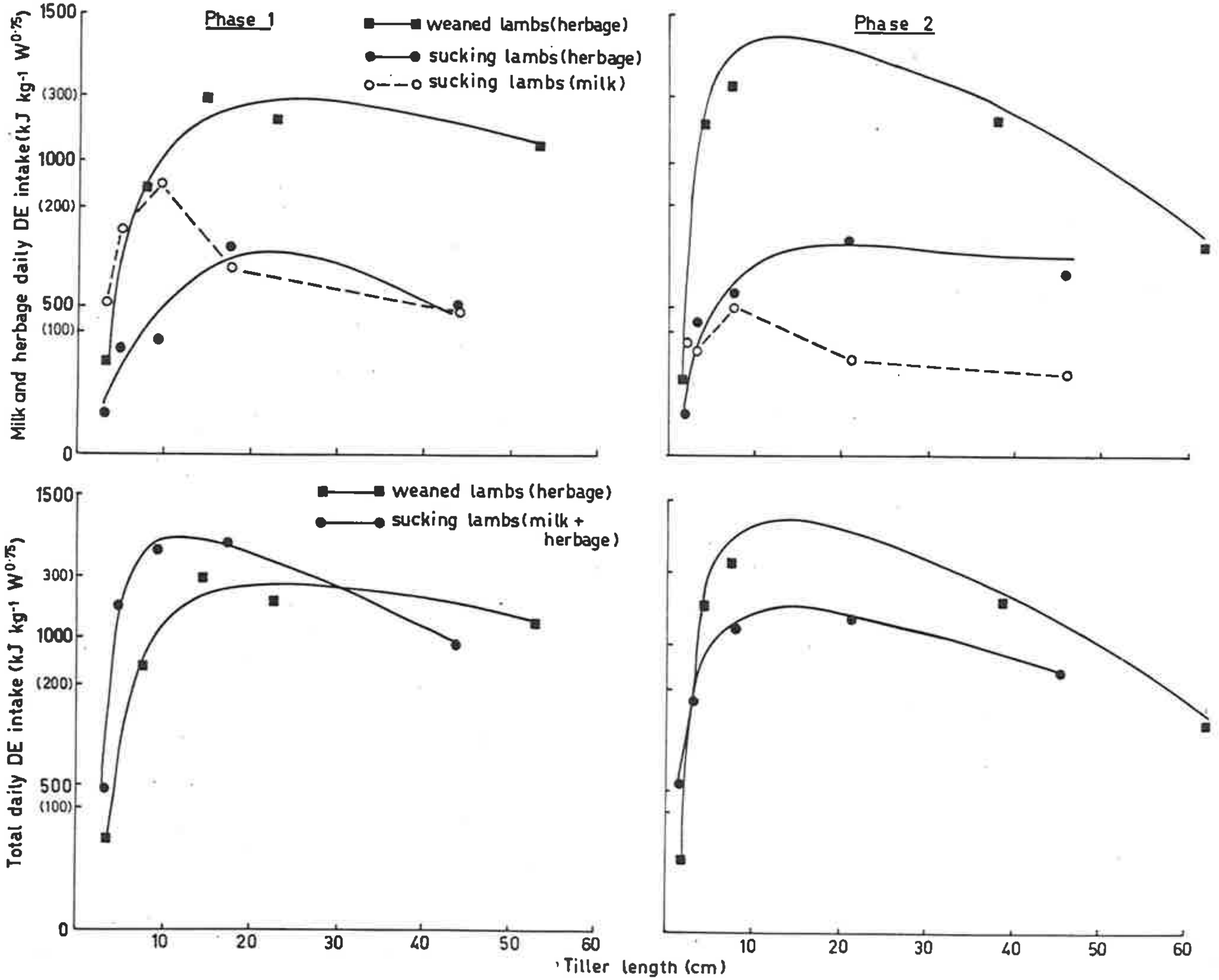
4.4.2 Intake

(a) Daily intake of herbage by lambs

Figure 8 shows that lamb intake was related to herbage availability in a curvilinear fashion. At each level of herbage availability weaned lambs consumed up to twice as much herbage as the sucking lambs. Maximum digestible energy (DE) intakes of herbage

Figure 8. The relation of the intake of DE from milk and from grass by sucking lambs and the intake of grass DE by weaned lambs to tiller length in phases 1 (Top, Left) and 2 (Top, Right). Figures in parentheses on the Y ordinate are kilocalories. Curves were drawn from fitted equations as described in Appendix Table 3.

Figure 9. The relation of the total daily intake of DE by weaned and sucking lambs to TL in phases 1 (Bottom, Left) and 2 (Bottom, Right).
Figures in parentheses on the Y ordinate are kilocalories. Curves were drawn from fitted equations as described in Appendix Table 3.



Phase 1
Phase 2
weaned lambs(herbage)
sucking lambs(herbage)
sucking lambs(milk)
weaned lambs (herbage)
sucking lambs(milk + herbage)
Milk and herbage daily DE intake (kJ kg-1 W0.75)
Total daily DE intake (kJ kg-1 W0.75)
1500
(300)
1000
(200)
500
(100)
0
10
20
30
40
50
60
Tiller length (cm)

where achieved by all lambs when the tiller length of pastures was from 10 to 15 cm (Figure 8 and Table 13). Although the relative differences in intake were similar at all levels of availability, the absolute differences in herbage intake between weaned and sucking lambs increased markedly at the higher tiller lengths (above 10 cm) giving rise to a significant interaction (Figure 8 and Table 13). The interaction, in respect of herbage intake between class of lamb and length of sward was significant in both phases (Table 13).

The relation of herbage DE intake (Y, kJ $kg^{-1}W^{0.75}$ day^{-1}) to tiller length (X, cm) for each class of lamb was examined using an equation of the form:

$$Y = A + BX + C\sqrt{X} + DX^2.$$

These relations for weaned and sucking lambs in both phases are presented in Appendix Table 3. In summary, the responses of both classes of lambs to TL were similar in relative terms but different in absolute terms. Presumably the ewe's presence (as a supplier of milk and a competitor for herbage) affected the herbage intake of sucking lambs. The intake data are summarised in Appendix Tables 4 and 5.

(b) Intake of milk by sucking lambs

Milk production of ewes grazing pastures of different availabilities was relatively constant in each phase (Figure 8). All milk yields have been joined by eye fitted lines since there were no significant differences between treatments (Table 14). Lambs receiving milk modified their intake by eating less herbage at all

Table 13. Analysis of variance and means of the daily DE intake of herbage (kJ $kg^{-1}W^{0.75}$) by weaned and sucking lambs in phases 1 and 2.

(a) Phase 1

Source of variation	DF	Mean square	F	Probability
Availability	4	581523	22.7	***
Class (weaned vs sucking)	1	2526771	98.6	***
Availability X class	4	111148	4.3	**
Residual	30			

Means

Nominal availability

1	2	3	4	5	LSD
225a	633b	802bc	919bc	781bc	211

Class of lamb

Weaned	Sucking	LSD
923a	421b	133

(b) Phase 2

Source of variation	DF	Mean square	F	Probability
Availability	4	744198	29.4	***
Class (weaned vs sucking)	1	1593966	63.1	***
Availability X class	4	176010	7.0	***
Residual	30	25237		

Means

Nominal availability

1	2	3	4	5	LSD
389a	971b	1172c	1115bc	815b	159

Class of lamb

Weaned	Sucking	LSD
906a	507b	100

**P < 0.01, ***P < 0.001.

* Means with different subscripts within rows are significantly different at P < 0.05.

availabilities. The decline in milk consumption by lambs from phase 1 to 2 is probably a reflection of the normal decline of lactation with time (Perrin 1958; Langlands 1977). However, lambs did not increase their herbage intake during this period to compensate fully (in terms of lamb growth rate) for the reduced milk supply. Thus the total DE intake (unadjusted) of sucking lambs declined from phase 1 to phase 2 at all availabilities (Figure 8). The milk yield data are presented in Table 14.

(c) Relation of milk intake to herbage consumption

The regression relating milk intake to herbage consumption of the sucking lambs was not significant in either phase (see Table 15). This was probably because ewe milk production was constant on all pastures within each phase (Table 14). Changes in intake with availability were associated with the herbage component of the diet only.

(d) Total intake of DE by lambs

Maximum total intakes of DE by weaned and sucking lambs were achieved when pastures were 10 cm in tiller length or longer (Figure 9). The total intake of DE (unadjusted intake as described in Section 4.3.2f) by sucking lambs in phase 1 was significantly greater at all availabilities than that of weaned lambs. However there were no significant differences in phase 2 or when the intake data were meaned over the two phases (Tables 16 and 17). The greater growth rates of sucking lambs compared to weaned lambs at all availabilities could have been due either to a synergistic effect of milk and grass when fed together, or to the fact that milk DE is used with a greater efficiency for lamb growth than is DE of herbage origin as has been shown by Jagusch and Mitchell (1971).

Table 14. Analysis of variance of daily intake of DE from milk (i.e. kJ $kg^{-1}W^{0.75}$) by sucking lambs at phase 1 and 2.

(a) Milk DE intake in phase 1

Source of variation	DF	Mean square	F	Probability
Availability	4	130509	3.1*	n.s.
Between lambs within availability	3	28919	0.69	n.s.
Residual	12	42095		

Means

Nominal availability					
1	2	3	4	5	LSD
511a	762a	921a	637a	488a	n.s. (P < 0.05)

(b) Milk DE intake in phase 2

Source of variation	DF	Mean square	F	Probability
Availability	4	27978	0.7	n.s.
Between lambs within availability	3	39289	1.0	n.s.
Residual	12	39346		

Means

Nominal availability					
1	2	3	4	5	LSD
385	347	507	335	285	n.s.

n.s. = not significant at P < 0.05.

* significant at P < 0.1.

Table 15. Regression analyses of milk DE intake (Y) against grass DE intake (X) of sucking lambs in phases 1 and 2.

Period	Source of	DF	Mean square	F	Probability
(a) Phase 1	Regression	1	387.7	0.01	n.s.
	Deviations	18	52269.2		
(b) Phase 2	Regression	1	61477.5	1.25	n.s.
	Deviations	18	49323.8		

n.s. = not significant.

Table 16. Analysis of variance of the total daily intake of DE (kJ kg^{-1}W$^{0.75}$) by weaned and sucking lambs in phases 1 and 2.

(a) Phase 1

Source of variation	DF	Mean square	F	Probability
Availability	4	790832	17.7	***
Class	1	259146	5.8	*
Availability X class	4	48766.6	1.1	n.s.
Residual	30	44540.6		

Means

Nominal availability

1	2	3	4	5	LSD
481a	1014b	1263c	1237c	1025b	211

Class of lamb

Weaned	Sucking	LSD
923a	1084b	133

(b) Phase 2

Source of variation	DF	Mean square	F	Probability
Availability	4	785456	22.3	**
Class	1	7426	0.6	n.s.
Availability X class	4	131858	3.7	
Residual	30	35181		

Means

Nominal availability

1	2	3	4	5	LSD
390a	971b	1172c	115bc	815b	188

Class of lamb

Weaned	Sucking	LSD
906a	879a	n.s.

n.s. = not significant, *P < 0.05, **P < 0.01, ***P < 0.001

Means with different subscripts within rows are significantly different at P < 0.05.

Table 17. Analysis of variance of the total intake of DE (kJ $kg^{-1}W^{0.75}$) by weaned and sucking lambs, when DE intake is the mean of phase 1 and 2 intake.

Source of variation	DF	Mean square	F	Probability
Availability	4	780541	27.3	***
Class	1	44709	1.6	n.s.
Availability X class	4	42786	1.5	n.s.
Residual	30			

n.s. = not significant, ***P < 0.001

Means

Nominal availability					
1	2	3	4	5	LSD
435a*	993b	1217c	1176c	920b	169

Class of lamb		
Weaned	Sucking	LSD
915a	982a	n.s.

* Means with different subscripts within rows are significantly different at P < 0.05.

Values (unadjusted) for the proportion of the total intake of DE of herbage origin in the diet of sucking lambs were calculated from the equations in Appendix Table 3 and are presented in Table 18.

Of all treatments the herbage component of the sucking lamb's diet became more important as the milk yield of ewes declined from phase 1 to 2 (Section 4.4.2b).

4.4.3 Utilization of dietary energy

The relation of total intake of DE to weight change for weaned and sucking lambs is illustrated in Figure 10. The intake of DE by sucking lambs is presented in both unadjusted and adjusted forms. The adjustment was based on the increased efficiency of utilization of milk compared to grass for lamb maintenance and growth as described in Section 4.3.2f.

There is clearly a displacement of the regression lines for the weaned and (unadjusted) sucking lamb data which suggests that the inclusion of milk in the diet had a synergistic effect on gain. However when the milk intake of the sucking lamb was adjusted for the increased efficiency of utilization of milk for lamb growth the resultant regression line did not differ in slope or displacement from that of the weaned lambs (Figure 10 and Tables 19a and b). The latter two regression lines fall between the values reported by Allden (1968b, 1969b) in pen and field studies. The DE intake requirements of weaned and sucking lambs for maintenance was 637 and 645 kJ $kg^{-1}W^{0.75}$ day^{-1}, respectively (Table 19a).

Table 18. Contribution of herbage to the diet of sucking lambs (i.e. proportion of the total DE intake (unadjusted)* of herbage origin).

Tiller length	Phase 1	Phase 2
5	21	26
10	27	48
15	28	57
20	45	57
25	51	63
50	46	65

* Total DE intake unadjusted for the increased nutritive value of milk compared to herbage.

<u>Figure 10.</u> Relation of daily DE intake (kJ $kg^{-1}W^{0.75}$) to live weight change for weaned lambs and sucking lambs and also the values for sucking lambs after adjusting for the reported increased efficiency of utilization of milk DE compared to grass DE for lamb growth. Data from 20 lambs were used to derive each regression line (see Table 21a). Also presented are values obtained from:-

(1) Garrett *et al.* (1959) —·—·—·—·—·—·—and
(2) Allden (1968b) in pen studies ....and from
(3) Allden (1969b) - - - - - - - - - - - - - - - - - - -in

field studies. Daily DE intake data expressed as kcal $kg^{-1}W^{0.75}$ are given in parenthesis on the Y ordinate.

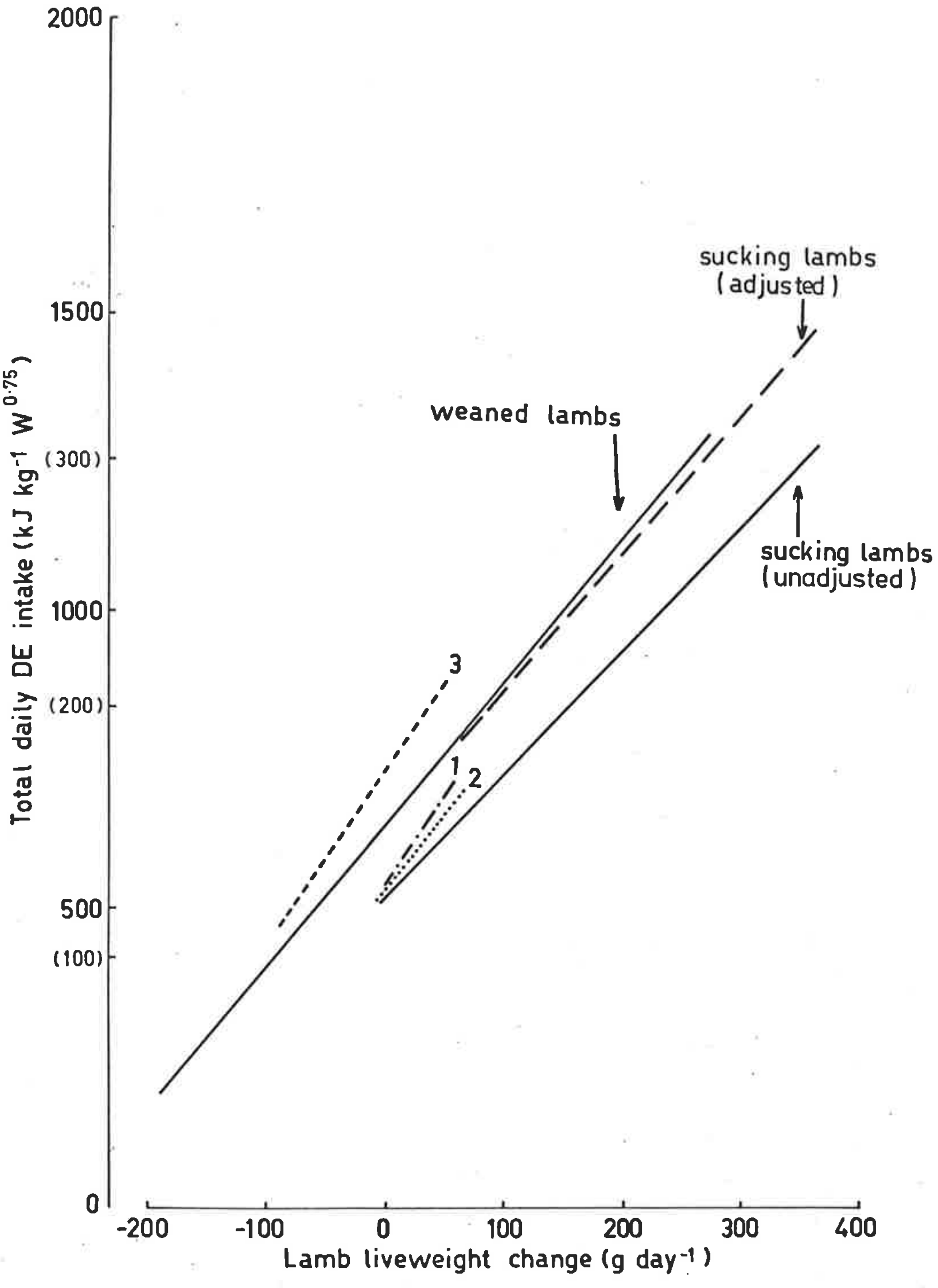

2000
1500
1000
500
0
(300)
(200)
(100)
Total daily DE intake (kJ kg-1 W0.75)
sucking lambs (adjusted)
weaned lambs
sucking lambs (unadjusted)
3
1
2
-200
-100
0
100
200
300
400
Lamb liveweight change (g day-1)

Table 19a. Linear regression analysis of the relationship between daily intake of DE by lambs (Y, kJ $kg^{-1}W^{0.75}$) and liveweight change (X, kg day^{-1}).

Class of lamb	Regression equation	r^2	Daily intake of DE for maintenance (kJ kg^{-1} $W^{0.75}$)
Weaned	Y = 637.3 + 2387.9X	0.94	637.3 (153)*
Sucking	Y = 519.9 + 2072.4X	0.86	519.9 (124)
Sucking (adjusted)	Y = 644.9 + 2298.8X	0.79	644.9 (154)

* Data in parentheses are daily intake of DE expressed in kcal $kg^{-1}W^{0.75}$.

Table 19b. Analysis of variance and t tests for differences between slopes and displacements of the three regression lines relating the intake of DE to liveweight change.

Source of variation	DF	Mean Square	F	Probability
Slopes	2	4801.4	0.3	n.s.
Displacements	2	90429.8	5.1	**
Residual	54	17754.0		

n.s. = not significant, **P < 0.01

t tests

Comparison of classes of lambs	Slopes	Displacements
Weaned vs sucking	0.43 n.s.	2.03*
Weaned vs sucking (adjusted)	-0.41 n.s.	-0.81 n.s.
Sucking vs sucking (adjusted)	-0.74 n.s.	-3.11**

n.s. = not significant, *t < 0.05, **t < 0.01

4.4.4 Components of herbage intake

(a) Grazing time and rate of intake

The dynamic interrelationships between total daily herbage intake (I) and its components, grazing time (T) and rate of intake (R) as herbage availability changes may influence the lamb's response to weaning. Total daily intake, rate of intake and potential rate of intake were all related to herbage availability in a curvilinear fashion (Figure 11). The intake data are summarised in Appendix Table 6. Maximum total intake and rates of intake were achieved on swards of approximately 15 cm TL or longer.

When herbage was short the intakes and components of intake of weaned and unweaned lambs were similar. Only when herbage was plentiful was there a marked difference in the intake,rate of intake and grazing time of the different classes of lambs. Thus when the intake data were meaned over all availability treatments the weaned lambs had significantly greater total herbage intake and components of intake compared to sucking lambs (Table 20 and Figure 11). It seems that milk consumption and/or competition from the ewe reduced the intake of herbage and the grazing activity of the sucking lamb compared to that of the weaned lamb grazing alone on similar pastures.

Bearing in mind that intake is the product of rate of intake and grazing time, Figure 11 shows quite clearly that as the amount of herbage present commenced to decline the animals' total daily intake (I) and its components (RT) were at first unaffected; then a stage was reached when the availability of herbage apparently imposed limitations on the rate at which the lamb ingested its feed, but this was compensated for by an increase in grazing time. Thereafter the lamb extended its

Figure 11. The relationships between tiller length of swards and:

(a) (Top, Left) the total daily intake of herbage,

(b) (Top, Right) grazing time,

(c) (Bottom, Left) potential rate of intake, and

(d) (Bottom, Right) daily rate of intake.

The lines are drawn from fitted equations which are presented in Appendix Table 3.

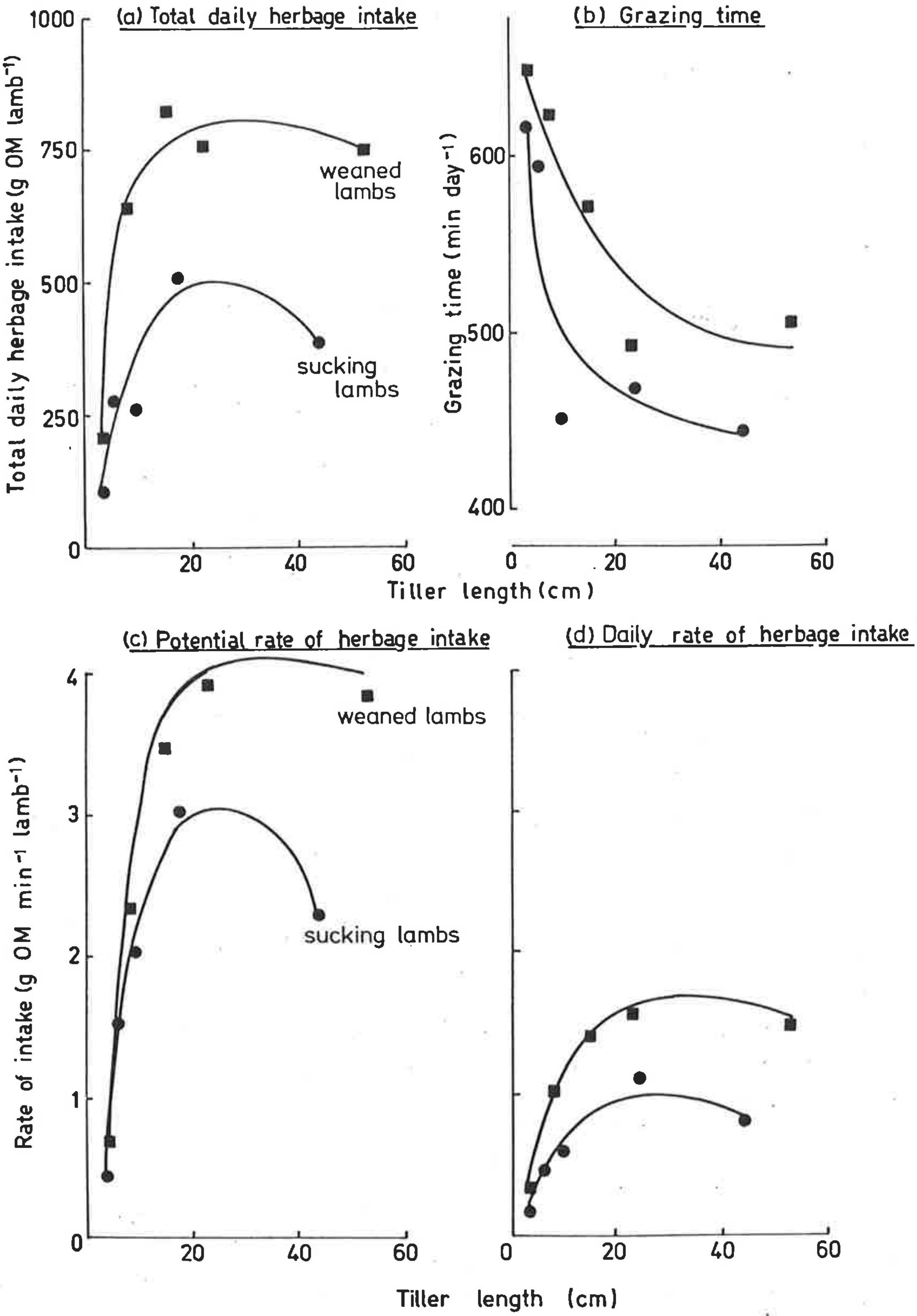

(a) Total daily herbage intake
Total daily herbage intake (g OM lamb⁻¹)
1000
750
500
250
0
weaned lambs
sucking lambs
(b) Grazing time
Grazing time (min day⁻¹)
600
500
400
0
20
40
60
Tiller length (cm)
(c) Potential rate of herbage intake
Rate of intake (g OM min⁻¹ lamb⁻¹)
4
3
2
1
0
weaned lambs
sucking lambs
(d) Daily rate of herbage intake
20
40
60
Tiller length (cm)

Table 20. Analyses of variance and means of (a) the total daily intake of herbage and its components, namely (b) grazing time and (c) daily rate of intake. Similar analyses of the potential rate of herbage intake are given in (d).

(a) Total daily herbage intake (g OM day^{-1} $lamb^{-1}$)

Source of variation	DF	Mean square	F	Probability
Availability	4	270686.0	9.2	***
Class	1	1088208.0	37.0	***
Availability X class	4	58064.9	2.0	n.s.
Residual	30	29409.4		

Means

Nominal availability

1	2	3	4	5	LSD
162a	457b	546bc	638c	549bc	171

Class of lamb

Weaned	Sucking	LSD
635a	305b	108

(b) Grazing time (min day^{-1})

Source of variation	DF	Mean square	F	Probability
Availability	4	40167.0	10.2	***
Class	1	35640.0	9.1	**
Availability X class	4	3069.9	0.8	n.s.
Residual	30	3931.5		

Means

Nominal availability

1	2	3	4	5	LSD
632a	602a	509b	479b	483b	63

Class of lamb

Weaned	Sucking	LSD
571a	511b	40

Table 20 (continued).

(c) Daily rate of herbage intake (g OM min^{-1} $lamb^{-1}$)

Source of variation	DF	Mean square	F	Probability
Availability	4	1.37	13.1	***
Class	1	2.65	25.5	***
Availability x class	4	0.12	1.1	n.s.
Residual	30	0.10		

Means

Nominal availability

1	2	3	4	5	LSD
0.3a	0.7b	1.0c	1.3d	1.1cd	0.3

Class of lamb

Weaned	Sucking	LSD
1.2a	0.6b	0.2

(d) Potential rate of intake (g OM min^{-1} $lamb^{-1}$)

Source of variation	DF	Mean square	F	Probability
Availability	4	10.71	21.2	***
Class	1	10.01	19.8	***
Availability X class	4	0.53	1.05	n.s.
Residual	30	0.50		

Means

Nominal availability

1	2	3	4	5	LSD
0.5a	1.9b	2.7c	3.4c	3.0c	0.7

Class of lamb

Weaned	Sucking	LSD
2.8a	1.8b	0.4

n.s. = not significant, **$P < 0.01$, ***$P < 0.001$.

period of grazing further, but compensation became progressively more incomplete and the total intake fell dramatically.

(b) A comparison of the potential and daily rates of intake

Figure 11 shows that differences in the rate of herbage intake between lamb classes were greatest at the high availabilities and least when the herbage was in short supply. Rates of intake of lambs are compared on a per animal basis, since the live weights of all lambs were similar at that time (Appendix Table 7). At 40 cm TL the potential rate of intake was 4.1 and 2.8 g OM min^{-1} for weaned and sucking lambs, respectively (a 32% difference), whereas at 5 cm TL the values for the two classes were 0.7 and 0.5 g OM min^{-1} respectively (a 29% difference). Corresponding figures for the daily rate of intake were 1.9 and 0.9 g OM min^{-1} at TL of 40 cm (a 53% difference) and 0.5 and 0.3 g OM min^{-1} at TL of 5 cm, respectively (a 40% difference). It is evident that the rate of intake of a lamb during its first hour of grazing (the potential) is related to the rate of intake sustained during a full day's grazing in relative but not in absolute terms.

The potential rate of intake was highly correlated ($P < 0.001$) with both total intake and the daily rate of intake by weaned lambs, and less so for sucking lambs ($P < 0.01$). These relations are shown in Table 21. The potential rate of herbage intake has little value in terms of predicting a lamb's daily rate of intake in absolute terms. However it can be measured quickly, and since it is correlated with the daily rate of intake it is an accurate guide in relative terms for describing a lamb's intake response to tiller length.

Table 21. Matrix of simple correlation coefficients between potential rate of intake, total daily herbage intake, the components of intake, grazing time and daily rate of intake for two classes of lambs.

Variables	Daily rate of OM intake		Grazing time		Total daily herbage OM intake	
Class of lamb	Weaned	Sucking	Weaned	Sucking	Weaned	Sucking
Potential rate of OM intake (g OM min^{-1} 25 kg $lamb^{-1}$)	0.87	0.54	-0.63	-0.36	0.82	0.55
Daily rate of OM intake (g OM min^{-1} 25 kg $lamb^{-1}$)	-	-	-0.60	-0.53	0.97	0.95
Grazing time (min day^{-1})	-	-	-	-	-0.40	-0.29

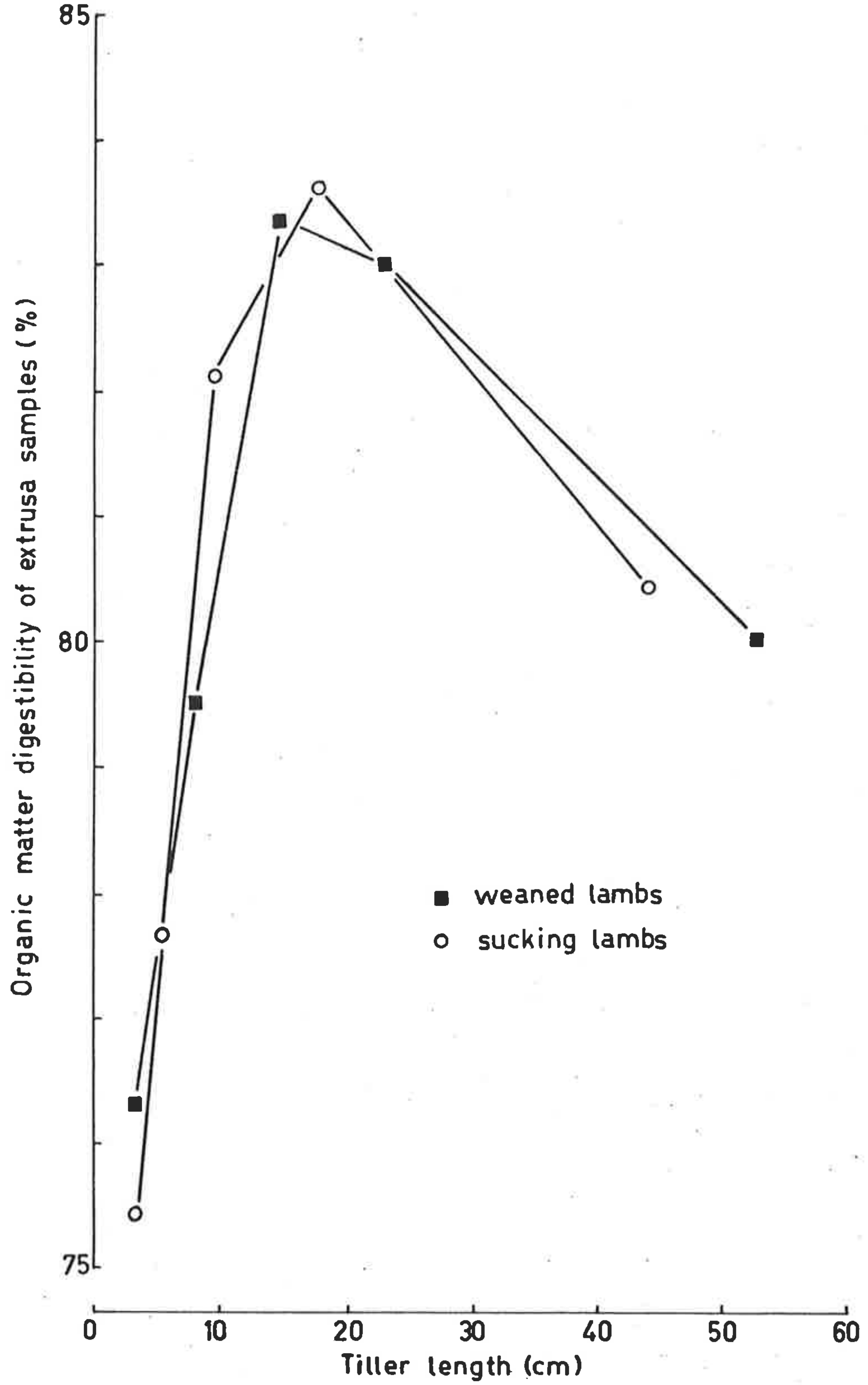
$P < 0.05 \simeq 0.44$*, $P < 0.01 \simeq 0.56$**, $P < 0.001 \simeq 0.81$***

4.4.5 Digestibility of herbage

There was a rapid increase in the *in vitro* OMD of grass as the tiller length of pastures increased from 3 cm up to about 15 cm for both weaned and sucking lambs, whereas on swards longer than 30 cm in TL there was a decrease in OMD with increase of tiller length.

These relations can be seen in Figure 12 and are summarised in Appendix Table 8. In phase 1, over all availabilities, weaned lambs selected a diet which was significantly more digestible than that selected by sucking lambs (Table 22). The difference in the *in vitro* OMD of herbage consumed by weaned and sucking lambs was relatively small, being less than one unit of OMD. In phase 2, similar trends occurred but the difference was not significant. When data from phase 2 were pooled over all availabilities weaned lambs selected a diet 0.9 units of OMD greater than that of sucking lambs but this difference was not statistically significant at $P < 0.05$ (Appendix Table *0. It should be remembered that a less intensive sampling procedure was used in phase 2 compared to phase 1. Thus the OMD of the diet consumed by all lambs over all availabilities was within 1 unit of OMD irrespective of whether lambs has been weaned or were sucking.

Figure 12. Relation between the *in vitro* organic matter digestibility of the diet selected by weaned and sucking lambs and the tiller length of swards in phase 1.



85
80
75
Organic matter digestibility of extrusa samples (%)
weaned lambs
sucking lambs
0
10
20
30
40
50
60
Tiller length (cm)

Table 22. Analysis of variance and means of the *in vitro* organic matter digestibility (OMD) of herbage extrusa samples from O.F. lambs in phase 1 (Split plot Latin Square Analysis (Steele and Torrie 1960)).

Source of variation	DF	Mean square	F	Probability
Between treatments (class of lamb weaned vs sucking)	1	5.31	8.55	*
Within treatments between animals	4	1.39	2.24	n.s.
Residual	4	0.62	0.29	n.s.
Availabilities	4	93.63	44.1	***
Day of sampling X class of lamb	8	1.39	0.65	n.s.
Availability X class of lamb	4	3.15	1.48	n.s.
Residual	24	2.12		

Means

Main effects	Nominal availability 1	2	3	4	5	LSD
Between treatments (weaned vs sucking)	80.5a†	79.8b				0.5
Between animals within treatment	80.4	80.2	80.6	79.6	80.1	n.s.
Day of sampling	79.5	79.8	80.5	80.3	80.8	n.a.
Availabilities	75.9a	78.6b	82.8c	83.2c	80.3d	1.3

n.s. = not significant, n.a. = not available, *P < 0.05, ***P < 0.001.

† Means with different subscripts within rows differ significantly at P < 0.05.

4.5 Discussion of Experiment 1

Weaning consistently increased herbage consumption by lambs but consistently decreased the weight gain and estimated body energy retention of lambs during the period of study. In practice, the ewe/lamb unit does not exist for a 'long term' (i.e. a number of years). Management decisions have to be made to deal with the short term (i.e. a period of weeks) situations when feed shortage dictates a need for livestock movement or supplementary feeding.

The design of the experiment made it possible to estimate the responses of lambs when weaned on to pastures of different availabilities. Weaning on to pastures of similar or shorter tiller length resulted in a depression in lamb growth. The only advantage of early weaning noted was when lambs were weaned and transferred from very sparse to abundant pastures - in this experiment from pastures of less than 5 cm in tiller length (TL) to pastures of greater than 10 cm in TL.

Although weaned lambs consumed more herbage than sucking lambs at all availabilities this increase in herbage intake did not compensate fully for the loss of ewe's milk. At the very low herbage availability the absolute differences in herbage OM intake by weaned and unweaned lambs was 97 grams, whereas at availability 2, the difference had risen to 365 grams, and remained at about that level on higher availability pastures. Thus, the level of herbage availability and the presence of the ewe restricted herbage intake of lambs on sparse swards. However, the benefits of the ewe's milk supply to the 8 and 11 week old sucking lamb outweighed the effects of a reduced herbage intake by sucking lambs compared to weaned lambs at all herbage availabilities.

The stocking rate adopted in this experiment allowed weaned lambs to maintain the initial levels of herbage throughout the experiment. Thus a stable situation between herbage supply and animal demand was produced. Whereas, ewes with and without lambs substantially reduced the pasture available.

The data on rate of tiller length change indicated that when the sward area was divided equally between a ewe and her weaned lamb the grazing pressure of the ewe was greater and of the lamb less than when the ewe/lamb combination grazed the whole area. Furnival and Corbett (1976) found that herbage availabilities increased on plots grazed by weaned lambs compared with areas grazed by their dams or areas grazed by ewes and sucking lambs at the same total stocking rate. Thus competition for feed between ewe and lamb ensures the maximum use of herbage inthe short term. However, if the herbage supply is depleted too rapidly it may not be possible to produce a prime, saleable lamb before the next breeding season.

During the currency of this short term experiment there was no indication that the milk intake of the lambs on the lowest availability treatment differed from that on the high availabilities at each period of measurement. One of the intermediate availability groups showed a tendency to produce higher yields (Figure 8) but this was attributable to random error. Presumably lactating ewes grazing sparse pastures were able to sacrifice their body tissue reserves to sustain milk intake of the lamb in the short term. These results should not be extrapolated beyond the conditions under which they were determined. If periods of adverse nutrition are prolonged ewe milk production could be expected to decline far below that produced by ewes grazing abundant pastures, as found by Langlands (1977).

At each level of herbage availability the overall digestible energy intakes of all lambs were similar, but sucking lambs gained more weight than weaned lambs. Thus when weight responses of weaned and unweaned lambs were related to energy intake there was some discrepancy. However, the discrepancy was eliminated when energy intake was adjusted for the higher efficiency of use of milk for fattening compared to grass commonly reported in the literature (Jagusch and Mitchell 1971; Black 1971).

After adjusting intake for the higher value of milk for fattening the maintenance requirements of weaned and sucking lambs were found to be similar at 637 and 645 kJ $kg^{-1}W^{0.75}$ day^{-1}, respectively values which are intermediate between those reported for pen-fed and grazing sheep of similar breeding in this environment (Allden 1968b, 1969b).

The DE intake data was fitted to the simple linear equation relating intake to live weight and liveweight gain, as used by Garrett et al. (1959). Adjustment of the DE intake data of sucking lambs raised the energy requirements for maintenance and growth of the sucking lambs to similar levels to that of weaned lambs. The equation produced estimates of the DE requirement for maintenance of live weight of a 30 kg lamb (Table 23), which are reasonably consistent with the results of other workers (Allden 1969b; Joyce and Rattray 1970). However, slightly lower values for DE requirements for liveweight gain were recorded compared to other values in the literature (Allden 1969b; Joyce and Rattray 1970; Langlands and Bennett 1973c). For example, from 25 to 31 mJ (6.1 to 7.3 mcal) of DE intake were required above maintenance for each kg of liveweight gain by a 30 kg lamb. Joyce and Rattray (1970) found that 32 to 40 mJ (7.5 to 9.6 mcal) DE were required for each kg liveweight gain above maintenance and Allden (1969b) found 38 to 42 mJ (9.0 to 9.9 mcal) of DE were required per kg of liveweight gain.

Table 23. A comparison of the DE requirements for maintenance (kJ) of 30 kg lamb and for a gain of one kilogram in live weight.

Class of lamb	No. of lambs	Linear equation* $I = aW^{0.75}(1 + bG)$	Main-tenance	Gain of 1 kg (kJ)
Weaned	20	$I = 637.3W^{0.75}(1 + 3.75G)$	8170 (1952)≠	30637 (7321)
Sucking	20	$I = 519.9W^{0.75}(1 + 3.99G)$	6665 (1593)	26593 (6354)
Sucking (adjusted)	20	$I = 644.9W^{0.75}(1 + 3.56G)$	8268 (1976)	29434 (7033)

* After Garrett *et al.* (1959).

≠ Figures in parentheses are DE intake data expressed in terms of kilocalories.

The general agreement with the results of other workers lends confidence to the intake data recorded in this experiment. The main purpose of the experiment was to determine differences in intake associated with weaning and herbage availability. Because of the short term measurements the live weight data might be expected to be less precise than direct measures of intake. Since herbage intake was estimated in an identical fashion in all treatments it is likely that any errors would be similar for all treatments and that relative differences in intake would remain unchanged.

Presence or absence of ewes was associated with significant differences in the time spent grazing and the rate of herbage intake by lambs. These differences were relatively small when lambs grazed very short swards but became divergent on abundant pasture. Weaned lambs grazed for longer periods and had greater rates of herbage intake compared to sucking lambs when pastures were 15 cm in TL and longer. Likewise, there was some evidence to show that weaned lambs consumed feed of slightly greater *in vitro* digestibility (about 1 unit of OMD) compared to unweaned lambs grazing similar swards.

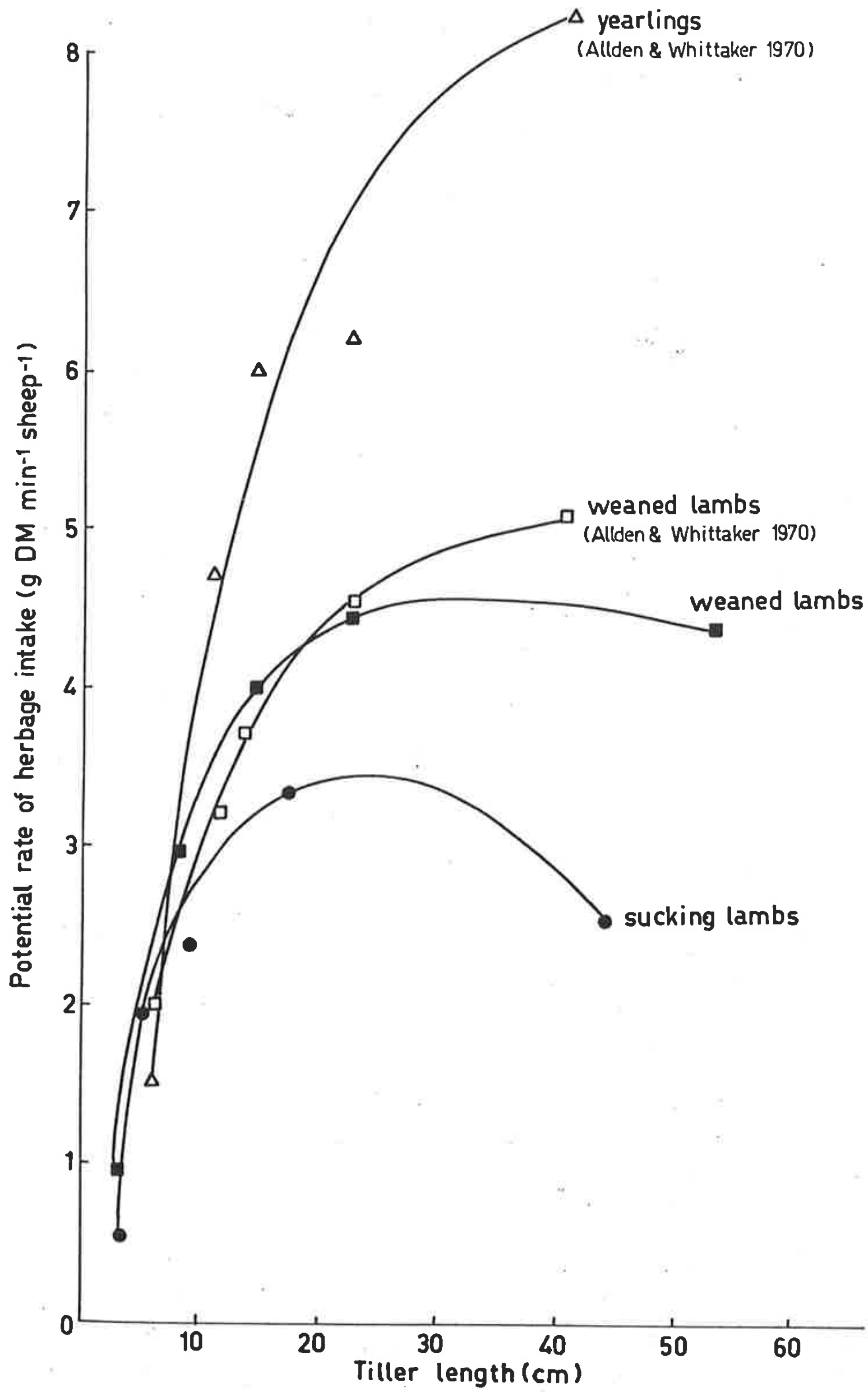
The experiment provided an opportunity to compare the rate of intake determined indirectly over a full daily grazing period with estimates determined by the method of Allden (1962) over a one hour period (Figure 13). There were big differences in the order of magnitude of rates of intake but there was good correlation between the two methods in relation to the point at which rate of intake declined (i.e. the point of inflexion) and in the relative responses.

Equations relating the potential rate of intake (Y, g DM min^{-1} $sheep^{-1}$) to tiller length (X, cm) as described in Section 4.3.4,

Figure 13. A comparison of relationships between tiller length and the potential rate of herbage DM intake in the current experiment (in phase 1) with results obtained from field studies on similar swards by Allden and Whittaker (1970). Equations relating potential rate of intake (Y, g DM minute^{-1} sheep^{-1}) to tiller length (X, cm) of the form:

$$Y = A + BX + C\sqrt{X}$$

were established for each class of stock. Details of the constants and coefficients in these equations are given in Appendix Table 3.


yearlings
(Allden & Whittaker 1970)
weaned lambs
(Allden & Whittaker 1970)
weaned lambs
sucking lambs
Potential rate of herbage intake (g DM min-1 sheep-1)
Tiller length (cm)
0
1
2
3
4
5
6
7
8
10
20
30
40
50
60

were established for each class of stock (Figure 13) and accurately described these relationships (Appendix Table 3). For 25 kg weaned lambs there were no significant differences in the constants and coefficients in the equations relating rates of intake to TL for lambs in the present work and in the equation fitted to the results of Allden and Whittaker (1970) as depicted in Figure 13.

Although sucking lambs grew faster than weaned lambs at all herbage availabilities there was evidence that this greater gain was at the expense of their dam. The experiment was not designed to examine the residual effects of early weaning in terms of ewe reproductive capacity at a later time. Therefore the work presented does not permit a long term estimation of the effects of feed derpivation on the ewe/lamb unit, neither does it measure that amount of feed needed to restore the weight losses of the deprived ewes nor the residual effects of such treatments on future reproductive performance. Such factors would clearly need to be taken into consideration in management strategies relating to early weaning. In a once a year lambing situation where the ewe suckles her lamb for 3-4 months, there would be about 3 to 4 months available to the ewe to regain lost body tissues before being remated. Whereas, weaning the lamb at 2 months would allow the ewe 5 months to recover. If the frequency of lambing were increased it might be difficult for ewes to regain lost tissues. For example, Corbett and Furnival (1976) found that the longer the lactation of ewes subsisting on a low plane of nutrition the lower was their live weight at joining and lambing. Consequently, mating and lambing percentages were depressed. Thus, the effect of herbage availability in relatively short term situations when feed shortages are critical for survival of the ewe/lamb unit may have important residual effects on later ewe reproductive capacity.

Profitability in the prime lamb flock depends on the channelling of maximum energy into the saleable commodity (lamb) consistent with the maintenance of a high fertility rate. In the current study a crude estimate was made of the partition of the energy of weight changes between ewe and lamb. Since, approximately two-fold differences have been reported in the literature (Hutchinson 1969; Allden 1970b) in the energy content of the body weight of the lamb and the ewe, the weight changes were expressed in units of energy.

The results indicated that the overall balance was comparable at each level of herbage availability, although when pasture was abundant there was a suggestion of an overall advantage to the sucking lamb and lactating ewe unit. The significant point was that at all levels of herbage availability a greater proportion of energy was channelled into the saleable commodity, i.e. the lamb, in the unweaned units.

In addition to ensuring a maximum channelling of nutrients to the lamb, it is necessary to maintain high fertility in the prime lamb producing flock. Management decisions have to be made to deal with the short term situation when feed shortage dictates a need for livestock movement or supplementary feeding. Studies that measure the amount of feed needed to restore the weight losses of the deprived ewes and the residual effects of such losses on future reproductive performance are needed to ensure that management strategies relating to early weaning are consistent with the maintenance of a high level of ewe fertility (Coop 1962; Large 1970; Curll 1976).

The present work has indicated the need for studies to define more precisely the requirements of milk and herbage for maximum growth rate of lambs grazing annual pastures. Annual pastures may senesce any time from September to December at Clare, South Australia. In general, only dry herbage residues remain for stock feed during the period of summer drought (Donald and Allden 1959). It is desirable to finish lambs for market before pastures have senesced otherwise lambs must be carried over summer on poor quality feed or fed a supplement. Pastures of differing herbage availabilities can be generated as in the current experiment and the time of senescence (i.e. quality) of pastures could be varied by applying dessicants to kill the pasture or irrigation to prolong pasture growth. Further treatments/ experiments which include milk feeding by the ewe and by bottle would permit isolation of the effects of the ewe's presence (grazing competition) and her milk supply on lamb growth. Furthermore weaning treatments could be included in such experiments to evaluate this practice which may be necessary when feed is in short supply or in accelerated lambing systems.

This experiment has illustrated the uses and limitations of short term studies of this kind. It has permitted a close examination of many of the processes within lambing systems without many of the confounding effects which commonly occur in experiments on continuing systems. For example, in the present study it was possible to examine the responses of ewes and lambs to early weaning over a wide range of herbage availabilities which are representative of many of the seasonal conditions encountered in a Mediterranean environment. Provided the results are viewed within the context of the design, they have proved to be valuable in providing an understanding of the effects of different levels of herbage availability on the outcome of weaning. Also certain pasture situations have been identified in which weaning is either a restrictive or a justifiable management practice.

5. EXPERIMENT 2

5.1 Objectives

The major aim of experiment 2 was to examine the influence of a wide range of seeding rates and plant densities on plant and animal production from annual pastures in the year of establishment. The objectives of this experiment extend beyond the boundaries of animal productivity (e.g. sheep live weight and wool) responses, and examine the growth of plants and changes in plant and tiller characteristics (such as plant number and weight, tiller length, number and weight and the number of tillers per plant) in grazed and ungrazed pastures over a wide range of plant densities. In addition, the effects on sheep intake of herbage yield and the components of yield, plant density and weight were studied in order to gain further understanding of mechanisms in operation in plant/animal associations in swards of different plant density. The experiment also provided the opportunity to compare the herbage intake of grazing animals when estimated by two methods, namely from herbage cutting (McIntyre 1951) and faecal collection techniques (Garrigus 1934).

5.2 Experimental Design

Natural plant populations in autumn in grazed annual pastures range from near zero (after prolonged droughts) to several thousand plants per square metre (Sharkey *et al.* 1964; Smith 1968c, 1972; Smith *et al.* 1972). Smith (1972) among others has recorded plant populations in autumn equivalent to sowing 700 kg seed per hectare.

5.2.1 Experimental treatments

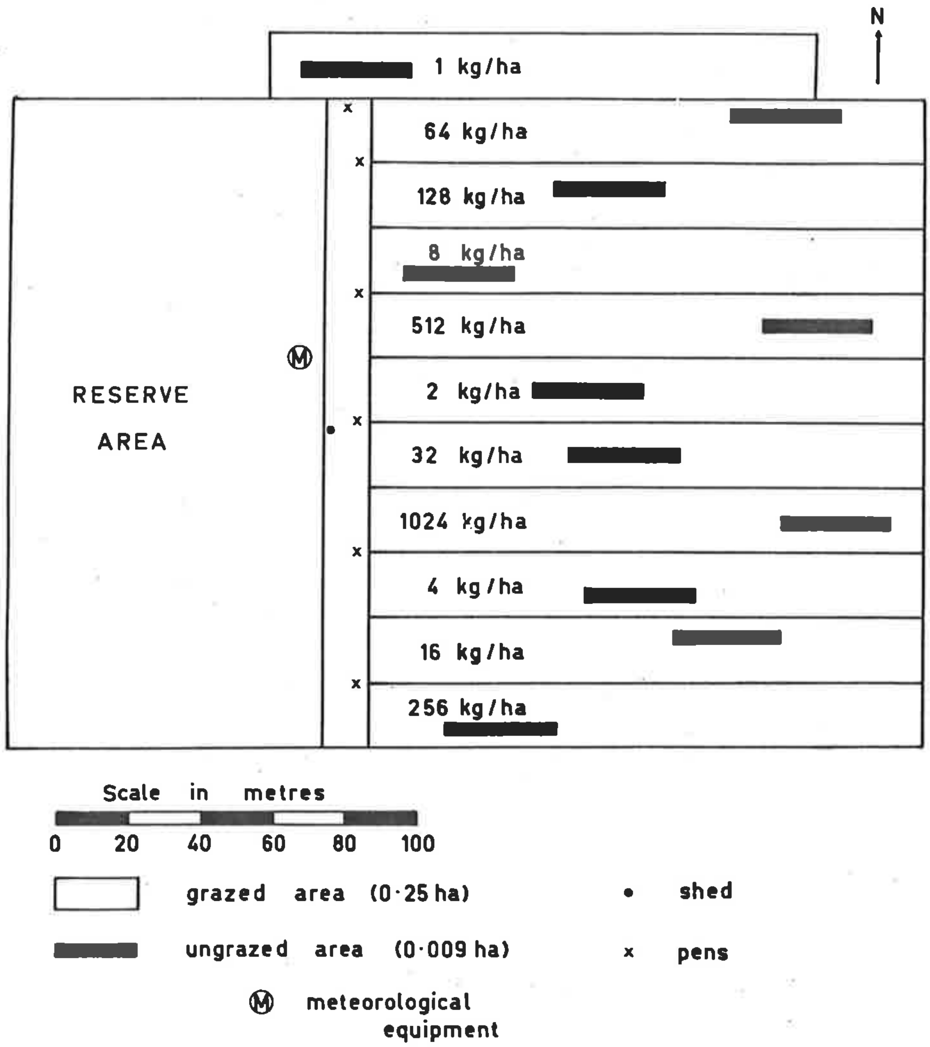
The objective was to establish a wide range of plant densities per unit area in order to produce the full range of plant populations which are likely to be encountered by animals grazing annual pastures over a number of years. It was more important to obtain swards with incremental increases in density rather than a restricted number of treatments with replication, since it is not physically possible to obtain exact replicates of plant establishment per unit area over large areas in field conditions. Eleven plots were sown at different seeding rates (from 1 to 1024 kg ha^{-1}) with a grazed and an ungrazed treatment within each seeding rate. Pastures of Wimmera ryegrass were sown on May 15th,1971 at the rates of:

1, 2, 4, 8, 16, 32, 64, 128, 256, 512 and 1024 kg seed ha^{-1}.

The seeding rate treatments were allocated at random to the eleven plots (each of 0.259 ha) as shown in Figure 14. An enclosed (ungrazed) area of 0.009 ha was allocated at random within each seeding rate treatment. Livestock were excluded from this area throughout the experiment. The remaining area of each plot (0.25 ha) was designated as the grazed plot area. On July 5th, 51 days after sowing, the grazed areas were stocked with 20 Merino wethers ha^{-1}. On October 4th, 143 days after sowing, the stocking rate was reduced on all plots to 12 wethers ha^{-1}, to reduce mortalities, until the completion of the experiment.

Five harvests were taken at approximately six week intervals after sowing, detailed measurements being made of plant and animal variables at each harvest.

Figure 14. Field plan of the experimental area showing the treatments in Experiment 2.


N
1 kg/ha
64 kg/ha
128 kg/ha
8 kg/ha
512 kg/ha
2 kg/ha
32 kg/ha
1024 kg/ha
4 kg/ha
16 kg/ha
256 kg/ha
RESERVE AREA
Scale in metres
0 20 40 60 80 100
grazed area (0·25 ha)
ungrazed area (0·009 ha)
shed
pens
meteorological equipment

5.2.2 Pasture establishment and management

Swards of Wimmera ryegrass were sown on May 15th, 1971 into a well prepared, weed-free seedbed at seeding rates of 1 to 1024 kg ha^{-1}. An adjacent area of 1.7 ha (termed the reserve area) was also sown with 20 kg ha^{-1} of Wimmera ryegrass seed. This area was used for holding animals with oesophageal fistulae.

5.2.3 Animals and their management

(a) The experimental animals

The sheep used were three year old, medium woolled, South Australian Merino wethers (Bungaree strain). From a uniform flock of 115 wethers, five sheep were allocated at random to each of the 11 treatments on the basis of live weight. A flock of five wethers was placed on each grazed plot on July 5th, 1971.

(b) Sheep mortalities

Sheep that died during the experiment were replaced with wethers of similar age. The pool of reserve sheep was maintained on an adjacent Wimmera ryegrass dominant pasture at a moderate stocking rate (10 sheep ha^{-1}) to minimize mortalities. The live weight of a replacement animal was invariably greater than the animal for which it was a substitute. Replacement animals were not used for animal data, but were necessary to maintain a uniform number of grazing animals per plot. When deaths occurred, the dead animals were weighed and the dyebands and fleece removed (as described in Section 5.3.4b) within approximately 15 hours of death. A *post mortem* examination was carried out on each carcass. Deaths were always associated with severe nutritional stress and no significant disease conditions were observed.

(c) Oesophageally fistulated (O.F.) sheep

Twenty Merino wethers from the original flock were selected at random and fistulated at the oesophagus on April 22nd, 1971. The fistulation procedure is described in Section 4.2.2. These animals were used to obtain samples of the diet of sheep grazing the experimental plots. The 20 O.F. sheep grazed the Wimmera ryegrass pasture in the reserve area (Figure 14) throughout the experiment, except when samples were being collected on the treatment plots.

5.3 Measurements

5.3.1 General

The major objective was to measure plant and animal production from pastures of different plant densities in the year of establishment. Measurements were also made of many plant characteristics such as plant number per unit area and individual plant weight to isolate plant factors associated with low or high levels of production from pastures of different plant density. In addition to measurements of sheep live weight and wool production, the intake of herbage by sheep and the components of intake (rate of intake and grazing time) were also estimated, the aim being to study the ways in which animals alter their intake and grazing behaviour on pastures of different plant densities and the effects of these changes on plant and animal production.

5.3.2 Variables measured

As mentioned earlier, five harvests were taken at approximately six-weekly intervals after sowing, at which detailed measurements were made of the plant and animal variables. A list of the variables measured in experiment 2 is given in Table 24, and details of their measurements follow.

5.3.3 Pasture measurements

Plant measurements were made in order to estimate the significance of changes in the plant population with time to plant growth and plant characteristics in grazed and ungrazed swards. The characters under study are listed in Table 24. Plant number per unit area, plant weight, tiller length, number and weight and the number of tillers per plant were measured at each harvest in grazed

Table 24. Variables measured in Experiment 2.

Variables measured
(i) Plant
(a) Tiller length, tillers per plant, plant weight and number
(b) Tiller number and weight (derived)
(c) Herbage dry matter yield on offer (availability)
(d) Herbage growth rate and cumulative yield (production)
(e) Digestibility of whole plants
(f) Herbage intake (estimated by a herbage cutting technique)
(g) Seed yield
(ii) Animal
(a) Live weight and survival
(b) Wool
(c) Herbage intake (estimated by a faecal collection method) and digestibility of the diet
(d) Comparison of two methods of estimating intake
(e) Components of intake, the daily rate of intake and grazing time

* All variables were measured at each of 5 harvests (the dates of sampling are given in Table 26) except for seed yield which was estimated at the end of the experiment.

swards from core samples (Hutchinson 1967).

Grazed plots were divided into 20 equal areas (strata) and ungrazed plots were divided into ten strata and one core sample (80.7 cm^2 in area) was taken at random within each strata at each harvest. However, on the very low density plots (seeding rates 1 to 4 kg ha^{-1}) it was necessary to take 10 cores per strata to obtain sufficient plant material for measurement. It was only possible to accurately core sample ungrazed plots at the first three harvests. At later harvests, the height of the pasture in ungrazed plots made accurate core sampling impossible and an alternative method of sampling was used. This involved taking 50 plants at random from each plot in the field. This material and the cores of pasture were stored at 4°C until the plant material could be harvested and measured.

(a) Tiller length, tillers per plant, plant weight and number

Five plants were selected at random from each core then tiller length was measured as described in Section 4.3.1b. The number of tillers per plant were counted and recorded. Then plants were washed to remove soil, combined and oven dried at 80°C for 24 hours and weighed (Sample A) and the mean dry weight of individual plants per core calculated. The remainder of the herbage in the core was then cut at ground level, washed, dried and weighed (Sample B).

Plant number per unit area in core samples was calculated by dividing the total weight of dry matter per core by the mean individual plant weight (i.e. (A+B)/0.2A).

The above sward characteristics were measured in ungrazed plots at harvests 4 and 5 from the 50 plants that were harvested from each plot. Also, plant number per unit area was estimated by dividing dry matter yield per unit area (estimated by the visual method as described in Section 5.3.3c) by the mean individual plant weight.

(b) Tiller number and weight (derived)

Tiller numbers per unit area were derived from the product of plant number and the number of tillers per plant. Individual tiller weight was derived by dividing plant weight by the number of tillers per plant.

(c) (i) Herbage dry matter (DM) yield on offer (availability)

Herbage yield present or availability was estimated in all swards using the visual method of Morley et al. (1964). Grazed plots were divided into ten equal areas (strata) with five trained observers each making 10 visual estimates of yield in each treatment (one estimate per strata). Conversely ungrazed plots were divided into five equal strata and the five observers made five estimates of yield per treatment (one per strata). Each observer visited fixed (compulsory) quadrats pegged out in each treatment. These quadrats were cut at ground level, after visual assessment, then washed, oven dried and weighed in order to convert the visual yield estimates to actual yield data using regression techniques.

(d) Growth rate and cumulative yield (production) of herbage

Herbage growth rates and cumulative yield in grazed plots were estimated by using the open and closed quadrat technique of McIntyre (1946, 1951). Six paired, 1.5 m by 1.5 m quadrat cages were placed at random on each grazed plot at each harvest. At the beginning (t_1) and end (t_2) of a period of enclosure a quadrat sample, 61 cm by 61 cm was harvested from the middle of each cage. The herbage was cut at ground level, washed to remove soil, oven dried and weighed.

The daily growth rate of herbage was calculated as:

$$\frac{W_c - W_o}{t_2 - t_1} \text{ kg DM ha}^{-1} \text{ day}^{-1}$$

where, W_o was the weight of DM on the grazed area at time, t_1. W_c was the yield of DM on the area enclosed at time, t_1, at a later time, t_2. Since livestock did not have access to the ungrazed plots, herbage growth rate was calculated as the difference in yield present between any two harvest occasions divided by the number of days between those harvests. In ungrazed swards herbage yield was measured as described in Section 5.3.3c.

(e) Digestibility of whole plants

At each harvest comparisons were made of the digestibility of whole plants in grazed and ungrazed swards. Subsamples were taken at random from the oven dried herbage material from compulsory quadrats that had been cut for the estimation of herbage yield (Section 5.3.3c). In plots of verylow density it was often necessary to collect further plant material at random in the field to obtain sufficient material for analysis. Organic matter and digestibility analyses were carried out as described in experiment 1 (Section 4.3.2c).

(f) Herbage intake (estimated by a herbage cutting technique)

A crude estimate of herbage intake was obtained from the difference between the production and availability of pasture

(Section 3.3.3d) as described by Carter and Day (1970). This method is termed the herbage cutting technique of intake estimation. The organic matter content and digestibility of whole plant samples, as measured in Section 3.3.3e were used to calculate the intake of digestible organic matter. The DE intake was calculated using the value for ryegrass of 19.7 kJ (4.7 kcal) per gram of digestible organic matter as reported by Kellaway (1969).

(g) Seed yield

Seed yield was measured at the end of the experiment in order to estimate the seed reserves present for pasture regeneration. Seed yield per unit area was estimated in January, 1972 by harvesting the herbage within 0.25 m^2 quadrats together with the seed on the ground. Ten samples were harvested from each grazed and ungrazed plot from seven seeding rate treatments (i.e. 1, 4, 16, 32, 64, 256, 1024 kg seed ha^{-1}). The samples were air dried, then the herbage was separated from soil by flotation and the herbage air dried and threshed. Then the seed was cleaned and weighed at a constant moisture content of 10 percent.

5.3.4 Animal measurements

A major aim of this experiment was to determine if different plant populations in annual swards generate differences in animal production. Measurements were made of liveweight changes, herbage digestibility, herbage intake and the components of intake - rate of intake and grazing time with the object of relating these characters to plant productivity at the different density treatments.

(a) Sheep live weight and survival

Sheep were weighed at measured intervals during the experiment after being confined overnight in pens to reduce gut fill (Gharaybeh et al. 1966). Live weights (kg) were adjusted for estimates of fleece carried as described in Section 5.3.4b. Sheep survival was recorded and sheep that died were replaced as described in Section 5.2.3b. Data from replacement sheep were not included in the analyses.

(b) Wool

Clean wool production was estimated for each of the interharvest periods and for the whole experiment using the dyeband method of Chapman and Wheeler (1963), and the scouring technique of Frazer and Short (1960). Two dyebands were applied to the left mid-side of each sheep on April 9th, 1971 and at each harvest.

For the determination of clean wool weights dyebanded samples were immersed several times in a degreasing solvent (Shell 'X4') with a liquor to wool ratio of about 200 : 1 (Williams and Chapman 1966). The moist sample was then cut along the bottom of the dyebands with sharp scissors, dried overnight at 100°C and weighed.

When an animal died, the length of wool grown was measured on the sheep's body before removing the dyebanded staple with Oster clippers (Williams and Chapman 1966). The length of wool grown was measured again on staples after removal from the animal and the ratio of the two measurements used to correct the pile error (Hutchinson 1969).

(c) Herbage intake (estimated by a faecal collection method) and digestibility of the diet

The herbage intake of grazing sheep was estimated from measurements of faecal output (F) and of the digestibility (D) of the pasture consumed and has been described in experiment 1, Section 4.3.2c. The DE intake of the Merino wethers was calculated using the value for ryegrass of 19.7 kJ (4.7 kcal) per gram of digestible organic matter as reported by Kellaway (1969). This technique is termed the faecal collection method.

(i) Faecal output

Faecal collections were made from all the experimental sheep on three successive days at each harvest. The sheep were fitted with canvas harnesses and bags. During a collection period the total output of faeces of each sheep was collected daily and treated as described in experiment 1 (Section 4.3.2c).

(ii) Digestibility of the diet

Extrusa samples were collected from O.F. sheep on the grazed plots at each harvest period (Section 5.2.3c). At each harvest, flocks of three O.F. wethers were placed at random on each grazed plot on alternative days of a four day collection period. Thus, at each harvest the herbage of each plot was sampled by a total of six O.F. wethers over a three day period. Extrusa samples were collected and analysed as in experiment 1 (Section 4.3.2c).

(d) Comparison of two methods of estimating intake

Intake as estimated by a faecal collection method (as described above) was compared with intake estimated from a herbage cutting technique as described in Section 5.3.3f. Relationships between intake and live weight, liveweight change and wool growth were examined for each method of determining intake.

(e) Rate of herbage intake and grazing time

Daily rate of intake was derived by dividing total daily herbage intake (of each animal) by the time spent grazing. The time spent grazing by each sheep was determined by visual observation over 36 hour periods during the final days of each harvest as described in experiment 1 (Section 4.3.2i).

5.3.5 Summary of experimental procedures

A schematic outline of the main events during the course of a harvest are given in Table 25 and the dates of sampling in Table 26.

5.3.6 Statistical analysis of the data

This experiment was a study of the responses of a constant number of animals to changes in seeding rate and in the subsequent plant population. The experimental design contained eleven unreplicated seeding rate treatments in a geometric progression from 1 to 1024 kg seed ha^{-1}. Most of the data were analysed from two dimensional response relationships using regression procedures which related plant and animal data to seeding rates and plant densities.

(a) Construction of plant growth curves

A logistic equation (Richards 1959) was used to describe plant growth in grazed and ungrazed swards and was fitted by an iterative method to each set of data points (for a given seeding rate treatment). The equation is:

Table 25. A schematic outline of the main events during the course of a harvest. Five such harvests were undertaken.

Day of harvest				
1.	Open and closed quadrats cut Visual assessment of herbage yield present			Weigh sheep
2.		Collection of O.F. extrusa and whole plant samples	Collection of faeces	
3.	Core sampling			
4.				
5.				
6.				Grazing time
7.				
8.	Dyeband wethers			

Table 26. Sampling programme in Experiment 2.

Harvest	Date	Days from sowing	Measurements: (i) Plant — Tiller length, tillers per plant, plant no. and weight, tiller no. and weight	(i) Plant — Herbage yield present in grazed and ungrazed swards	(i) Plant — Herbage growth rate, cumulative yield and intake (cutting technique)	(i) Plant — Digestibility of whole plants	(ii) Animal — Live weight	(ii) Animal — Intake (faecal and O.F. samples)	(ii) Animal — Grazing time	(ii) Animal — Wool
h_1	July									
	5th	51			*		*			
	6th	52		*		*				
	7th	53	*							
	8th	54						*		
	9th	55								
	10th	56							*	
	11th	57								
	12th	58								*
h_2	Aug.									
	9th	86			*					
	10th	87		*		*				
	11th	88	*							
	12th	89						*		
	13th	90								
	14th	91							*	
	15th	92								
	16th	93					*			*
h_3	Sept.									
	27th	135			*		*			
	28th	136		*		*				
	29th	137	*							
	30th	138						*		
	Oct.									
	1st	139								
	2nd	140							*	
	3rd	141								
	4th	142								*
h_4	Nov.									
	8th	177			*					
	9th	178		*						
	10th	179	*							
	11th	180						*		
	12th	181								
	13th	182							*	
	14th	183								
	15th	184					*			*
h_5	Dec.									
	13th	212			*		*			
	14th	213		*		*				
	15th	214	*							
	16th	215						*		
	17th	216								
	18th	217							*	
	19th	218								
	20th	219								
	21st	220					*			*

* Mean date of sampling.

$$Y = \frac{A}{1 + Be^{-CT}}$$

where Y = cumulative herbage DM yield (kg ha^{-1}) (shoot DM)

T = days from sowing (not emergence)

e = the base of natural logarithm

A defines maximum herbage production where T = ∞;

and B and C are constants which define the shape of the curve.

The following functions may be derived from the equation:

¼ AC, maximum plant growth rate (kg ha^{-1} day^{-1}),

½ A, point of inflexion, and the plant yield at which maximum plant growth rate occurs (kg ha^{-1}); and

$(\log_e B)/C$, days from sowing to maximum plant growth rate.

(b) Animal data

Certain animal data (e.g. live weight of sheep) were subjected to analyses of variance (Steel and Torrie 1960), the aim being to test for significant differences in animal performance on the different seeding rate treatments. Least significant differences (LSD) were calculated when the F test was significant. Such significant differences were due to a summation of animal and plant density effects within treatments. Regression analysis was used to examine trends in productivity associated with plant density.

Differences between two methods of intake estimation were examined. Linear regression equations were calculated relating intake (estimated by the two methods) to sheep liveweight change. These equations were then compared by testing for significant differences between the slopes and displacements of these lines.

5.4 Results of Experiment 2

Some comment is needed to explain the order of presentation of results. Logically, one might expect to examine in the first place all the changes in the plant characteristics of the swards and then proceed to examine the effects of these changes on the animal population. However, this approach would involve the presentation of much plant data without any indication of the final outcome on animal performance. To overcome this problem, the major effects of the plant density treatments on pasture yield and animal productivity are first described so that the more detailed plant and animal responses can then be outlined against a background of the overall production trends generated within the experiment. Comparisons of grazed and ungrazed swards are made in the final section.

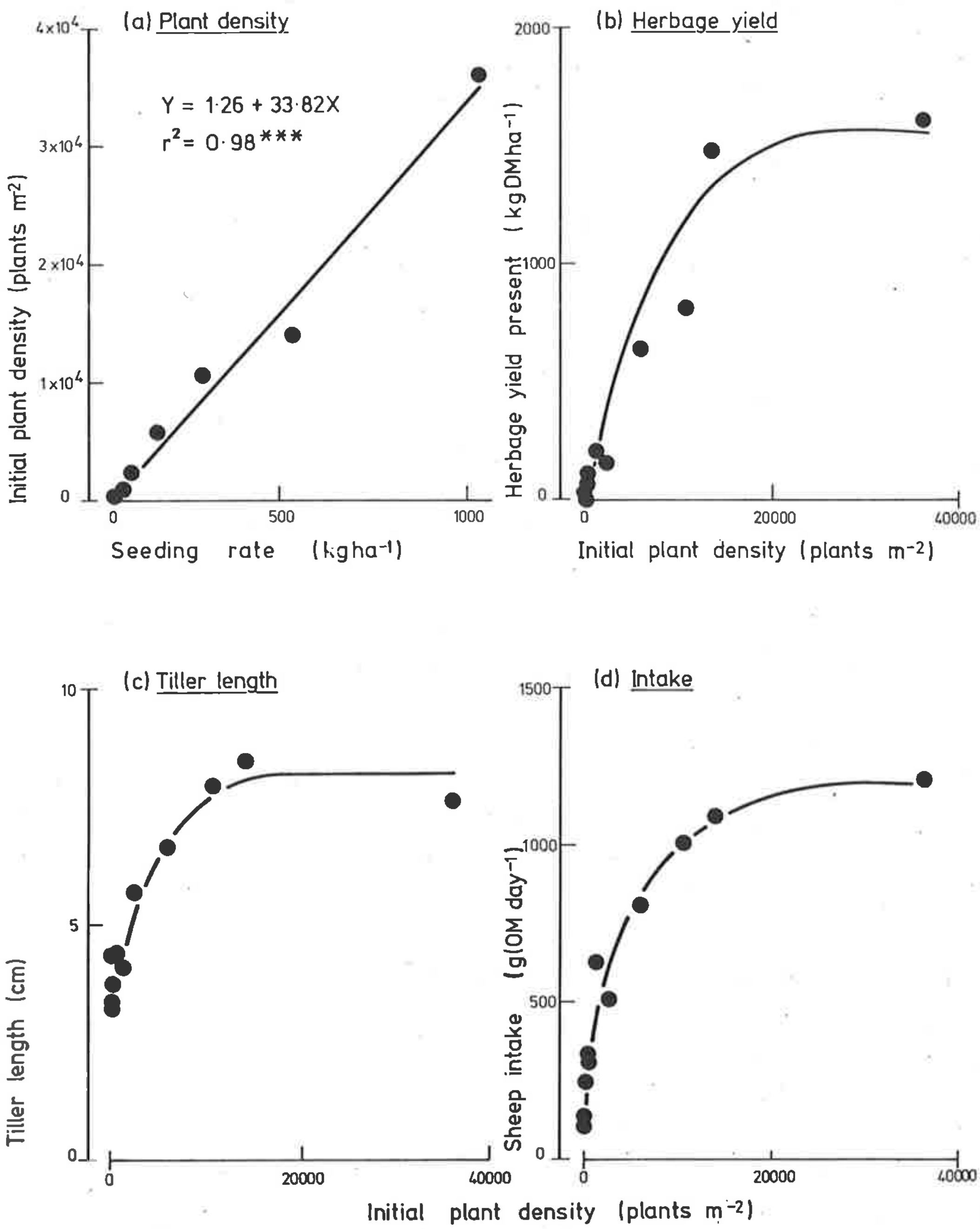
5.4.1 Plant density, yield, tiller length and herbage intake at the onset of grazing

The objectives of obtaining swards with a wide range in plant density and herbage yield were achieved. The seeding rates from 1 to 1024 kg ha^{-1} produced pastures with an approximately 950-fold range in plant density and a 200-fold difference in herbage yield, at harvest 1 when the grazing of plots began (Figure 15a, b).

Each additional 1 kg ha^{-1} of seed sown (i.e. 50 seeds m^{-2}) on 15th May produced 34 plants m^{-1} on the 7th July, 53 days after sowing (Figure 15a). Thus the terms seeding rate and initial plant density (IPD) will be interchanged freely in the text. Plant yield,

Figure 15. (a) (Top, left) The relation of initial plant density (Y, plants m^{-2}) on 7th July, 53 days after sowing to seeding rate (X, kg ha^{-1}) for the grazed treatments. The relations of (b) (Top, right) herbage yield present (c) (Bottom, left) tiller length and (d) (Bottom, right) sheep intake at harvest 1 to initial plant density.

Harvest 1



(a) Plant density
4x10⁴
3x10⁴
2x10⁴
1x10⁴
0
Y = 1·26 + 33·82X
r² = 0·98***
Initial plant density (plants m⁻²)
0
500
1000
Seeding rate (kgha⁻¹)
(b) Herbage yield
2000
1000
0
Herbage yield present (kgDMha⁻¹)
0
20000
40000
Initial plant density (plants m⁻²)
(c) Tiller length
10
5
0
Tiller length (cm)
0
20000
40000
(d) Intake
1500
1000
500
0
Sheep intake (g(OM day⁻¹)
0
20000
40000
Initial plant density (plants m⁻²)

tiller length and herbage intake all increased in an asymptotic fashion as IPD increased (Figure 15b, c and d). When sheep were placed on the experimental swards, the wide range in plant density and herbage yields present led to a 12-fold range in herbage intake (from 104 to 1211 g OM day^{-1}, see Figure 15d).

5.4.2 Animal production

(a) Sheep live weight and survival

The seeding rates used induced markedly different responses in the liveweight change and survival of grazing sheep (Figures 16 and 17). Swards of different seeding rates were found to fall into three distinct categories: low, medium and high, based on sheep live weight and survival in time. Swards could also be termed stable or unstable on the basis of animal survival and productivity.

The three categories are:

(i) Low density swards (unstable) - seeding rates of 1-16 kg ha^{-1}; IPD of 38-495 plants m^{-2},

(ii) Medium density swards (stable) - seeding rates of 32-64 kg ha^{-1}; IPD of 1124-2444 plants m^{-2},

(iii) High density swards (stable) - seeding rates of 128-1024 kg ha^{-1}; IPD of 5750-35993 plants m^{-2}.

(i) Low density swards (unstable)

On swards of low density sheep were unable to maintain their initial live weight, except for sheep on the 16 kg ha^{-1} treatment which gained weight for a brief period in spring (Figure 16). Thus, the fleece-free live weights of wethers on low density swards at the end

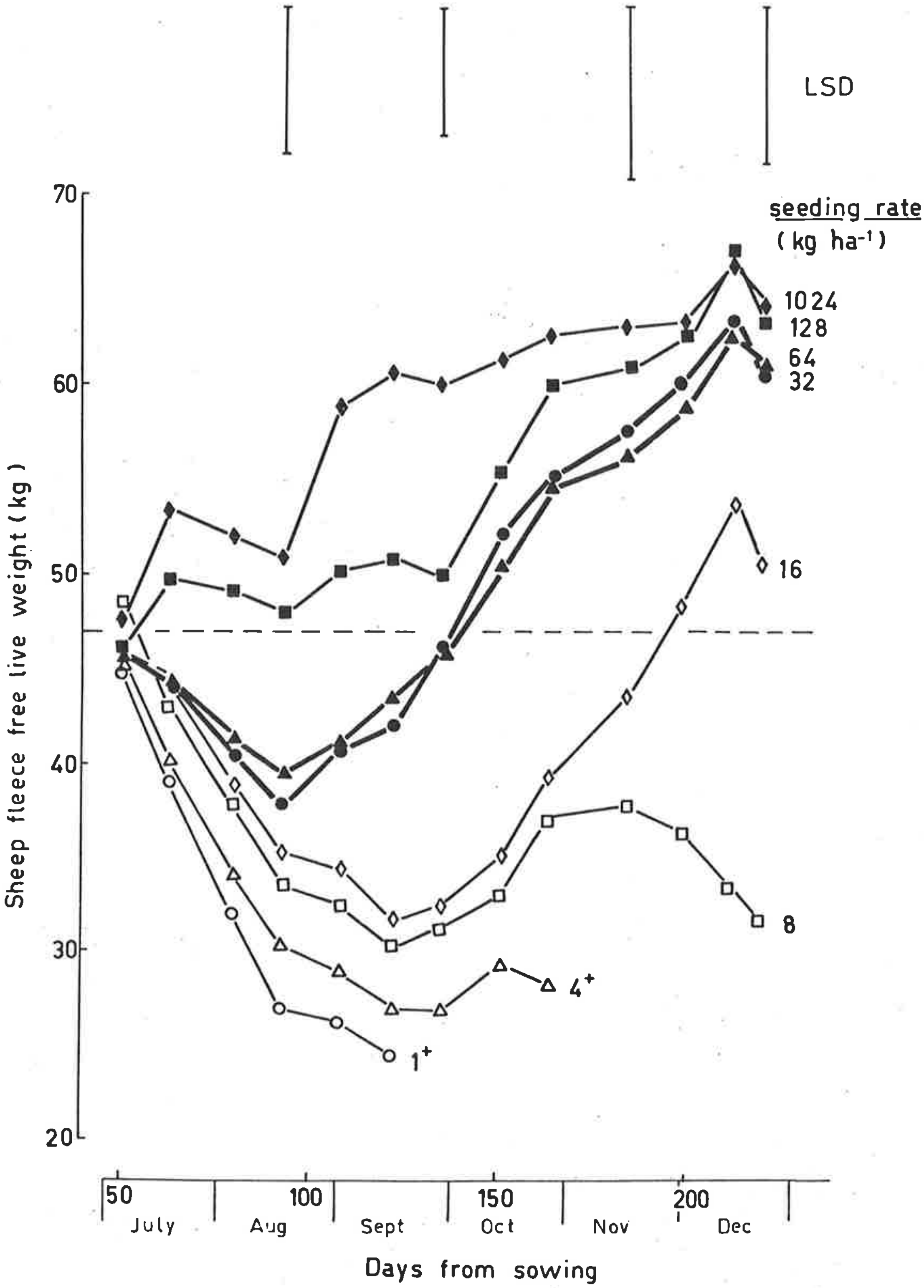
Figure 16. A comparison of changes in sheep fleece free live weight with time for sheep grazing swards sown at a selected range of seeding rates. Data for original animals only are presented. Analyses of variance for computation of LSD's are presented in Appendix Table 10.

(i) Low density swards (seeding rates 1-16 kg ha^{-1}) are represented by the thinnest lines;

(ii) Medium density swards (seeding rates 32-64 kg ha^{-1}) by the thickest lines; and

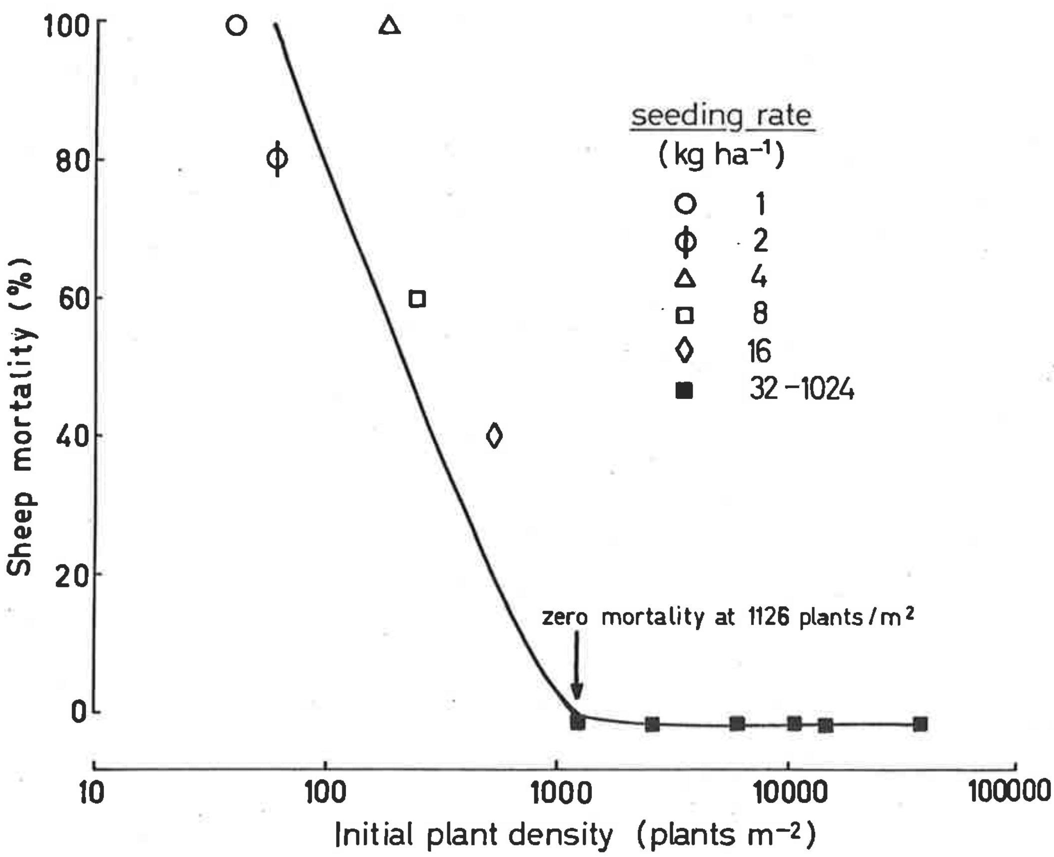
(iii) High density swards (seeding rates 128-1024 kg ha^{-1}) by lines of intermediate thickness.

\+ On the seeding rate treatments, 1 and 4 kg ha^{-1}, all the original experimental sheep died before the end of the experiment.



LSD
70
60
50
40
30
20
seeding rate
(kg ha-1)
1024
128
64
32
16
8
4+
1+
Sheep fleece free live weight (kg)
50
100
150
200
July
Aug
Sept
Oct
Nov
Dec
Days from sowing

Figure 17. The relation of sheep mortality to initial plant density (logarithmic scale). Mortality of original animals only is presented.
The curve is eye fitted.



100
80
60
40
20
0
Sheep mortality (%)
seeding rate
(kg ha⁻¹)
1
2
4
8
16
32 - 1024
zero mortality at 1126 plants / m²
10
100
1000
10000
100000
Initial plant density (plants m⁻²)

of the experiment ranged from 25 to 50 kg and were substantially less than those of sheep grazing higher density swards (the latter sheep weighed 63 kg). Sheep mortality occurred at the low seeding rates; ranging from 100% losses at 1 kg ha^{-1} to 40% deaths at 16 kg ha^{-1} (Figure 17). Sheep mortality tended to occur earlier in time the lower the seeding rate of the sward (Appendix Table 9).

(ii) Medium density swards (stable)

No mortalities were recorded on swards of medium and high densities (seeding rates of 32 kg ha^{-1} and greater) and the final live weights of wethers grazing these swards were similar (c. 63 kg). Although sheep on medium density swards lost 15-20% of their initial live weight during the early part of the experiment, these animals compensated for this loss of production during the spring period. Live weight of these animals at the end of the experiment (61 kg) did not differ from those grazing higher density swards (64 kg).

(iii) High density swards (stable)

Wethers grazing high density swards (seeding rates of 128 kg ha^{-1} and greater) gained weight throughout the experiment.

Views of swards and sheep for a range of seeding rate treatments at different harvests are presented in Appendix Plates 4-7.

(b) Total herbage yield, intake, liveweight change and wool growth

Live weight, intake and wool data for the individual plots are summarized in Appendix Tables 10-12. Figure 18 shows that during the complete experimental period a minimum IPD of 1126 plants m^{-2} was required for maximum total herbage yield, intake, liveweight gain and wool production. There was a tendency for sheep intake and

Figure 18. The relations of

(a) (Top, left) total herbage yield,

(b) (Top, right) sheep intake^{+},

(c) (Bottom, left) liveweight change^{+},

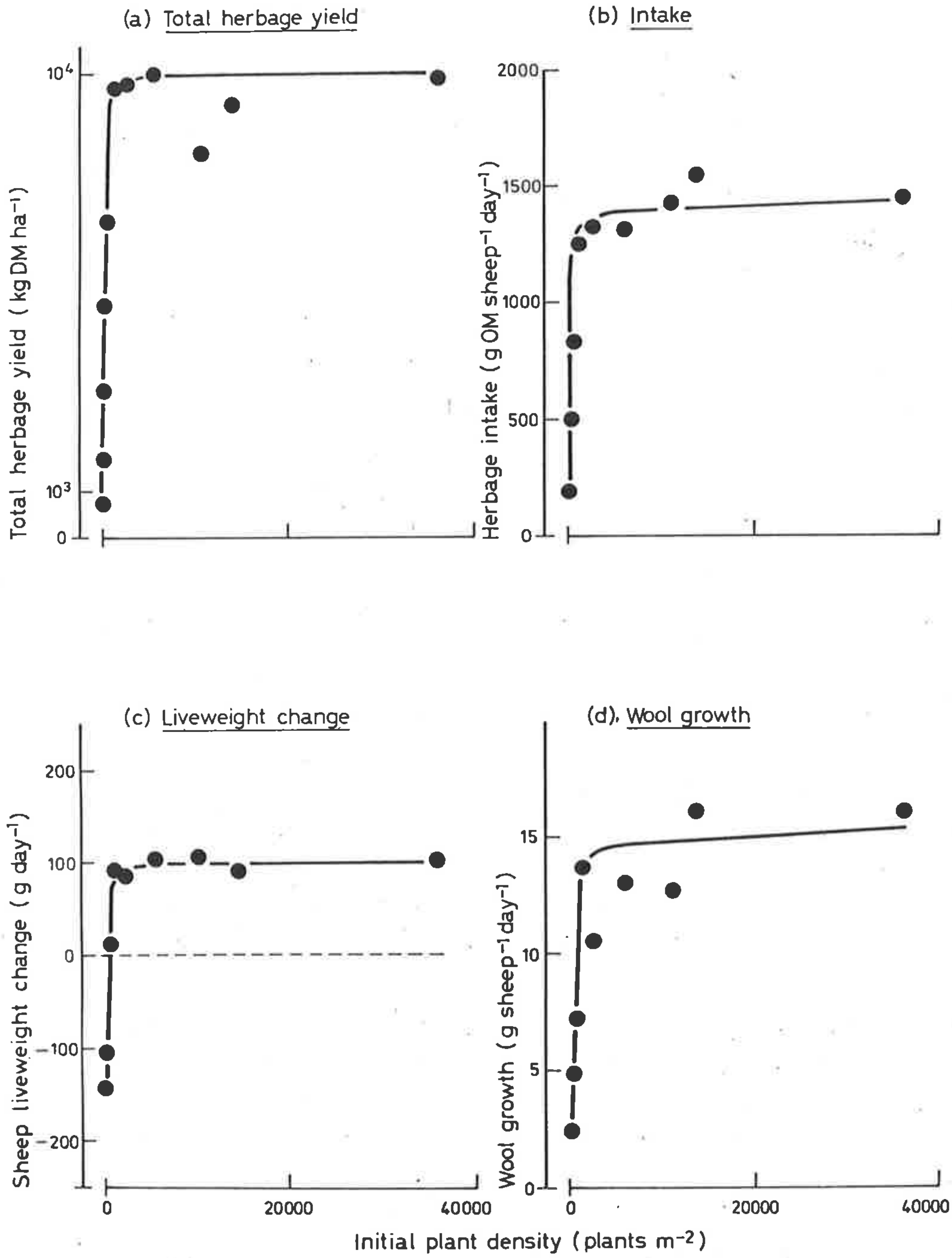
and

(d) (Bottom, right) wool growth^{+} produced over the full experiment to initial plant density.

\+ Data for nine seeding rate treatments are presented since all original experimental sheep died before the end of the experiment on the 1 and 4 kg ha^{-1} treatments.

Curves are eye fitted.

Full Experiment



wool growth to increase slightly as IPD increased above 1126 plants m^{-2}. Sheep grazing swards seeded with 16 and 1 kg seed ha^{-1}, produced 8 and 2 g of clean wool day^{-1}, respectively (Figure 18). On higher density swards, wool growth ranged from 11 to 16 g day^{-1}.

5.4.3 Herbage yield and plant density

(a) Herbage yield on offer and cumulative yield

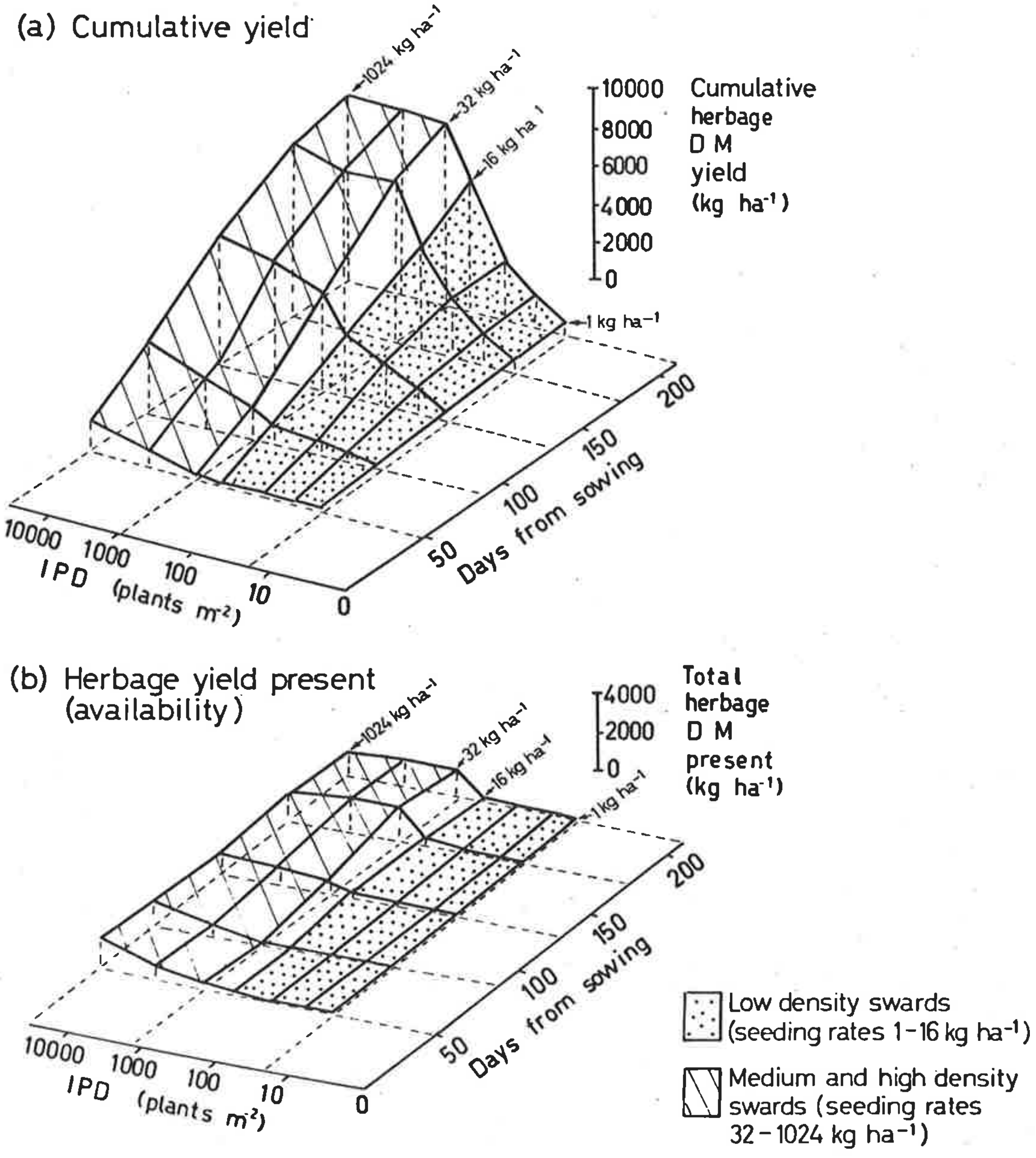
Figure 19a, b shows how the initial plant density influenced both herbage yield (the amount of herbage on offer) and cumulative yield of grazed swards on five harvest occasions. Appendix Tables 13 and 14 summarise the herbage yield data. The seeding rates from 1 to 1024 kg DM ha^{-1} produced swards with an initial 270-fold difference in yield when grazing treatments were imposed (Figure 15); this was reduced to 14-fold by the end of the experiment, 212 days after sowing (Figure 19a). Over the seeding rates 1-16 kg ha^{-1}, the low density swards gave total herbage yields of 7% to 75%, respectively of those from swards of higher density; an effect which was reflected in the large differences in animal production recorded in the previous section. A minimum IPD of 1126 plants m^{-2} (a seeding rate of 32 kg ha^{-1}) was required for maximum total yield and for maximum yield on offer at harvests 3 to 5.

In terms of herbage availability the initial 270-fold difference in herbage yield on offer between pastures of different densities persisted throughout the experiment (Figure 19b and Appendix Table 14). A minimum herbage yield on offer ranging from 670 to 1800 kg DM ha^{-1} is required for maximum animal production from annual pastures (Scott Young 1960; Arnold 1964a; Allden and Whittaker 1970). It is clear that on the low density swards the limited herbage

Figure 19a, b. (a) (Top) Changes in cumulative herbage yield in relation to IPD (logarithmic scale) and time in grazed swards sown at a selected range of seeding rates.

(b) (Bottom) Changes in herbage yield present (availability) in relation to IPD (logarithmic scale) and time in grazed swards sown at a selected range of seeding rates.

Seeding rate treatments of 1, 16, 32 and 1024 kg ha^{-1} have been identified on each figure.



(a) Cumulative yield
1024 kg ha-1
32 kg ha-1
16 kg ha-1
1 kg ha-1
10000
8000
6000
4000
2000
0
Cumulative herbage D M yield (kg ha-1)
10000 1000 100 10 0
IPD (plants m-2)
50 100 150 200
Days from sowing
(b) Herbage yield present (availability)
1024 kg ha-1
32 kg ha-1
16 kg ha-1
1 kg ha-1
4000
2000
0
Total herbage D M present (kg ha-1)
10000 1000 100 10 0
IPD (plants m-2)
50 100 150 200
Days from sowing
Low density swards (seeding rates 1-16 kg ha-1)
Medium and high density swards (seeding rates 32-1024 kg ha-1)

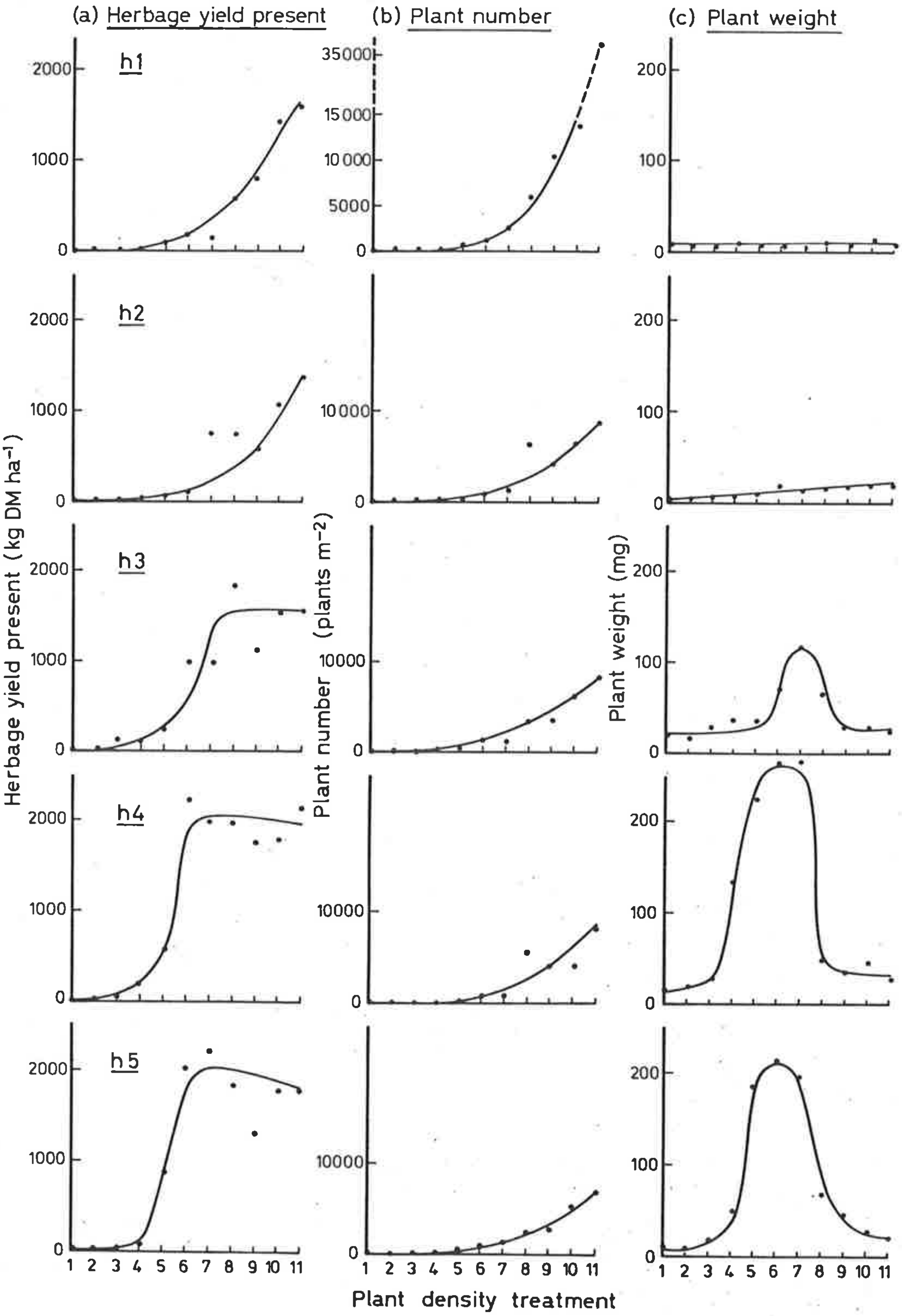
yields on offer were always less than the above range (Figure 19b), and thus associated with suboptimal levels of animal production recorded in Section 5.4.2. In summary, the most significant aspects of the yield data were that swards with seeding rates from 1 to 16 kg ha^{-1} produced far less herbage than those of higher density and that the time to produce maximum herbage yields (both on offer and accumulated) increased as the seeding rate decreased (Figure 19a, b). Thus at a comparable stocking rate, plant density had a very significant effect on total herbage yield and on the amount of herbage available to the grazing animal throughout the experiment. A minimum IPD of 1126 plants m^{-2} (seeding rate 32 kg ha^{-1}) was required for maximum total yield and for maximum herbage yield on offer at harvests 3 to 5.

5.4.4 Plant number and weight in relation to plant density

Herbage yield on offer (availability) is the product of plant number per unit area and individual plant weight. Data for ryegrass plant numbers and weights for individual plots are given in Appendix Tables 15-17. Figure 20 shows the effects of the density treatments on herbage yield on offer and its components plant weight and plant number at 5 harvests.

The scales on the Y ordinates for each pasture characteristic are identical for all harvests to facilitate visual comparisons of the data down the page in Figure 20. There were remarkably consistent responses of herbage availability and its components, plant number and weight to incremental changes in plant density. At harvest 1, there was an exponential relationship between density and availability, herbage yield on offer increased over the full range of plant density. These increases were mainly associated with increases in the number of plants present, individual plant weight being relatively constant (approximately

Figure 20. Changes in (a) (Left) herbage yield on offer (availability) and its components, (b) (Centre) plant number, and (c) (Right) plant weight in relation to plant density treatments in grazed swards at 5 harvests.
All curves are eye fitted.



(a) Herbage yield present
(b) Plant number
(c) Plant weight
h1
h2
h3
h4
h5
Herbage yield present (kg DM ha⁻¹)
Plant number (plants m⁻²)
Plant weight (mg)
2000
1000
0
35000
15000
10000
5000
200
100
1 2 3 4 5 6 7 8 9 10 11
Plant density treatment

10 mg). There was a progressive increase in plant weight at harvest 2 as density increased . At the later harvests (3 and 4) there was an asymptotic relationship between density and availability, there being a rapid increase in herbage availability from density treatment 1 up to treatment 6 (i.e. up to seeding rate of 32 kg ha^{-1}); whereas availability remained relatively constant at higher plant densities. Herbage availability was less on the high compared to medium density swards at harvest 5. The highest density swards tended to mature earliest. At the three later harvests, there was a substantial increase in the weight of individual plants in the intermediate density treatments 4 to 8, with little change evident in the other treatments. The highest weight of individual plants recorded (264 mg) occurred in density treatment 6 (i.e. a seeding of 32 kg ha^{-1}) at harvest 4.

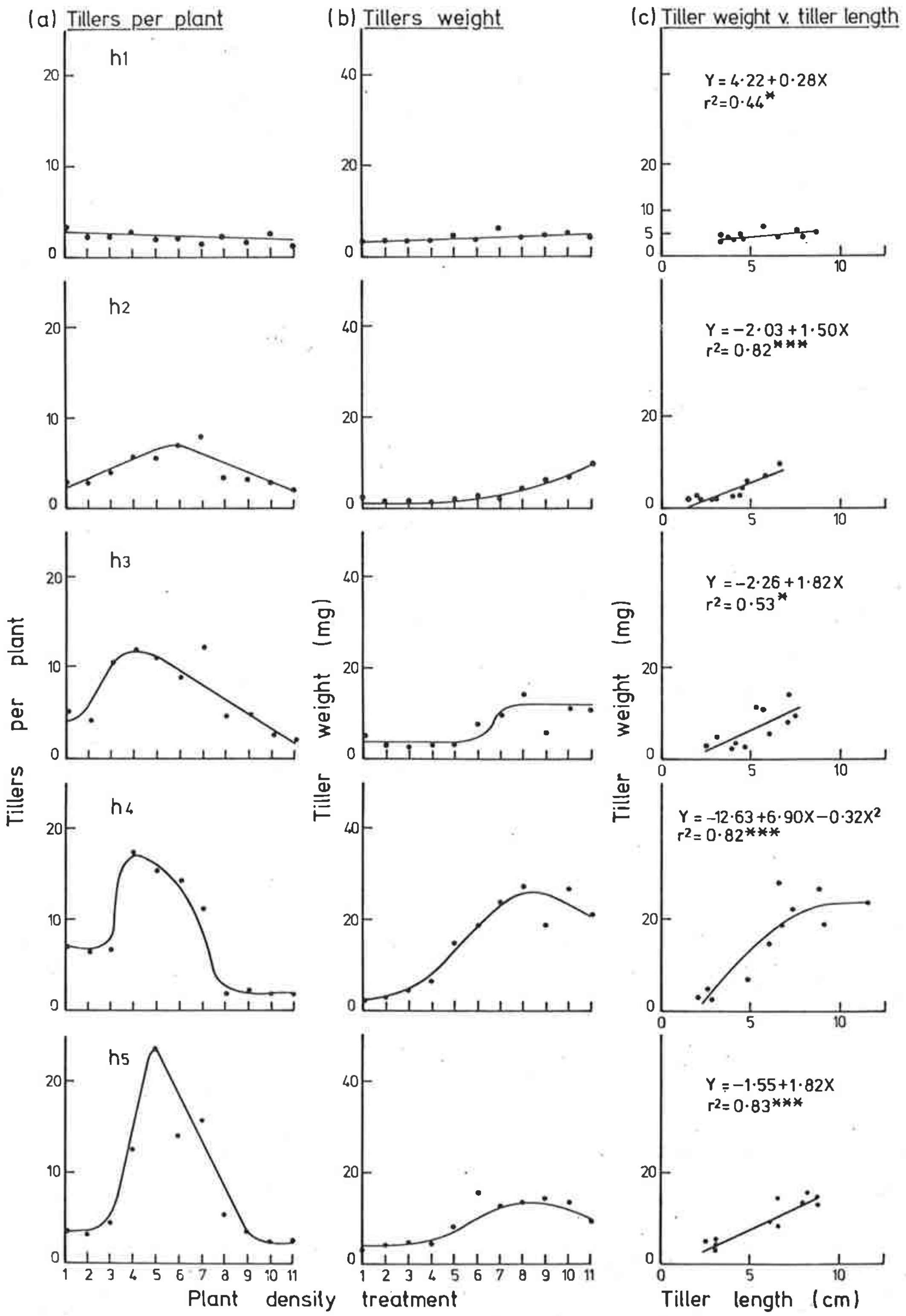
The most significant aspect of the relationship between herbage yield and its components was that in low density swards, increases in individual plant weight were not sufficient to compensate fully for the paucity of plants so that at all times herbage yield was substantially less than for swards of higher density (Figure 20). In swards sown at 32 kg ha^{-1} and higher the increases in individual plant weight fully compensated for any deficiency in plant numbers in terms of the total yield and availability of herbage at harvests 3 to 5 (Figures 19a, b and 20). Swards in which this compensatory mechanism was not fully expressed were those which produced sub-optimal levels of animal production (Section 5.4.2). Thus instability and associated low productivity in annual pastures occurred when a deficiency in one component of herbage yield could not be fully compensated for by an increase in another component during the growing season.

Differences in plant survival in time are obscured in Figure 20 because of the great range in the plant population present. At high plant densities there was a marked decline in plant numbers present in time (Appendix Tables 15 and 16). At the highest seeding rate (1024 kg ha^{-1}), plant density fell from 35993 plants m^{-2} at establishment to only 6964 plants m^{-2} on December 12th, a survival rate of 19%. Intense inter-plant competition in the dense swards was associated with high plant mortality. The plant population in the intermediate seeding rate treatment (32 kg ha^{-1}) remained constant throughout the experiment at c. 1000 plants m^{-2}. However, there were high plant mortalities in the very low density grazed swards (seeding rates 1 to 4 kg ha^{-1}). For the lowest seeding rate treatment, the density at establishment was 38 plants m^{-2}, of which only 11% or 4 plants m^{-2} were present at harvest 5. These small, light (c. 10 mg in weight), plants suffered high mortalities in the spring (Appendix Tables 15 and 16) because of the high grazing pressure.

5.4.5 Tillers per plant and per unit area, tiller weight and tiller length in relation to plant density

Individual plant weight is the product of the number of tillers per plant and tiller weight. Tiller data for individual plots are given in Appendix Tables 18-20. Figure 21 shows the changes in tillering and tiller weight of plants in the different density treatments. Again the scales for each sward characteristic are identical for all harvests to facilitate visual comparisons of the data. There were remarkably consistent responses of the tiller characteristics to incremental changes in plant density. The tillering capacity and tiller weight of all pastures were low and

Figure 21. Changes in (a) (Left) Tillers per plant and (b) (Centre) Tiller weight in relation to plant density treatments in grazed pastures at the 5 harvests.
All curves are fitted by eye in (a) and (b).
(c) (Right) Relations of tiller weight to tiller length in grazed pastures at 5 harvests. Regression techniques were used to relate tiller length (X, cm) to tiller weight (Y, mg) in (c).


(a) Tillers per plant
(b) Tillers weight
(c) Tiller weight v. tiller length
h1
h2
h3
h4
h5
Y = 4·22 + 0·28X
r²= 0·44*
Y = −2·03 + 1·50X
r²= 0·82***
Y = −2·26 + 1·82X
r²= 0·53*
Y = −12·63 + 6·90X − 0·32X²
r²= 0·82***
Y = −1·55 + 1·82X
r²= 0·83***
Tillers per plant
Tiller weight (mg)
Tiller weight (mg)
Plant density treatment
Tiller length (cm)

relatively uniform at harvest 1. At later harvests there was a substantial increase in the tillering capacity of swards in the intermediate density treatments 3 to 7, with little change evident in other treatments. The highest number of tillers per plant (23) occurred in density treatment 5 (a seeding rate of 16 kg ha^{-1}) at harvest 5. However, this increase in tiller production (Appendix Tables 18 and 19) was not matched with a concomitant increase in tiller weight (Figure 21). Thus the increase in tiller production and weight in low density swards was inadequate to fully compensate for the paucity of plants and herbage yield was substantially less than in higher density swards at all harvests (Figures 19a, b and 21). In density treatments 6 and 7, although plants did not tiller as profusely as in treatment 5, there were greater increases in the weight of tillers and also in total yield and yield on offer at all harvests.

The tiller length of grazed swards ranged from 2 to 12 cm throughout the experiment (Figure 21 and Appendix Table 20). Tiller weight was related to tiller length (and indirectly yield) in a linear fashion in 4 of the 5 harvests (Figure 21c). Thus as swards became longer there was generally a concomitant increase in tiller weight, so that herbage yield and tiller length are likely to be highly interrelated in closely grazed, annual grass swards.

The effects of seeding rate on plant and tiller characteristics can be summarised as follows:

The frequency and severity of grazing in the seeding rate treatments 1 to 4 kg ha^{-1} was such that no substantial increase in herbage yield on offer or in individual plant weight, tillers per plant and per unit area and tiller weight occurred during the experiment.

However, between seeding rates of 8-16 kg ha^{-1}, there was a considerable increase in all the above variables but such increases were not sufficient to produce the total herbage yield and availabilities that were obtained in the higher density swards.

A most significant finding was that the transition from unstable swards of low productivity (1 to 16 kg ha^{-1}) to stable, productive pastures (32 kg ha^{-1} and over) occurred over a very narrow range in seeding rate and plant density. In this experiment a minimum seeding rate of 32 kg ha^{-1} was required to enable any deficiencies in plant numbers to be fully compensated for by increases in individual plant weight to produce maximum plant and animal production.

Components of herbage yield in addition to their direct effects on herbage yield, indirectly influence sheep intake through their influence on the ease with which herbage may be prehenced by the grazing animal, i.e. the 'intrinsic' availability of herbage as defined by Allden and Whittaker (1970). This experiment was not designed specifically to study such relationships. In the current work the majority of plant characteristic were most highly intercorrelated early in the growing season (Appendix Table 21) and there were large, fluctuating changes in plant characteristics (e.g. the substitution of plant weight for number) in relation to time and to plant density, both within harvests and from harvest to harvest (Figures 20 and 21). Simple correlation coefficients did not provide an effective summary of the data (Appendix Table 21, Figure 3). It is evident that any ranking of these sward characteristics as determinants of plant growth and sheep intake is likely to be extremely variable in time and is likely to have little long term biological meaning. Plant density and tiller length were highly correlated with plant growth and sheep intake early in the growing season. Later on plant weight became more important.

5.4.6 Plant/animal relationships

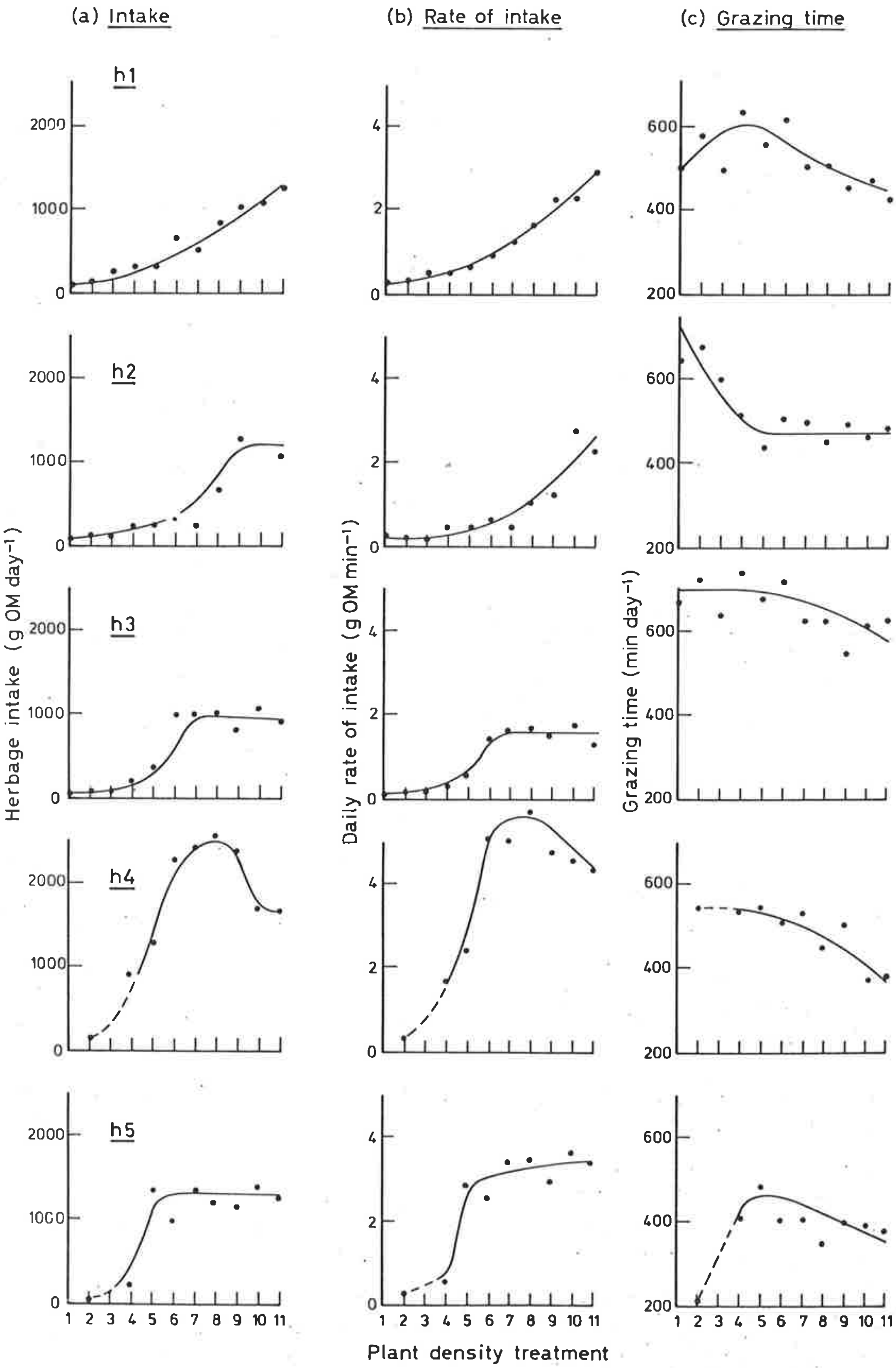
(a) Herbage intake and components of intake

Figure 22 illustrates changes in sheep intake, rate of intake and grazing time in relation to the different density treatments at the 5 harvests. The scales for each variable are identical for all harvests to facilitate visual comparisons of the data in time in the vertical plane. Examination of the data in a horizontal fashion provides a comparison of the components of intake at different density treatments for a given harvest.

At harvest 1, intake and rate of intake both increased over the full range of plant density treatments. As time progressed, these relationships changed (from exponential (h_1) to asymptotic (h_2, h_3 and h_5) to quadratic (h_4) forms). At harvests 3 to 5 a minimum seeding rate of 32 kg ha^{-1} was required for maximum intake and rate of intake (Figure 22). There was a trend for sheep to graze for a longer period on the low density swards compared to swards of higher density, except at the initial and final harvests on the lowest density swards where presumably previous grazing experience and animal fatigue, respectively, were associated with a reduced grazing time.

The intake of OM by sheep grazing swards sown at 1 to 4 kg ha^{-1} (treatments 1 to 3) was well below the maintenance level (c. 500 g OM day for 45 kg wethers, after Grimes 1966), throughout the experiment. Sheep on the 8 to 16 kg ha^{-1} (treatments 4 and 5) seeding rate treatments were able to increase their intake above maintenance at harvest 4 (in November), but this was not sufficient to completely overcome the effects of losing 30 to 40% of their initial

Figure 22. The relations of (a) (Left) The daily intake of organic matter by sheep and the components of intake; (b) (Centre) Daily rate of intake; and (c) (Left) Grazing time to plant density at the 5 harvests (h_1 to h_5). Data for original animals only is presented.
All curves are drawn by eye fit.
At harvests 4 and 5, curves from density treatment 4 to treatment 2 are dashed, since on the latter treatment the only data presented is that for the original animal which survived.



(a) Intake
(b) Rate of intake
(c) Grazing time
h1
h2
h3
h4
h5
Herbage intake (g OM day⁻¹)
Daily rate of intake (g OM min⁻¹)
Grazing time (min day⁻¹)
Plant density treatment

live weight during winter (Figure 16). Consequently, there was a marked decline in animal production on all these low density plots compared to that on higher density treatments (Section 5.4.2).

Figure 22 also shows that sheep grazing swards sown at 32 to 256 kg ha^{-1} (treatments 6 to 9) had substantially lower daily OM intakes at harvest 1 and 2 (in July and August) but greater OM intakes at harvest 4 (in November) compared to sheep grazing the highest density sward. The OM intake of the latter animals was relatively uniform throughout the experiment (c. 1000 g OM day^{-1}).

On swards of intermediate density (seeding rates 32 to 256 kg ha^{-1}) animals exhibited marked patterns of compensatory intake (Figure 22) and growth (Figure 16), whereas on swards of very low density (seeding rates 1 to 4 kg ha^{-1}) animal intake and production was relatively low and uniform. There was no opportunity for animals to compensate because herbage availability was very low at all times (Figure 19b).

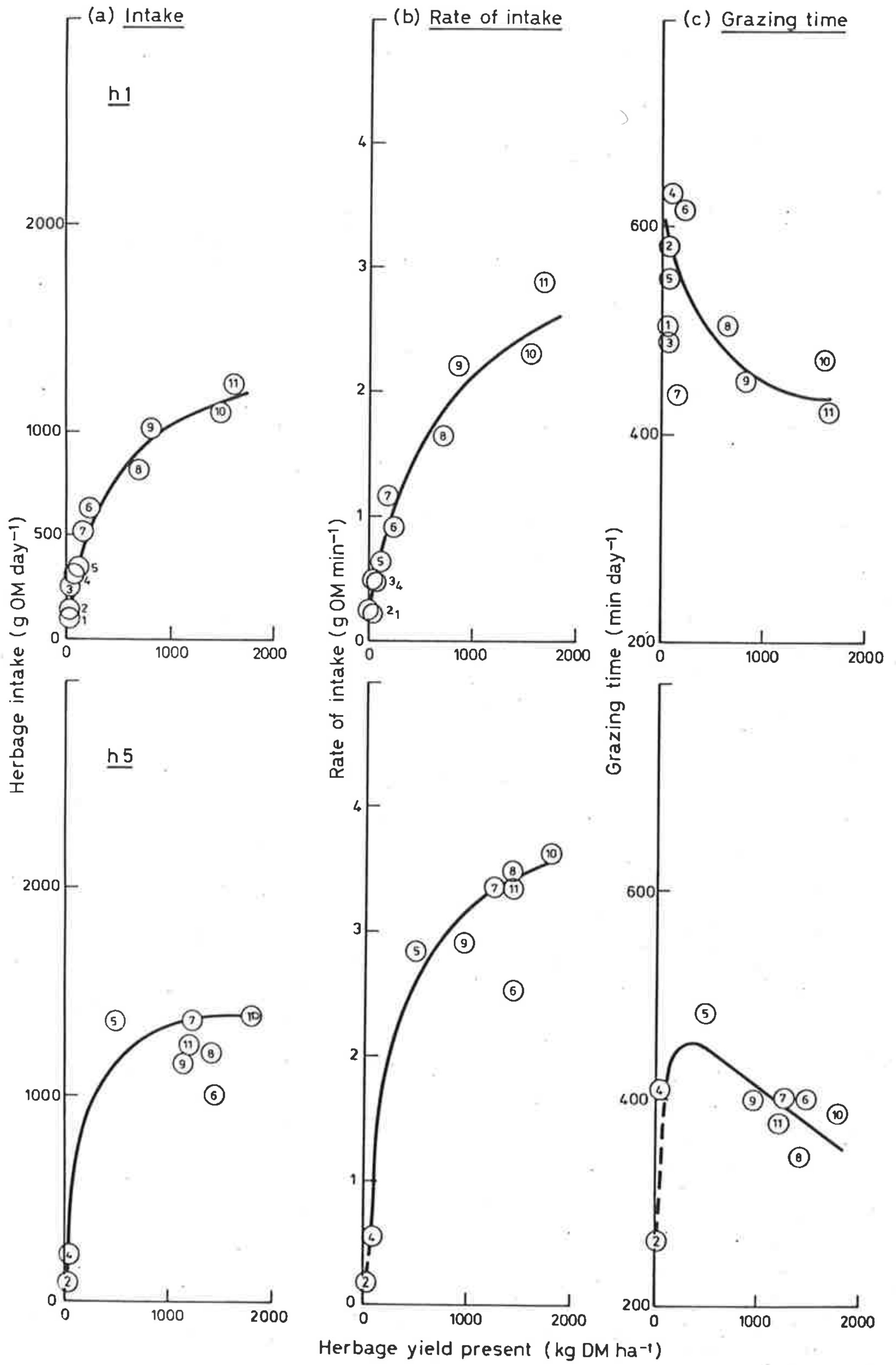
Figure 22 also shows that the relative changes in the rate of OM intake were similar to the changes in total daily OM intake as described above. As time progressed, the different previous nutritional histories of the sheep influenced their intake and the components of intake at later harvests. These effects are best illustrated by relating intake to herbage yield at the beginning of the experiment where no differences had been generated between groups in terms of physiological status of the animals, and at the end of the experiment when appreciable differences had been generated.

At the beginning of the experiment there were asymptotic relationships between daily intake, rate of intake and herbage availability (Figure 23) similar to other such relationships reported in the literature (Allden 1962; Arnold 1964a; Allden and Whittaker 1970). At the end of the experiment these effects were less clear cut, with appreciable differences in intake and rate of intake at similar herbage yields. In general, a minimum herbage availability of c. 1000 kg DM ha^{-1} was required for maximum daily herbage intake and rate of intake on the experimental swards (Figure 23). Also the time spent grazing tended to increase as herbage availability declined below 1000 kg DM ha^{-1}. The only exception was the reduced time spent grazing by the one surviving animal on density treatment 2 at harvest 5. This animal had a fleece-free live weight of 25 kg at harvest 5 and was in very poor condition.

(b) Digestibility and plant density relations

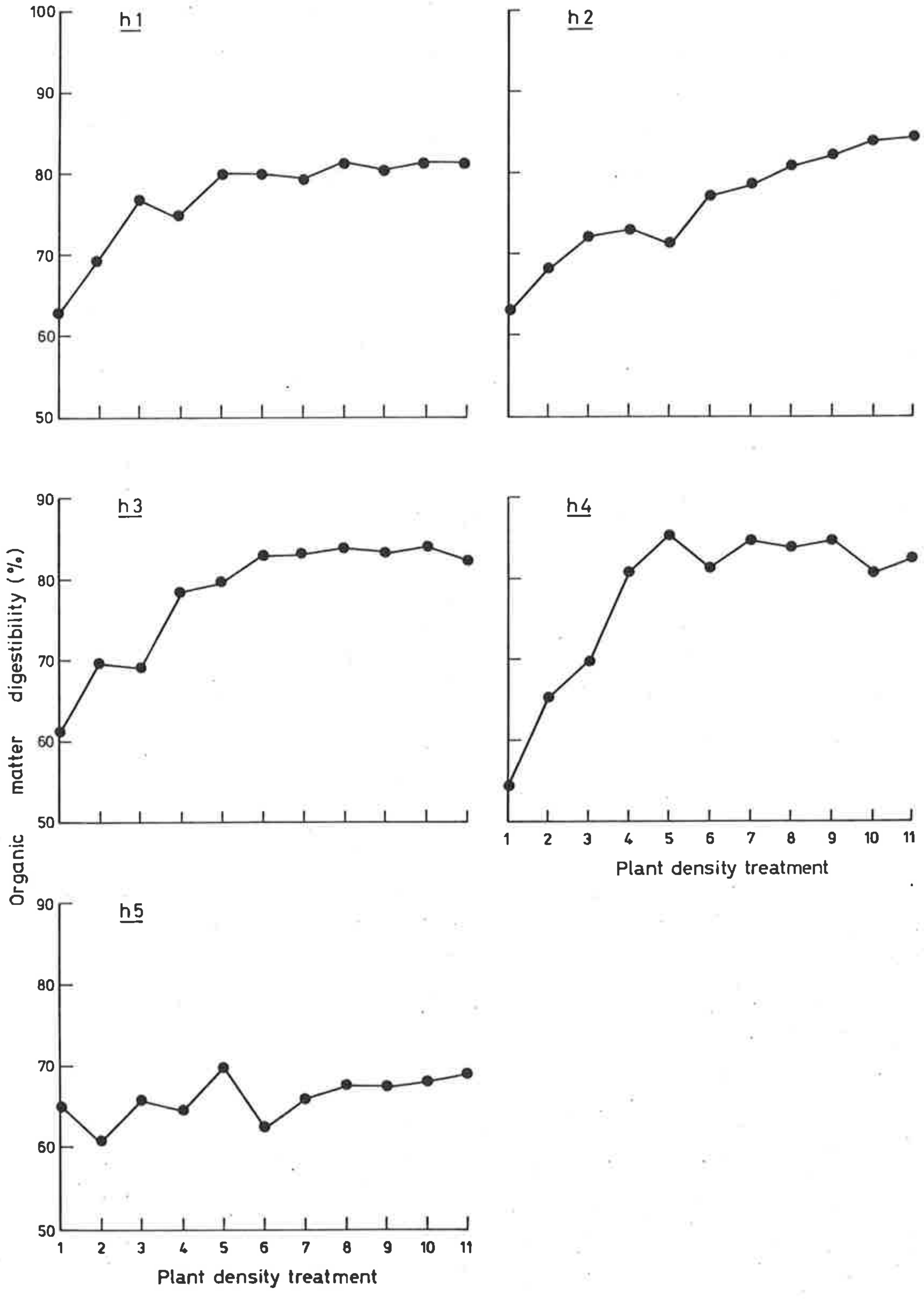
Figure 24 illustrates changes in organic matter digestibility (OMD) of oesophageal fistula (O.F.) samples obtained from swards of different densities at the five harvests. The OMD's of O.F. extrusa samples from low density swards (treatments 1 to 5) were less than that from swards of higher density, except at maturity when the OMD of all pastures were similar. Reasons for these differences were examined by comparing the OMD of O.F. and whole plant samples taken from the different swards (Figure 25). The data are summarized in Appendix Table 22. In the very low density, sparse swards (seeding rates 1 to 4 kg ha^{-1}) the OMD of O.F. samples was less than that of whole plant samples taken from the same swards. This was probably largely due to the ingestion of large quantities of soil and a greater intake of senescent herbage (including undecomposed root and stem residues from the previous year's crop) of low OMD by animals

Figure 23. The relations of (a) (Left) Daily intake of herbage by sheep and the components of intake; (b) (Centre) Daily rate of intake; and (c) (Right) Grazing time to the herbage yield present at harvests 1 (Top) and 5 (Bottom). The circled numbers refer to the density treatments 1 to 11.
All curves are fitted by eye.
At harvest 5, curves from density treatment 4 to treatment 2 are dashed, since on the latter treatment the only data presented is that for the one original animal which survived.



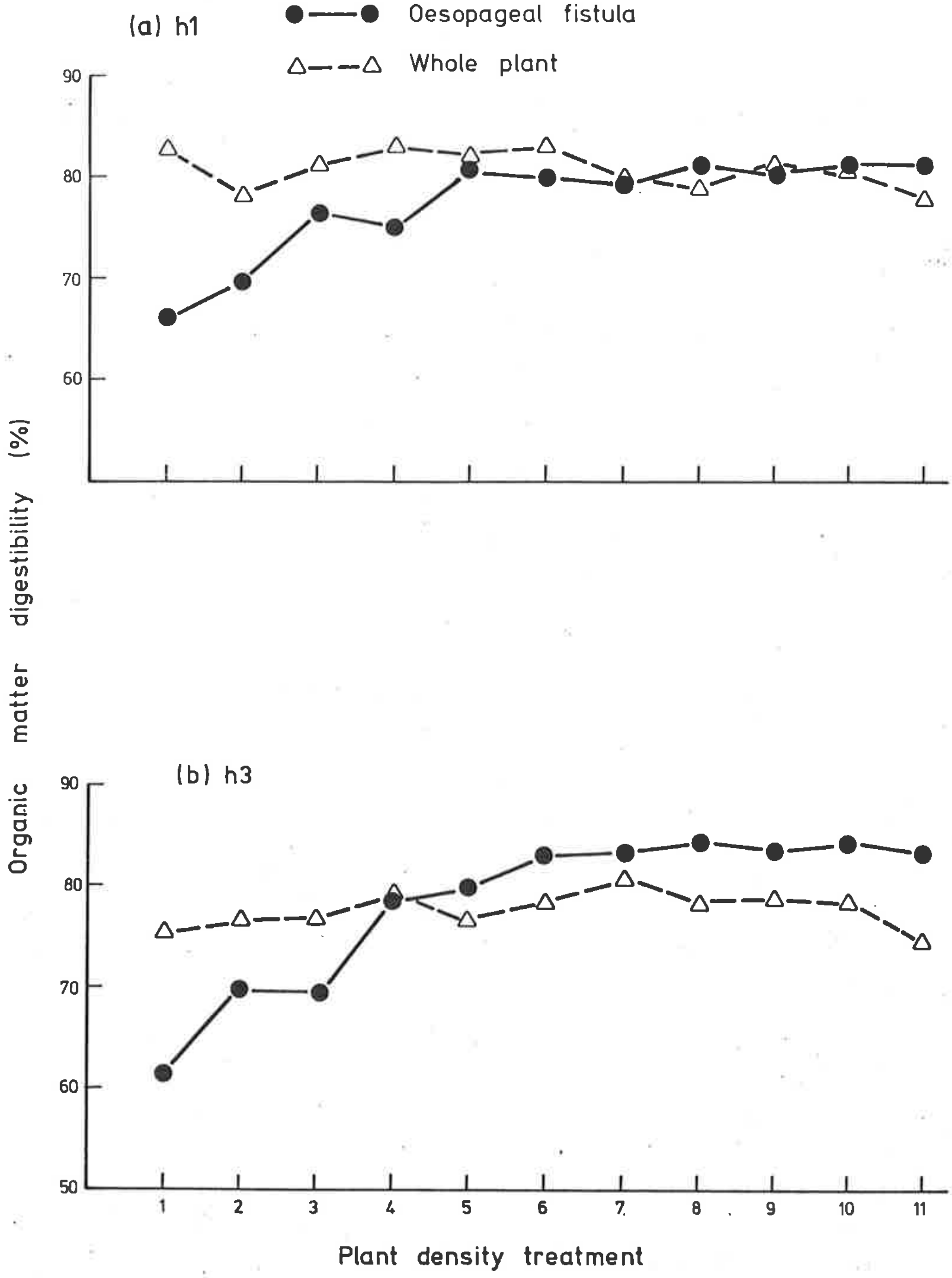
(a) Intake
(b) Rate of intake
(c) Grazing time
h1
h5
Herbage intake (g OM day⁻¹)
Rate of intake (g OM min⁻¹)
Grazing time (min day⁻¹)
Herbage yield present (kg DM ha⁻¹)

Figure 24. The relation of the OMD of O.F. extrusa samples to plant density treatments at the five harvests.



h1
h2
h3
h4
h5
100
90
80
70
60
50
Organic matter digestibility (%)
1 2 3 4 5 6 7 8 9 10 11
Plant density treatment

Figure 25. A comparison of the OMD of oesophageal fistula and whole plant samples from grazed swards of different plant density treatments at harvests 1 (Top) and 3 (Bottom).


(a) h1
Oesopageal fistula
Whole plant
90
80
70
60
Organic matter digestibility (%)
(b) h3
90
80
70
60
50
1
2
3
4
5
6
7
8
9
10
11
Plant density treatment

grazing low density swards. In medium and high density swards, the OMD of O.F. samples was greater than that of whole plant samples taken from the same swards at harvest 3, indicating the capacity of the animals to graze selectively.

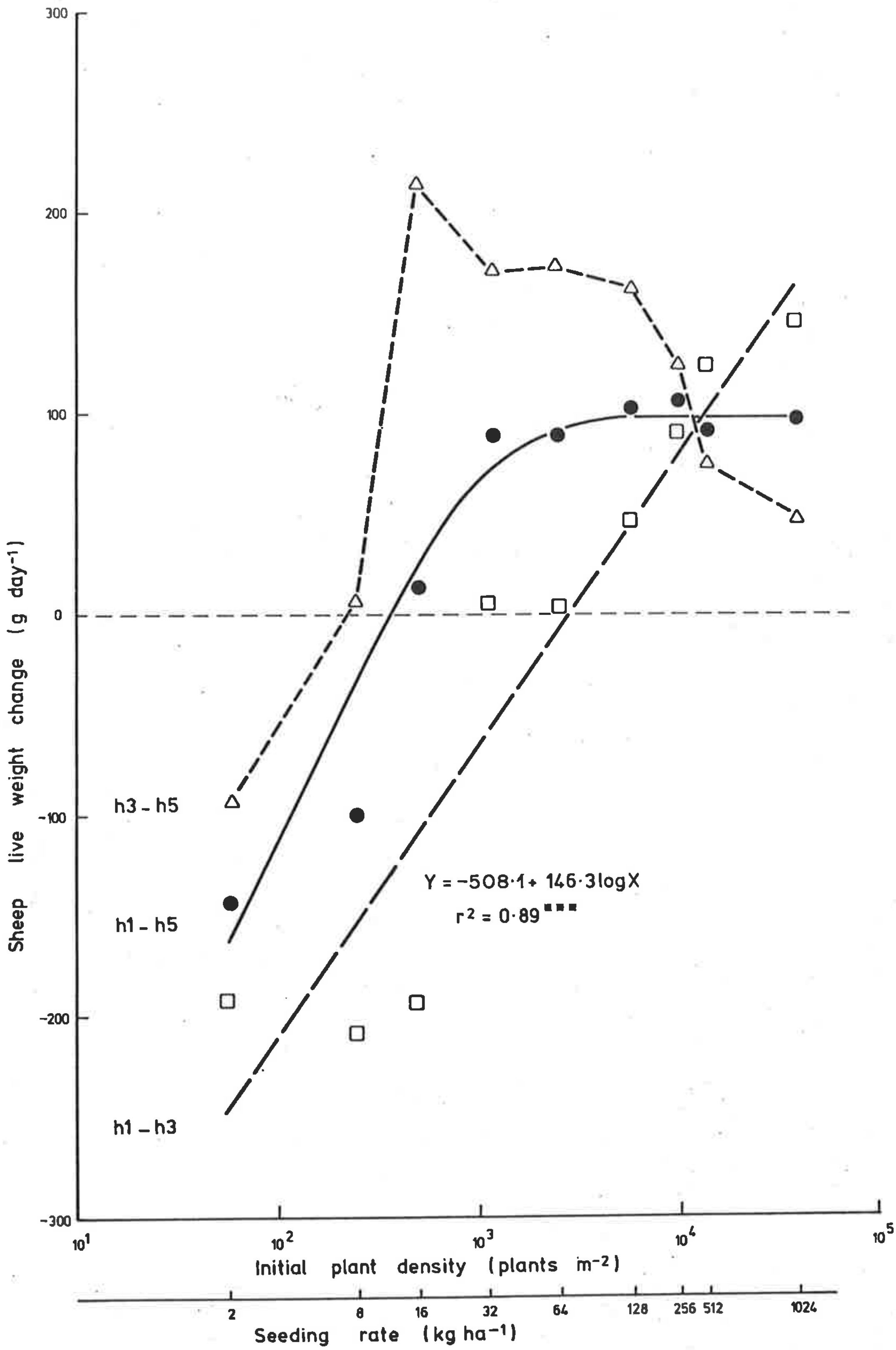
(c) Relations between sheep live weight, wool growth and plant density

Data in the preceding section showed that relations between plant characteristics and animal performance may change substantially in time. This is further exemplified by the different relations between sheep liveweight change, wool growth and plant density during different periods of the experiment (Figures 26 and 27). These results provide further evidence to the earlier observation (Figures 19 and 16) that plant density is a major determinant of plant and animal productivity during the early growth of annual pastures. Different measures of animal production responded linearly to the logarithm of the initial plant density at certain times of the year but for different periods of time (Figures 26 and 27). Different plant populations were required to maintain initial sheep live weight at different times of the year. In the first half of the experiment (h_1 - h_3), sheep liveweight change (Y, g day^{-1}) increased in a linear fashion as the logarithm of initial plant density (log X, plants m^{-2}) increased over the entire range of seeding rates studied. The equation is:

$$Y = -508.1 + 146.3 \log X \quad (r^2 = 0.89^{***}).$$

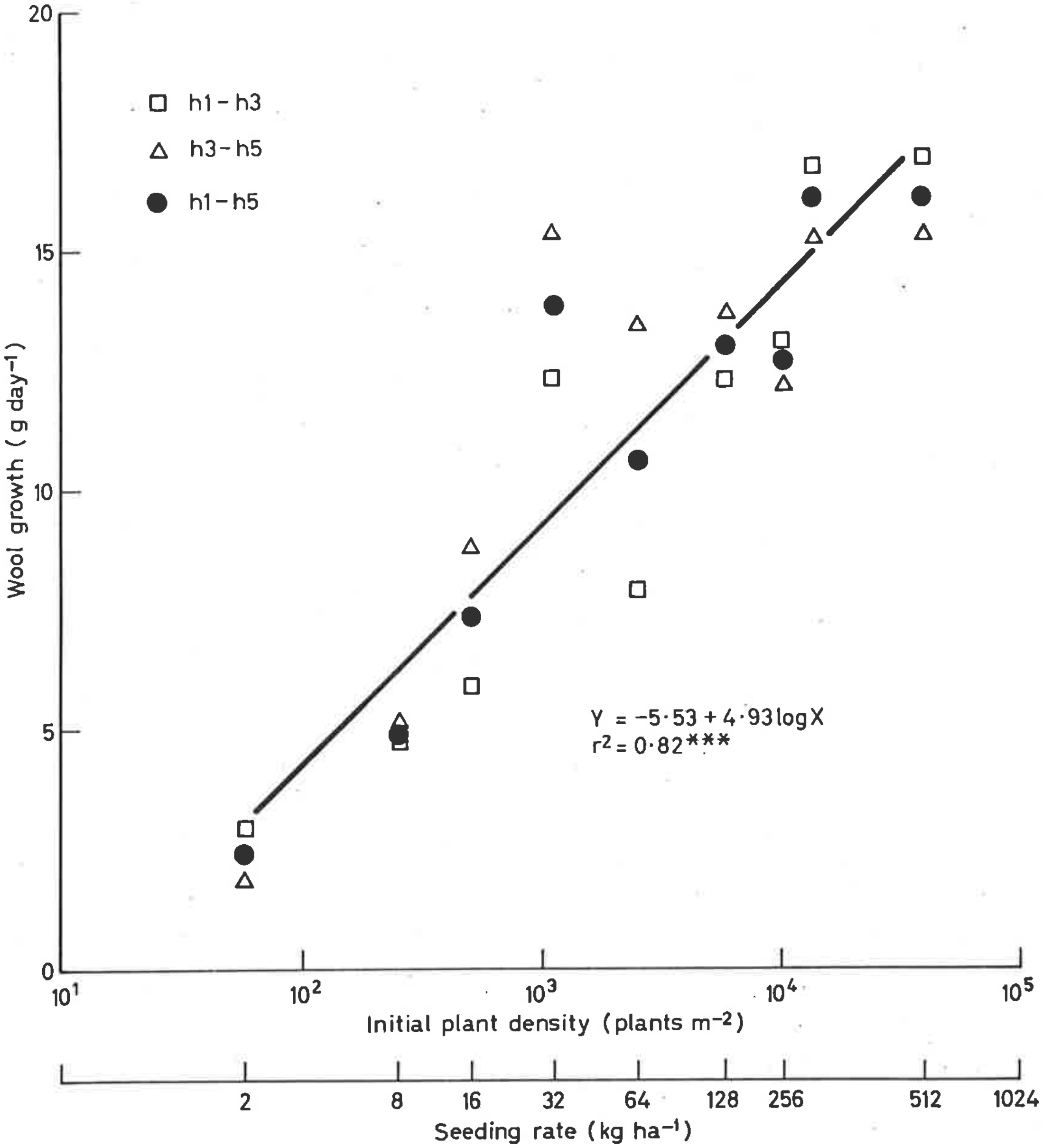
However, in the latter half of the experiment (h_3 to h_5) the relationship was curvilinear and for the whole experiment the response was asymptotic.

Figure 26. The relations between sheep liveweight change in the first half (h_1-h_3), second half (h_3-h_5) and over the full experimental period (h_1-h_5) to the logarithm of the initial plant density. Data for original, surviving animals only are used in calculating plot means.



300
200
100
0
-100
-200
-300
Sheep live weight change (g day⁻¹)
h3 – h5
h1 – h5
h1 – h3
Y = −508·1 + 146·3logX
r² = 0·89***
10¹
10²
10³
10⁴
10⁵
Initial plant density (plants m⁻²)
2
8
16
32
64
128
256
512
1024
Seeding rate (kg ha⁻¹)

Figure 27. The relations of wool growth during the first half (h_1-h_3), second half (h_3-h_5) and full experimental period (h_1-h_5) to the logarithm of the initial plant density.
Data for original surviving animals only are used in calculating plot means. Data for 9 density treatments are presented as 100% mortality of original animals occurred on treatments 1 and 3.



20
15
10
5
0
h1 - h3
h3 - h5
h1 - h5
Wool growth (g day⁻¹)
Y = -5·53 + 4·93 log X
r² = 0·82***
10¹
10²
10³
10⁴
10⁵
Initial plant density (plants m⁻²)
2
8
16
32
64
128
256
512
1024
Seeding rate (kg ha⁻¹)

Sheep maintained live weight in the first half of the experiment on swards with an IPD of 2972 plants m^{-2} (derived from the above equation). However, only c. 230 plants m^{-2} (read from Figure 26) were needed to provide the same function in the second half of the experiment. Thus, plant density became a less important determinant of sheep liveweight change with time. This was probably because there was a progressive increase in other plant and tiller characteristics, such as plant weight over time (Figure 20) and such increases compensated to varying degrees for any deficiencies in plant density.

Early in the growing season (harvest 1 and 2), herbage availability increased up to c. 1600 kg DM ha^{-1} as plant density increased over the full range of seeding rates studied (Figure 20). Thus, plant density was a major determinant of herbage yield early in the experiment. It was in the second half of the experiment (harvests 3 to 5) that increases in the weight of individual plants (Figure 20) and their components, tiller weight and tillers per plant (Figure 21) fully compensated for any deficiency in plant numbers in medium and high density (stable) swards, so that herbage availability was unaffected and remained high and relatively uniform at c. 2000 kg DM ha^{-1} (Figure 20). Whereas, in low density, unstable swards although there was a progressive increase in plant weight and its components over time, and as seeding rates increased from 1 to 16 kg ha^{-1}, such increases were insufficient to fully compensate for the paucity of plants and herbage availability was greatly reduced at all times (ranging from 1 to 500 kg DM ha^{-1}), compared to that of swards of higher density. In low density pastures, there was a trend for a linear response in sheep liveweight change to the logarithm of IPD at both periods, presumably because neither plants nor animals had expressed their full growth potential in both periods. In medium and high density pastures which produced similar levels of plant and animal output ha^{-1}, the initial positive linear response of sheep liveweight change to increases in IPD later became negative. This was probably because stock grazing on the highest density swards gained the most weight in the first period and exhibited far less if any compensatory gain in the later period - compared to sheep grazing medium density pastures (Figure 16).

In the three periods of assessment, sheep wool growth (Y, g day^{-1}) increased linearly as the logarithm of IPD (log X, plants m^{-2}) increased over the entire range of seeding rates studied (Figure 27). The equation for the data pooled for the three periods is:

$$Y = -5.53 + 4.93 \log X \quad (r^2 = 0.82^{***}).$$

This shows that in the later half of the experiment wool growth increased over a greater range of seeding rates than did liveweight change (Figures 27 and 26). Since wool growth is akin to an involuntary process, gains made at one point in time e.g. early in the growing season on high density swards are likely to persist (Figure 18), whereas body tissue reserves can be readily lost (Figure 16). Thus, different measures of animal production respond linearly to the logarithm of initial plant density (i.e. asymptotically to initial plant density *per se*) at certain times of the year but for different periods of time.

5.4.7 A comparison of two methods of estimating intake

In order to evaluate two methods of intake estimation, intake/production relationships were constructed to firstly estimate the intake requirements for liveweight and wool production and then assess the biological validity of such estimates.

(a) Relation of sheep liveweight change to DE intake

Figure 28a shows the relations between daily DE intake and liveweight change when intake is estimated by (i) a herbage cutting technique and (ii) a faecal collection method. Linear regression equations were calculated relating the daily DE intake of sheep (X, kJ kg^{-1} $W^{0.75}$) to their liveweight change (Y, g day^{-1}) using the intake values estimated by both methods. When intake was estimated from:

(i) the herbage cutting technique:

$$Y = -224.9 + 0.18X \quad (r^2 = 0.89^{***})$$

or from,

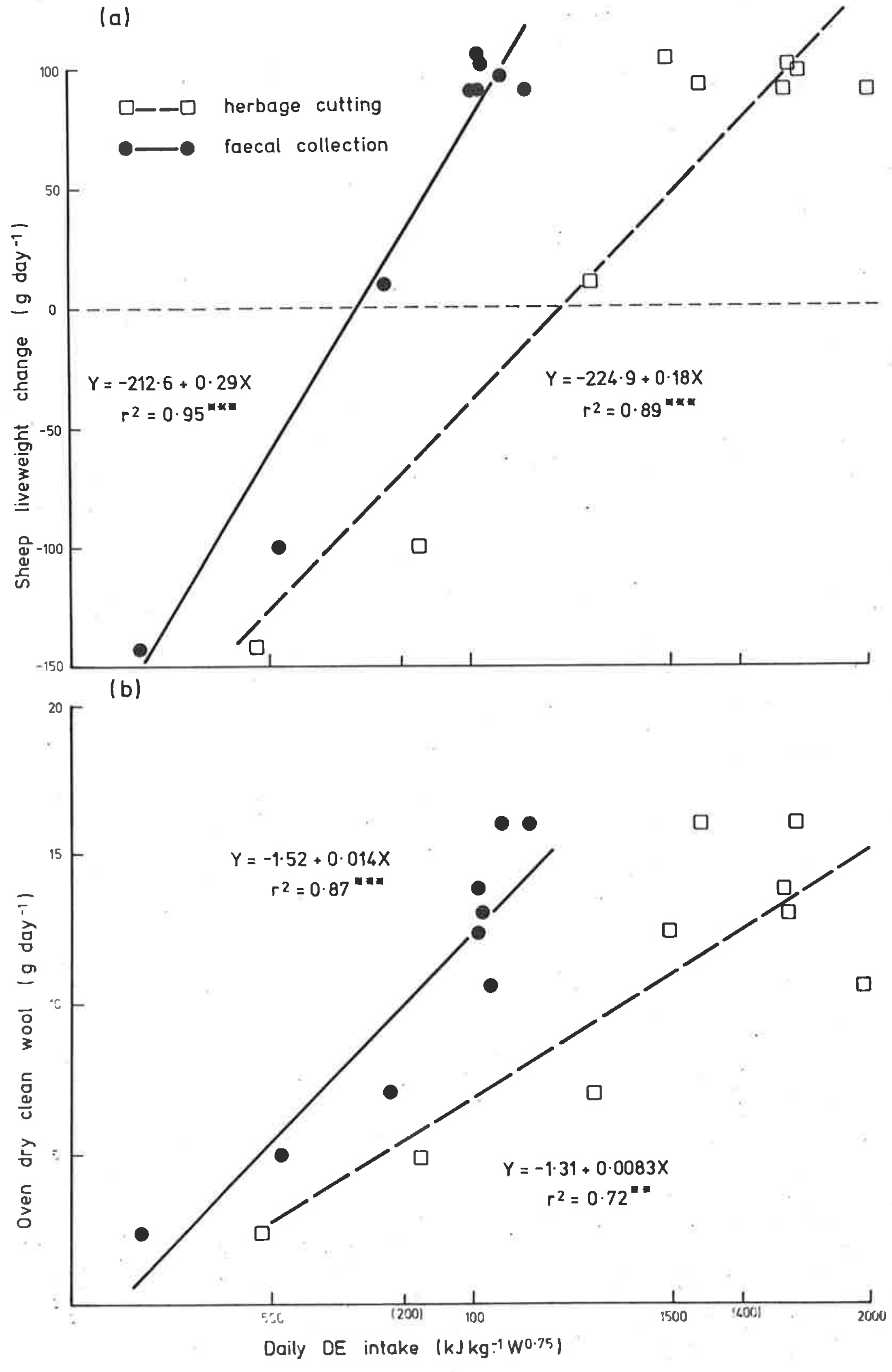
(ii) a faecal collection method:

$$Y = -212.6 + 0.29X \quad (r^2 = 0.95^{***}).$$

The two regression lines were significantly different in slope and displacement (a summary of the statistical analyses is given in Appendix Table 22). The model of Garrett _et al._ (1959) was used as described in experiment 1, Section 4.5 to calculate the DE requirements for maintenance and gain of 45 kg grazing wethers. This data is presented in Table 27.

The daily intake of DE per kg $W^{0.75}$ to maintain the live weight of a 45 kg wether when estimated from the herbage cutting technique was 1322 kJ (316 kcal) and from the faecal collection method was 770 kJ (184 kcal). The daily maintenance requirements of grazing sheep have been estimated by many workers, by different methods and ranges from 628 to 837 kJ (150 to 200 kcal) per kg $W^{0.75}$ (Grimes 1966; Allden 1969b; Langlands and Bennett 1973c). In the present

Figure 28. A comparison of relations between the intake of DE, when estimated by two methods and (a) (Top) Liveweight change and (b) (Bottom) Wool production of grazing sheep over the complete experimental period. Intake was estimated by two methods, namely from (i) a herbage cutting technique, and (ii) a faecal collection method.
Data for 9 density treatments only are presented as 100% mortality of original animals occurred on treatments 1 and 3. Figures in parentheses on the X axis are DE intake data expressed as kilocalories.



(a)
herbage cutting
faecal collection
Y = -212·6 + 0·29X
r2 = 0·95***
Y = -224·9 + 0·18X
r2 = 0·89***
Sheep liveweight change (g day-1)
100
50
0
-50
-100
-150
(b)
Y = -1·52 + 0·014X
r2 = 0·87***
Y = -1·31 + 0·0083X
r2 = 0·72**
Oven dry clean wool (g day-1)
20
15
500
(200)
100
1500
(400)
2000
Daily DE intake (kJ kg-1 W0·75)

Table 27. A comparison of estimates of the daily DE intake requirements of a 45 kg sheep when intake is estimated by two methods.

Method of intake estimation (for whole experiment)	Model Intake = $aW^{0.75}(1+bG)$	Maintenance (kJ)	Gain of 1 kg in live weight (kJ)
(i) Herbage cutting technique	$1322.9W^{0.75}(1 + 3.90G)$ (319)*	22979 (5491)	89617 (21414)
(ii) Faecal collection method	$768.4W^{0.75}(1 + 3.95G)$ (184)*	13344 (3188)	52707 (12594)

* Figures in parentheses are daily DE intake data expressed in terms of kilocalories.

study, the faecal collection method gave a value in keeping with those found by other workers, whereas, the herbage cutting technique was almost double the values commonly cited in the literature.

(b) Relation of wool production to DE intake

Equations relating sheep daily DE intake (Y, kJ kg^{-1} $W^{0.75}$) to wool production (Y, g day^{-1}) were calculated using intake estimated by two methods (Figure 28b). When intake was assessed from

(i) herbage cutting technique:

$$Y = -1.31 + 0.0083X \quad (r^2 = 0.72^{**})$$

or from

(ii) a faecal collection method

$$Y = -1.52 + 0.014X \quad (r^2 = 0.87^{***})$$

The above regression lines were significantly different in slope and displacement (Appendix Table 22). When intake was estimated by the faecal collection method, the production of each additional one gram of clean wool was associated with an intake of about 70 kJ (17 kcal) of DE per kg $W^{0.75}$. This value is very similar to the values of 71 kJ (17 kcal) and 78 kJ (19 kcal) of DE intake per kg $W^{0.75}$ per gram of clean wool as observed in pen and field experiments respectively, in this environment (Allden 1968b, 1969b).

When the DE requirements for wool production were estimated by the herbage cutting technique, the values were approximately twice those estimated by the faecal collection method in the present experiment and that estimated by Allden (1968b, 1969b).

Thus, the faecal collection method gave values of live weight and wool production which were similar to values commonly quoted in the literature for both field and pen fed animals. The herbage cutting technique gave estimates of intake which exceeded faecal collection data twofold. Reasons for this will be discussed in Section 5.5.

Furthermore, maximum intakes of herbage by sheep grazing abundant pastures are approximately 2 kg OM sheep^{-1} day^{-1} (Arnold Dudzinski 1967b; Young and Newton 1974). This was similar to the maximum intake of OM (estimated by the faecal collection method) by sheep in present experiment (Figure 22). However, the herbage cutting technique gave estimates of intake which exceeded faecal collection data twofold. The latter high intakes (4 kg OM sheep^{-1} day^{-1}) have not been recorded in the literature and do not seem to be biologically possible.

Figure 29 illustrates the relation of intake assessed over the complete experimental period to initial plant density using the preferred method of intake estimation (i.e. faecal collection method). Intake estimated by the herbage cutting technique is shown by a dashed line. Quadratic equations were used to describe both relationships. A minimum seeding rate of 32 kg ha^{-1} was required for maximum intake of herbage by the grazing animal during the experiment.

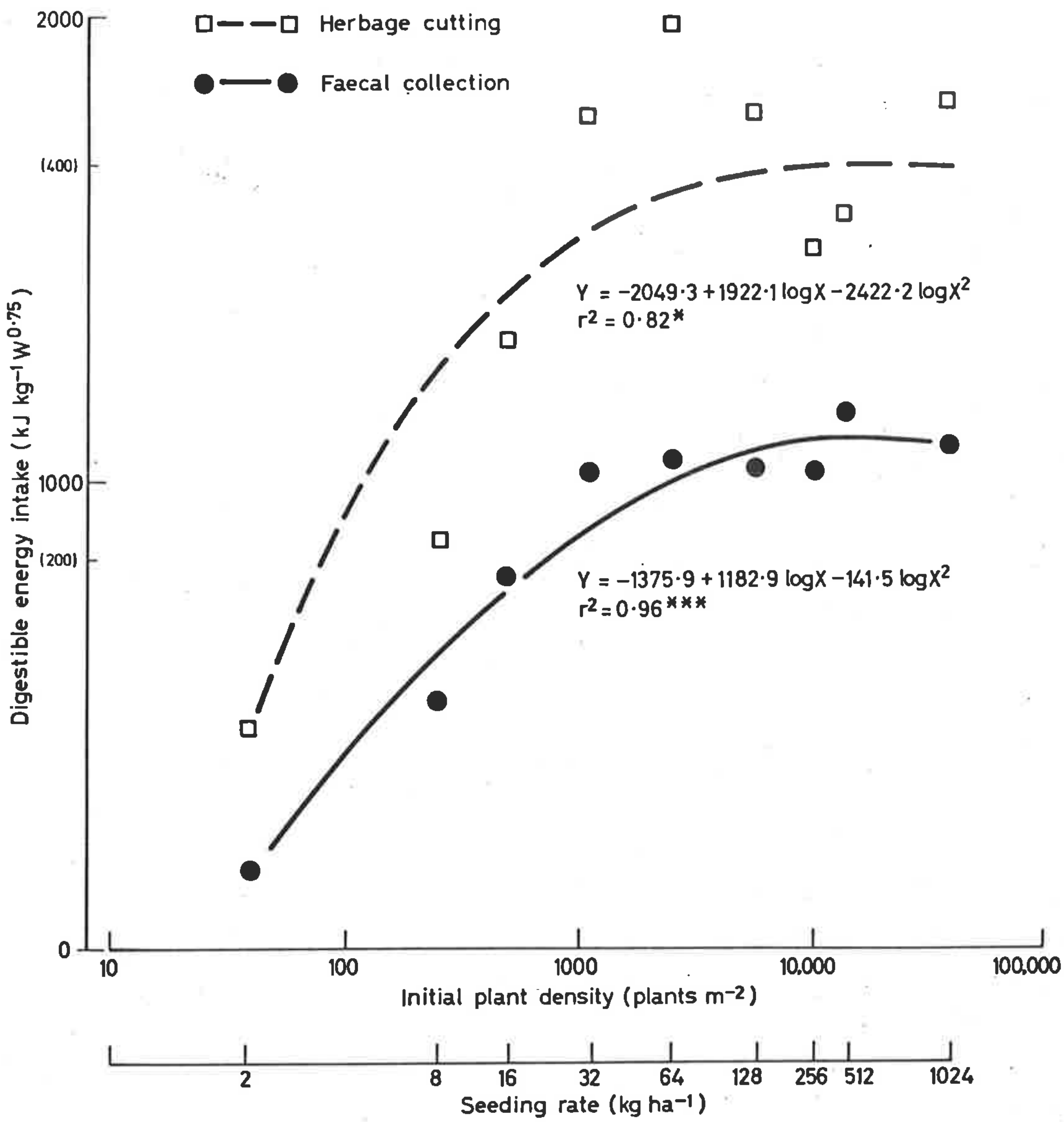
5.4.8 A comparison of grazed and ungrazed swards

Ungrazed areas were fenced off within each grazed seeding rate treatment. This permitted a separation of the effects of plant density from those of grazing pressure on herbage yield and plant characteristics. This also provided an opportunity to examine the relationship between the results obtained in ungrazed plots and grazing situations.

Figure 29. A comparison of relations between the intake of DE (when estimated by two methods) and initial plant density (on a logarithmic scale), when intake was estimated over the complete experimental period.

Intake was estimated by two methods, namely from (i) a herbage cutting technique and (ii) a faecal collection method.

Seeding rate treatments are shown on the lower X axis.


Herbage cutting
Faecal collection
Y = −2049·3 + 1922·1 logX − 2422·2 logX²
r² = 0·82*
Y = −1375·9 + 1182·9 logX − 141·5 logX²
r² = 0·96***
Digestible energy intake (kJ kg⁻¹ W⁰·⁷⁵)
2000
(400)
1000
(200)
0
10
100
1000
10,000
100,000
Initial plant density (plants m⁻²)
2
8
16
32
64
128
256
512
1024
Seeding rate (kg ha⁻¹)

(a) Relations between total herbage yield, cumulative yield and seeding rate

The logarithmic relationship between seeding rate and initial plant density was linear and similar in both grazed and ungrazed swards (Appendix Figure 4 and Table 23). Each additional 1 kg ha^{-1} of seed sown on May 15th produced 33 plants m^{-2} at establishment on July 7th (Appendix Figure 4). Cumulative herbage yield and availability data for the individual grazed and ungrazed plots are presented in Appendix Tables 13 and 14.

Figure 30 illustrates the relations of the cumulative yields of herbage in grazed and ungrazed swards to time and to the IPD. Early in the growing season, the cumulative yield of grazed and ungrazed swards were similar and were linearly related to IPD, but these relationships diverged as the season progressed (Figure 30). A minimum IPD of 1126 plants m^{-2} (a seeding rate of 32 kg ha^{-1}) was required for maximum herbage yield in grazed swards at harvests 3 to 5. In ungrazed swards yield became progressively less dependent on IPD with time; by harvest 5 there was no relationship between IPD and herbage yield over the full range of seeding rates studied (Figures 30 and 31).

Furthermore over the same range of seeding rates, grazing compared to no grazing reduced, had no affect or increased total herbage yield (Figures 30 and 31). At the lowest seeding rate of 1 kg ha^{-1}, there was a 12-fold difference in total yield in favour of the ungrazed sward; while at a seeding rate of 16 kg ha^{-1} total yield of grazed and ungrazed swards was similar. However at seeding rates of 32 kg ha^{-1} and higher, total yield from grazed swards was 17% greater than for ungrazed swards of similar density (Figure 31).

Figure 30. Changes in cumulative herbage yield in relation to time and to initial plant density in (a) (Top) Grazed; and (b) (Bottom) Ungrazed swards sown at a selected range of seeding rates.

IPD data are presented on a logarithmic scale.

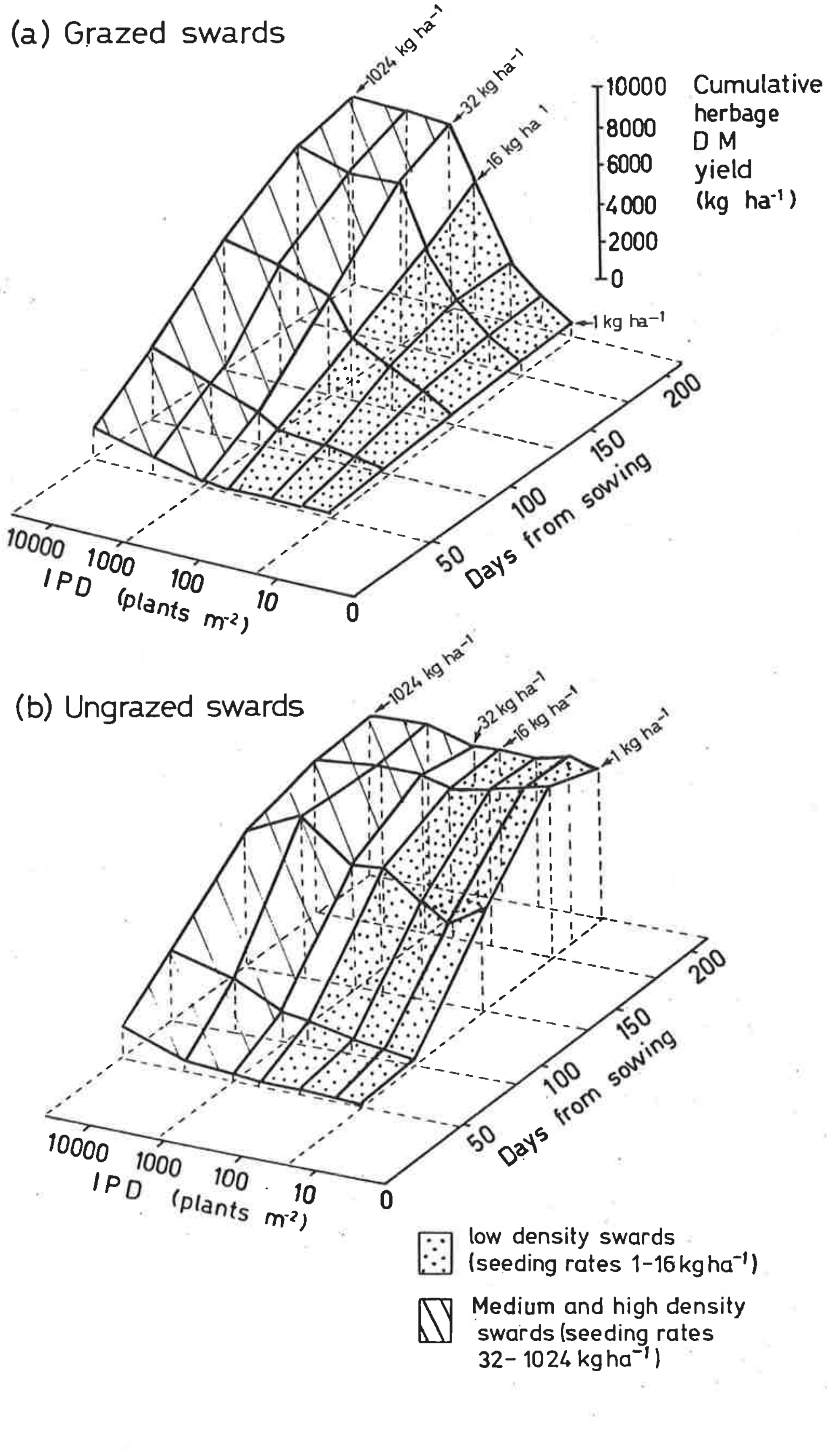
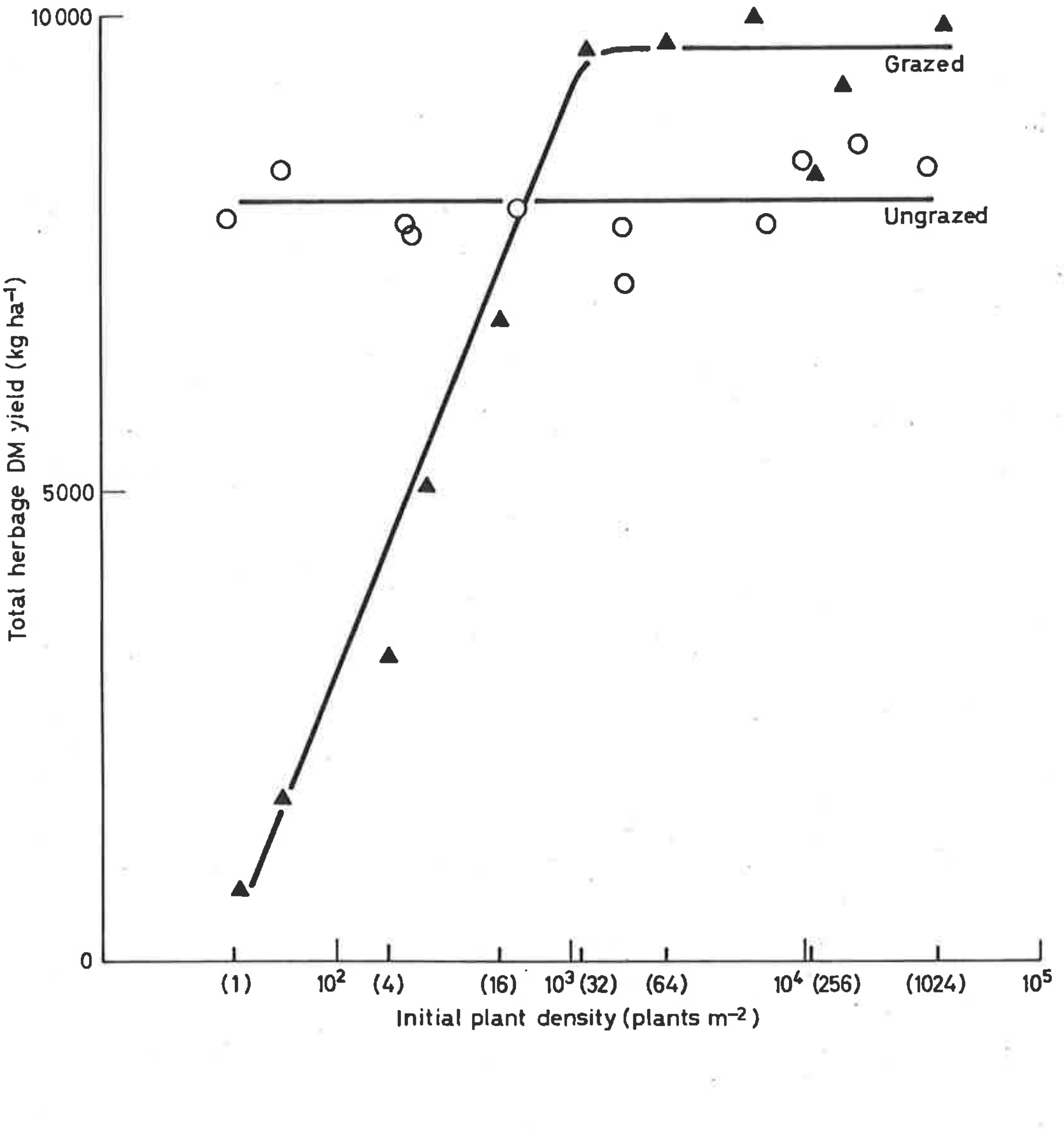

(a) Grazed swards
1024 kg ha-1
32 kg ha-1
16 kg ha-1
1 kg ha-1
10000
8000
6000
4000
2000
0
Cumulative herbage D M yield (kg ha-1)
10000 1000 100 10 0
IPD (plants m-2)
50 100 150 200
Days from sowing
(b) Ungrazed swards
1024 kg ha-1
32 kg ha-1
16 kg ha-1
1 kg ha-1
10000 1000 100 10 0
IPD (plants m-2)
50 100 150 200
Days from sowing
low density swards (seeding rates 1-16 kg ha-1)
Medium and high density swards (seeding rates 32-1024 kg ha-1)

Figure 31. The relationships between total herbage yield and initial plant density in grazed and ungrazed swards.



10 000
5000
0
Total herbage DM yield (kg ha⁻¹)
Grazed
Ungrazed
(1)
10²
(4)
(16)
10³ (32)
(64)
10⁴ (256)
(1024)
10⁵
Initial plant density (plants m⁻²)

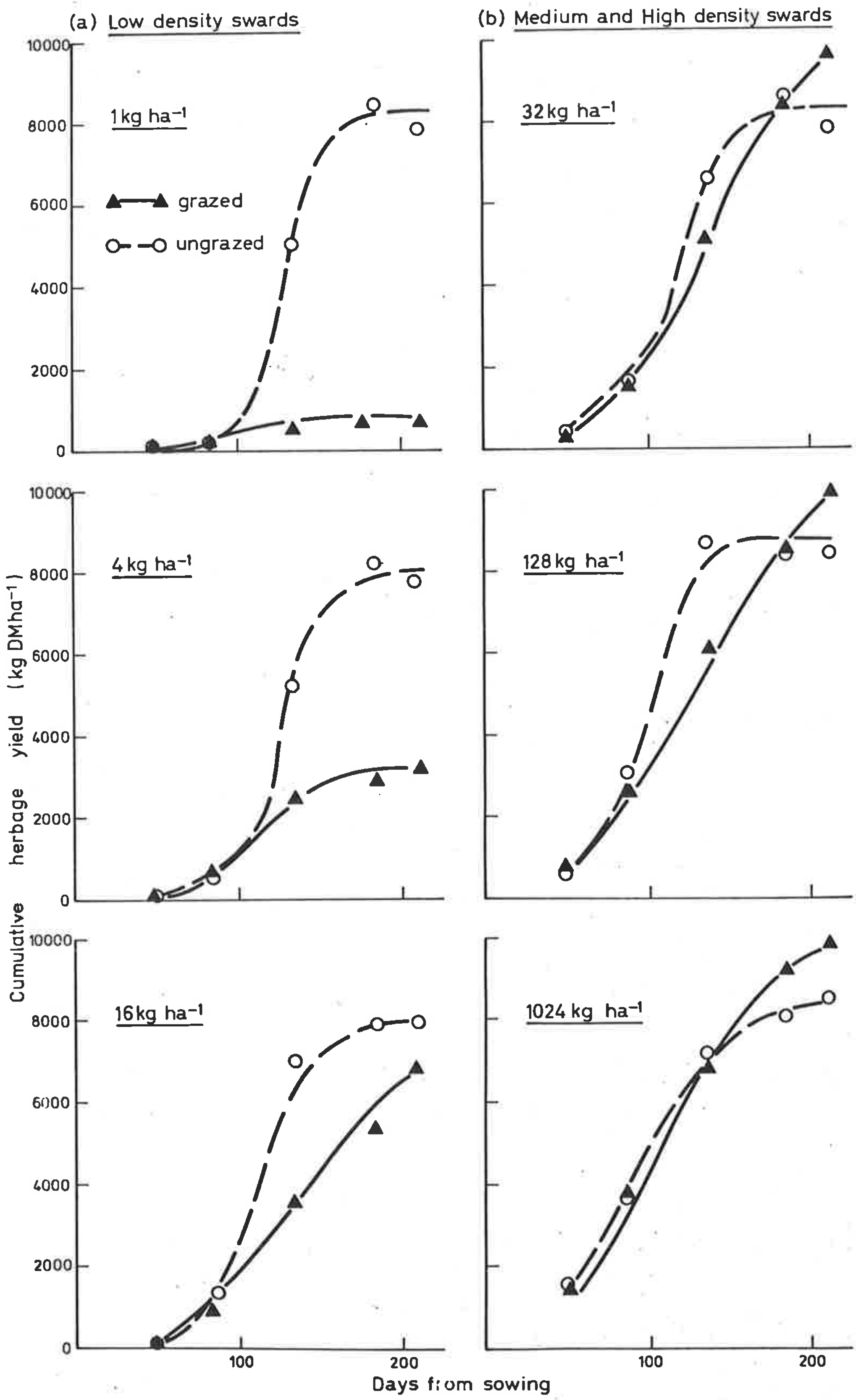
These results suggest that small plot, ungrazed studies may provide a reasonable estimate of plant growth in grazing situations early in the growing season but such relationships diminish in time.

(b) Plant growth, digestibility and seeding rate

Plant growth rate and digestibility data for the individual grazed and ungrazed plots are given in Appendix Tables 24 and 25. A logistic growth curve relating plant growth to seeding rate was fitted to each seeding rate treatment for all grazed and ungrazed plots (Section 5.3.6). Fitted growth curves for a range of seeding rate treatments in grazed and ungrazed swards are shown separately in Figure 32. They are combined in the one diagram in Appendix Figure 5. The equation gave a good fit for all treatments and estimates of plant growth attributes of each curve are presented in Table 28. Estimated maximum yield was influenced by plant density only in grazed pastures (as described in the preceding section). Maximum growth rate (maximum GR) was influenced by plant density, time and by grazing. In low density grazed pastures estimated maximum GR increased from 9 to 59 kg DM ha^{-1} day^{-1} as the seeding rate increased from 1 to 16 kg ha^{-1} (Table 28). However, such maximum GR's were far less than those achieved in both grazed swards of higher densities and in all ungrazed swards. In ungrazed plots, maximum GR increased as seeding rate decreased, but the number of days to achieve maximum GR and to produce 1500 kg DM ha^{-1} increased. There was a tendency for grazed swards to achieve a lower maximum GR at a later time in the growing season compared to ungrazed pastures of similar density. This was probably associated with the higher digestibility

Figure 32. Accumulation of herbage in time in grazed and ungrazed swards for a selected range of seeding rate treatments.

Curves are fitted logistic functions as described in Section 5.3.6.



(a) Low density swards
(b) Medium and High density swards
1 kg ha^{-1}
4 kg ha^{-1}
16 kg ha^{-1}
32 kg ha^{-1}
128 kg ha^{-1}
1024 kg ha^{-1}
grazed
ungrazed
Cumulative herbage yield (kg DM ha^{-1})
0
2000
4000
6000
8000
10000
100
200
Days from sowing

Table 28. Calculated values of plant growth attributes from fitted logistic curves.

Seeding rate (kg ha^{-1})	Plant no. m^{-2} at establish-ment (IPD)	(1) Predicted maximum yield (kg ha^{-1})	(2) DM at Max. G.R. (kg ha^{-1})	(3) Max. G.R. (kg ha^{-1} day^{-1})	(4) Time to Max. G.R. (days)	Date at Max. G.R.	Time* to produce 1,500 kg DM ha^{-1} (days)
(a) Grazed							
Low density							
1	38	700	350	9	101	Sept. 24th	n.a.
2	58	1697	849	23	106	Aug. 29th	109
4	165	3128	1564	40	110	Sept. 2nd	110
8	243	5134	2567	50	130	Sept. 22nd	108
16	495	7542	3771	59	147	Oct. 9th	103
Medium density							
32	1126	10168	5084	96	135	Sept. 27th	91
64	2444	10206	5103	113	136	Sept. 28th	97
High density							
128	5750	10499	5249	82	126	Sept. 18th	70
256	10543	8774	4387	60	122	Sept. 14th	65
512	13761	9666	4833	68	108	Aug. 31st	48
1024	35993	10323	5162	75	107	Aug. 30th	47
(b) Ungrazed							
Low density							
1	34	8203	4102	226	130	Sept. 22nd	108
2	47	8450	4225	168	136	Sept. 28th	105
4	185	8060	4030	144	126	Sept. 18th	103
8	202	8087	4040	126	120	Sept. 12th	97
16	581	7952	3976	210	101	Aug. 24th	87
Medium density							
32	1580	8110	4055	122	110	Sept. 2nd	85
64	2103	7706	3853	123	107	Aug. 30th	85
High density							
128	6568	8545	4273	189	92	Aug. 15th	77
256	9253	8697	4348	96	106	Aug. 29th	72
512	15982	8361	4180	96	87	Aug. 10th	54
1024	32694	8602	4301	83	93	Aug. 16th	54

n.a. Not available since this treatment did not produce 1500 kg DM ha^{-1}.

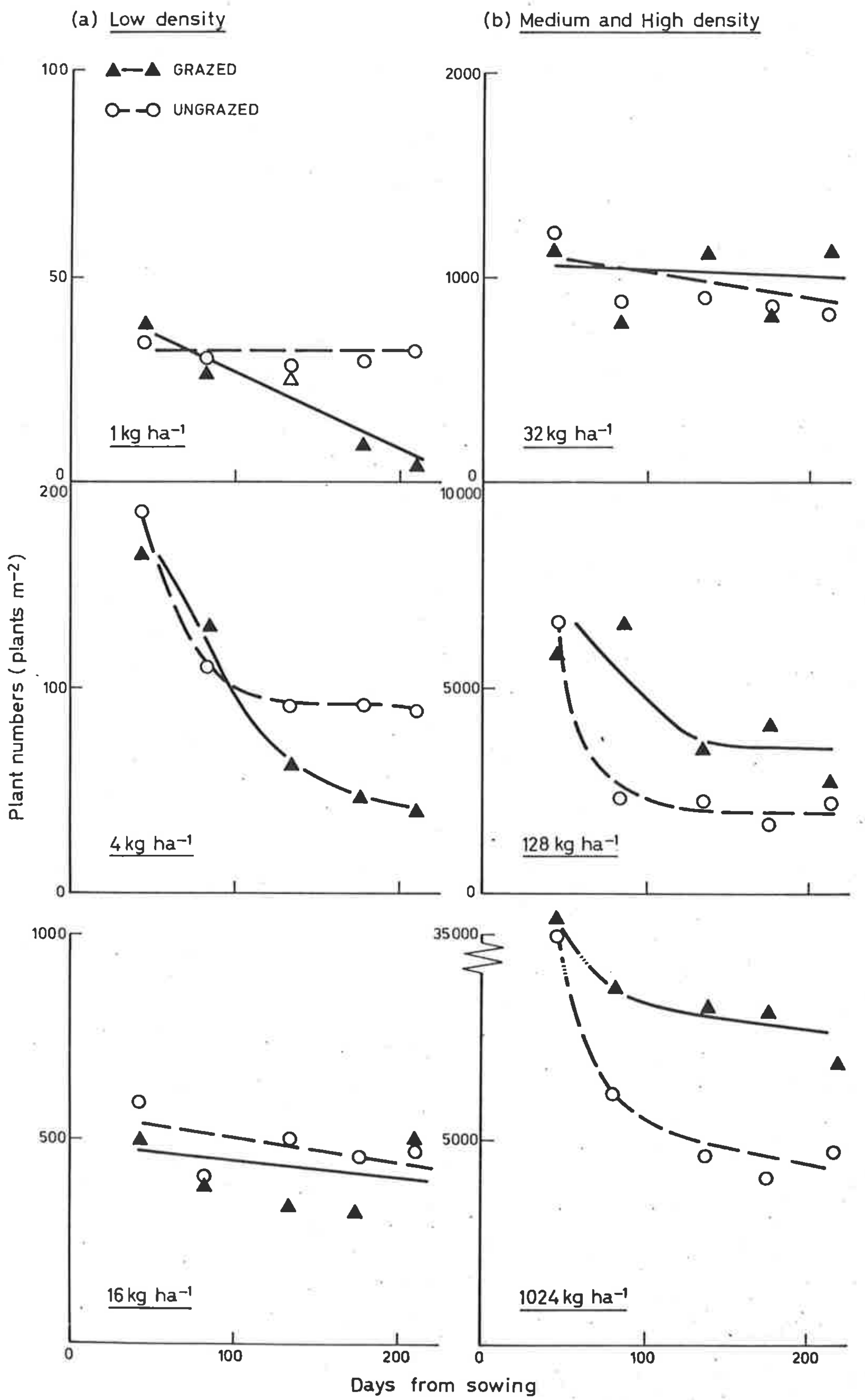
* Minimum herbage yield to form a closed canopy in perennial ryegrass (Alberda and Simba 1968).

$$Y = \frac{A}{1 + Be^{-CT}}$$

(1) A (2) $\frac{A}{2}$ (3) $\frac{AC}{4}$ (4) $\frac{1}{C}\log_e B$

Max. GR = Maximum rate of growth.

Figure 33. Changes in plant numbers per unit area in time in grazed and ungrazed swards of a selected range of seeding rates, encompassing (a) (Left) low density, and (b) (Right) medium and high density swards.



(a) Low density
(b) Medium and High density
GRAZED
UNGRAZED
1 kg ha⁻¹
32 kg ha⁻¹
4 kg ha⁻¹
128 kg ha⁻¹
16 kg ha⁻¹
1024 kg ha⁻¹
Plant numbers (plants m⁻²)
Days from sowing
100
50
0
200
1000
500
2000
10000
5000
35000

of grazed compared to ungrazed plants at harvests 4 and 5 (Appendix Table 25).

The characteristics of plant growth in grazed and ungrazed swards were similar in high density swards and differed markedly in low density situations.

(d) Plant and tiller characteristics and seeding rate

Plant number and weight and tiller number per plant for the individual grazed and ungrazed plots are given in Appendix Tables 15, 17 and 18. Figure 33 shows changes in plant numbers in relation to time in grazed and ungrazed swards sown at different seeding rates. Because of the great range in plant densities studied, the data are presented on a different scale for each seeding rate treatment. For example, the Y axis at 1 kg ha^{-1} is from 1 to 100 plants m^{-2} at 128 kg ha^{-1} seeding rate the scale is reduced 100-fold (from 1 to 10000 plants m^{-2}). However, the main comparison of interest is between grazed and ungrazed swards within a seeding rate. In grazed swards, the reduction in plant number in time was dramatic in the 1 to 4 kg ha^{-1} seeding rate treatments, whereas plant survival was far greater in ungrazed swards sown at the same seeding rates (Figure 33, Appendix Tables 15 and 16). Animal demand was always equal or greater than plant growth on these very low density grazed swards, so that the resultant small, heavily grazed plants suffered high mortality in spring.

In both grazed and ungrazed swards, plant numbers remained relatively constant in the 16 and 32 kg ha^{-1} seeding rate treatments. However, a 2 to 5-fold reduction in plant numbers occurred in all high density swards sown at seeding rates of 128 kg ha^{-1} and greater. Intense plant competition during early growth was associated with high plant mortality. The higher the seeding rate, the lower the percentage of original plant numbers which survived to maturity (Figure 33 and Appendix Table 16).

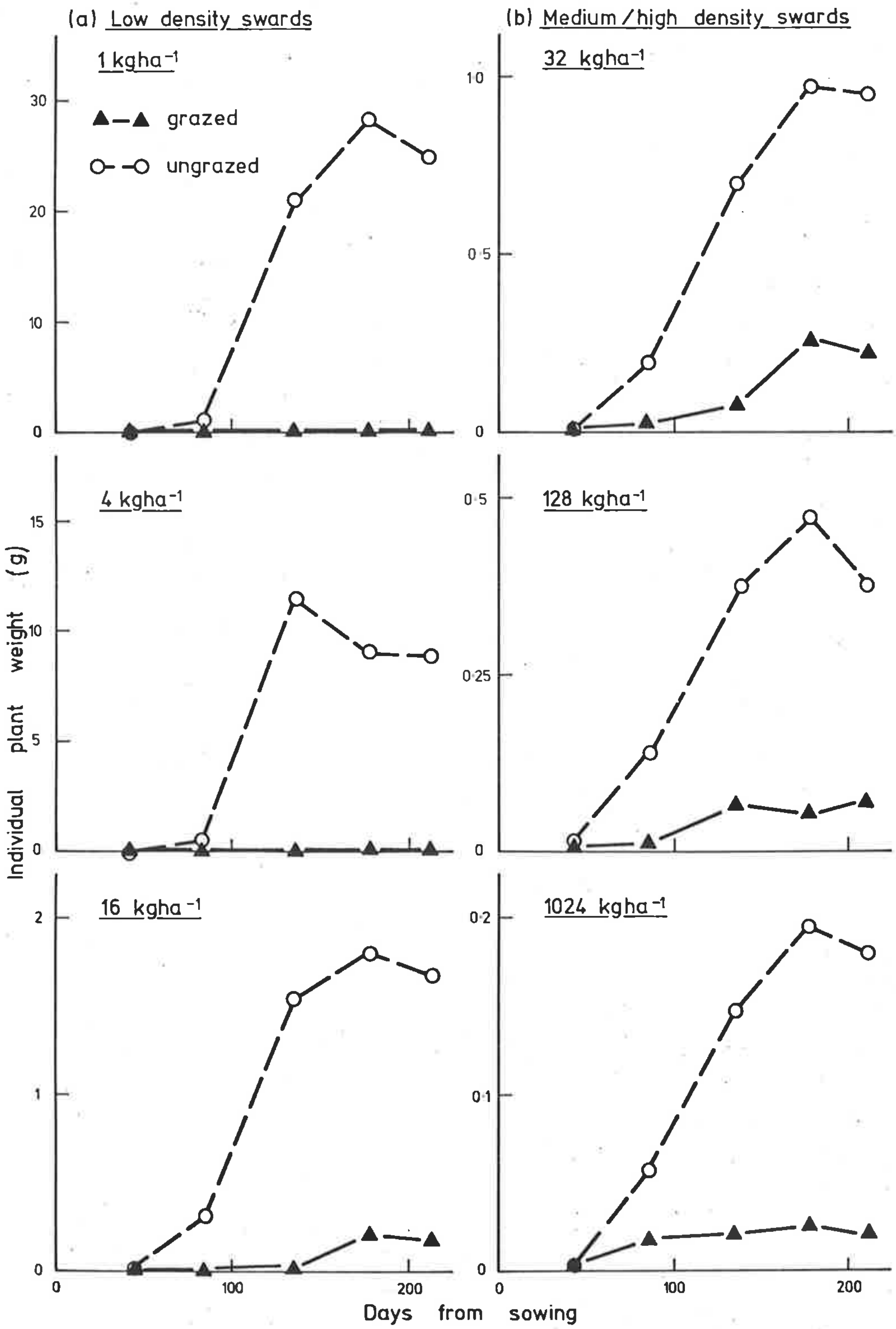
Herbage yield is the product of plant numbers and plant weight. The large differences in total herbage yield between grazed and ungrazed swards at the end of the season (Figure 31) were associated with large differences in individual plant weights in these swards (Figure 34). Again the major comparison of interest is between grazed and ungrazed swards within a seeding rate treatment. The 1000-fold range in initial plant densities generated produced c. a 136-fold range in plant weights (180 mg up to 24.5 g) in ungrazed pastures, whereas only a 22-fold range (10 mg - 217 mg) was generated in grazed swards at harvest 5.

It will be recalled that in low density grazed swards (seeding rates of 1 to 16 kg ha^{-1}) increases in plant weight did not fully compensate for deficiencies in plant numbers in terms of total herbage yield (Figure 20). By contrast, in ungrazed swards any deficiency in plant numbers was fully compensated for by increases in individual plant weight so that the total end of season yield was constant and independent of plant density over the full range of densities studied.

Figure 35 shows the relation of tiller number per plant in grazed and ungrazed swards for a selected range of seeding rate treatments. All data are presented on the same scale. Early in the growing season, tiller number per plant was low and constant in all swards. At later harvests, the plants in ungrazed plots exhibited the typical response to density of undefoliated plants, i.e. the more

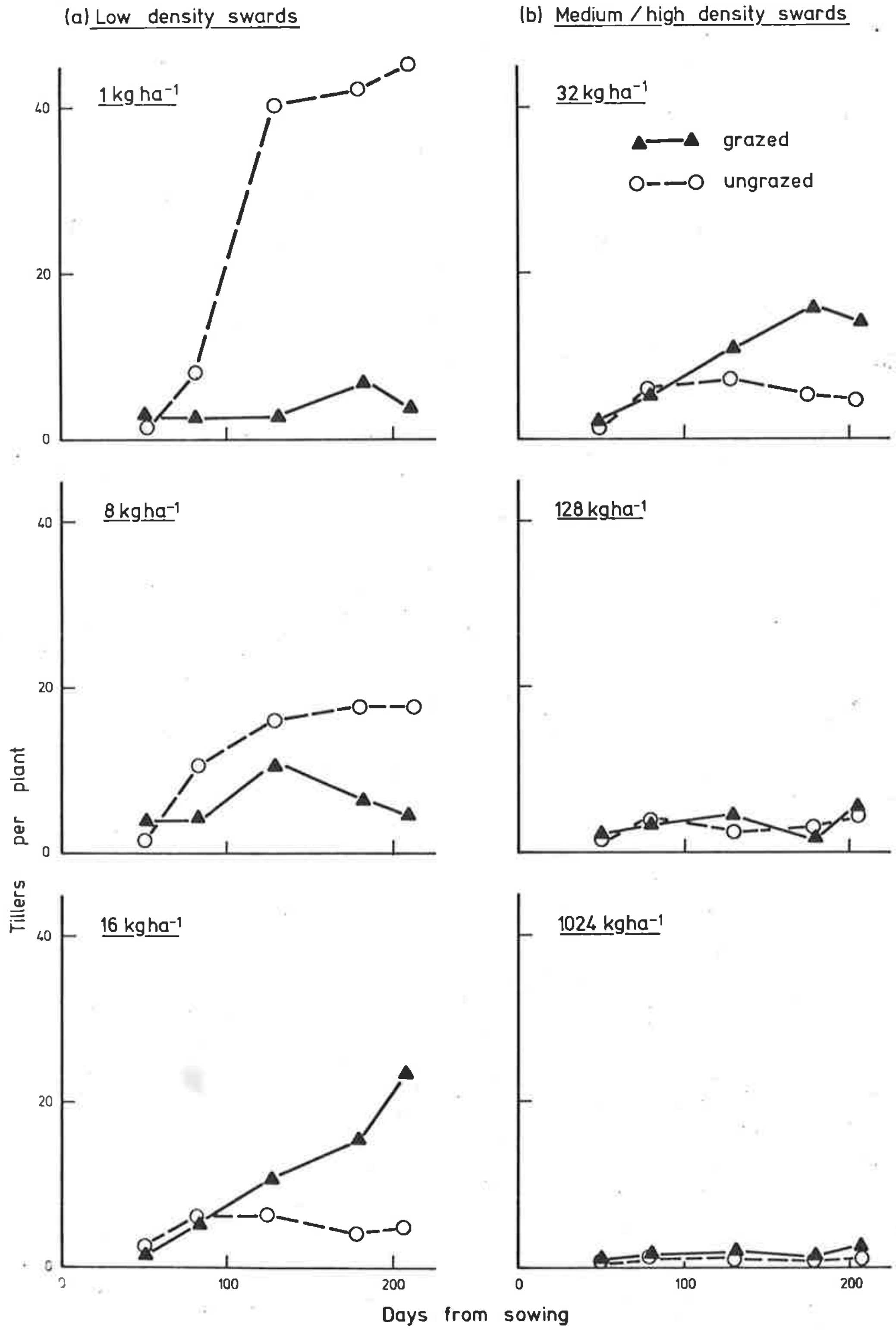
Figure 34. Changes in individual plant weight in time in grazed and ungrazed swards of a selected range of seeding rates.

Data for individual treatments are summarized in Appendix Table 17.



(a) Low density swards
(b) Medium / high density swards
1 kgha⁻¹
4 kgha⁻¹
16 kgha⁻¹
32 kgha⁻¹
128 kgha⁻¹
1024 kgha⁻¹
grazed
ungrazed
Individual plant weight (g)
Days from sowing

Figure 35. Changes in the number of tillers per plant in time in grazed and ungrazed swards of a selected range of seeding rates.



(a) Low density swards
(b) Medium / high density swards
1 kg ha-1
32 kg ha-1
8 kg ha-1
128 kg ha-1
16 kg ha-1
1024 kg ha-1
grazed
ungrazed
Tillers per plant
Days from sowing
0
20
40
0
100
200

plants present, the fewer tillers per plant and vice versa. There was a 50-fold range in tiller numbers per plant observed in ungrazed swards and only a 20-fold range in grazed swards of comparable density. It is of interest to study the relation of tillers per plant to plant density in grazed compared to ungrazed swards. All possible combinations were recorded depending on plant density, sampling occasion and grazing influences, namely: (i) reduced tillering, (ii) increased tillering, and (iii) similar tillering as shown in Figure 35.

(i) Reduced tillering

Tiller number per plant was greatly reduced by grazing in the very low density (1-8 kg ha^{-1} seeding rates) swards compared to ungrazed swards of similar density at all harvests (Figure 35).

(ii) Increased tillering

There was a large increase in tiller numbers per plant in grazed swards of intermediate density (seeding rates 16 to 64 kg ha^{-1}) compared to ungrazed swards of comparable density at harvests 3 to 5 (Appendix Table 18).

(iii) Similar tillering

Grazing had little effect on the number of tillers per plant in all higher density pastures (seeding rates 128 kg ha^{-1} and greater).

Plates 2 and 3 show the number of tillers per plant, tiller length and plant morphology of plants taken at random at harvests 2 and 5 from grazed and ungrazed swards, respectively. Grazing compared to nil grazing caused a reduction in tiller length at all densities and the number of tillers per plant, plant number, weight varied depending on sward density. It was not until a seeding rate of

Plate 2: The number of tillers per plant, tiller length and morphology of plants taken at random from grazed pastures of different densities at harvests 2 and 5.

(a) Top; h_2 (August 11th)

Left: seeding rate 1 kg ha^{-1}

Centre: seeding rate 32 kg ha^{-1}

Right: seeding rate 1024 kg ha^{-1}

(b) Bottom: h_5 (December 15th)

Left: seeding rate 1 kg ha^{-1}

Centre: seeding rate 32 kg ha^{-1}

Right: seeding rate 1024 kg ha^{-1}

All plants are shown in position for tiller length measurements.

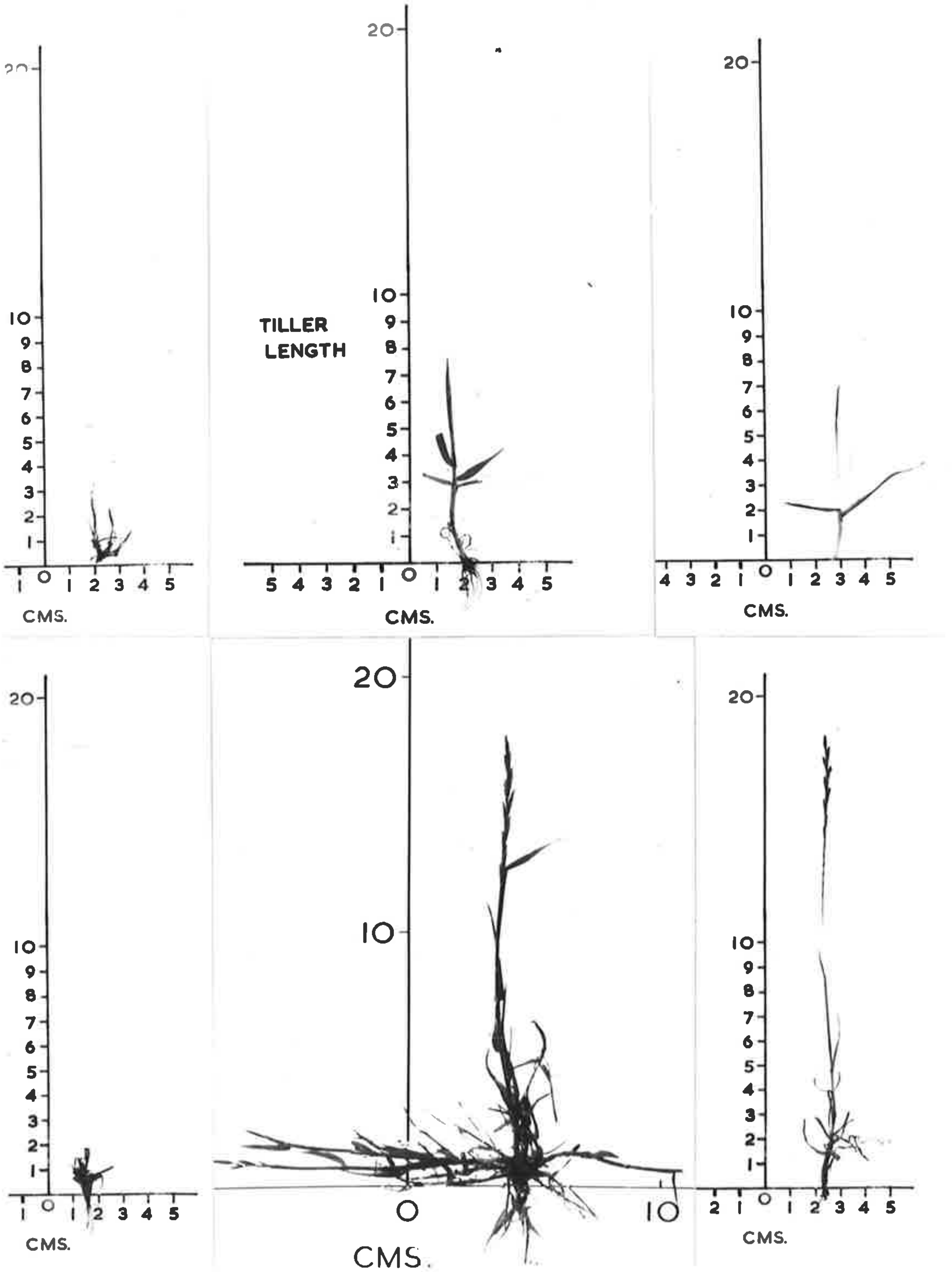

TILLER LENGTH
CMS.
CMS.
CMS.
CMS.
CMS.
CMS.

Plate 3. The number of tillers per plant, tiller length and morphology of plants taken at random from ungrazed pastures of different densities at harvests 2 and 5.

(a) Top: h_2 (August 11th)

Left: seeding rate 1 kg ha^{-1}

Centre: seeding rate 32 kg ha^{-1}

Right: seeding rate 1024 kg ha^{-1}

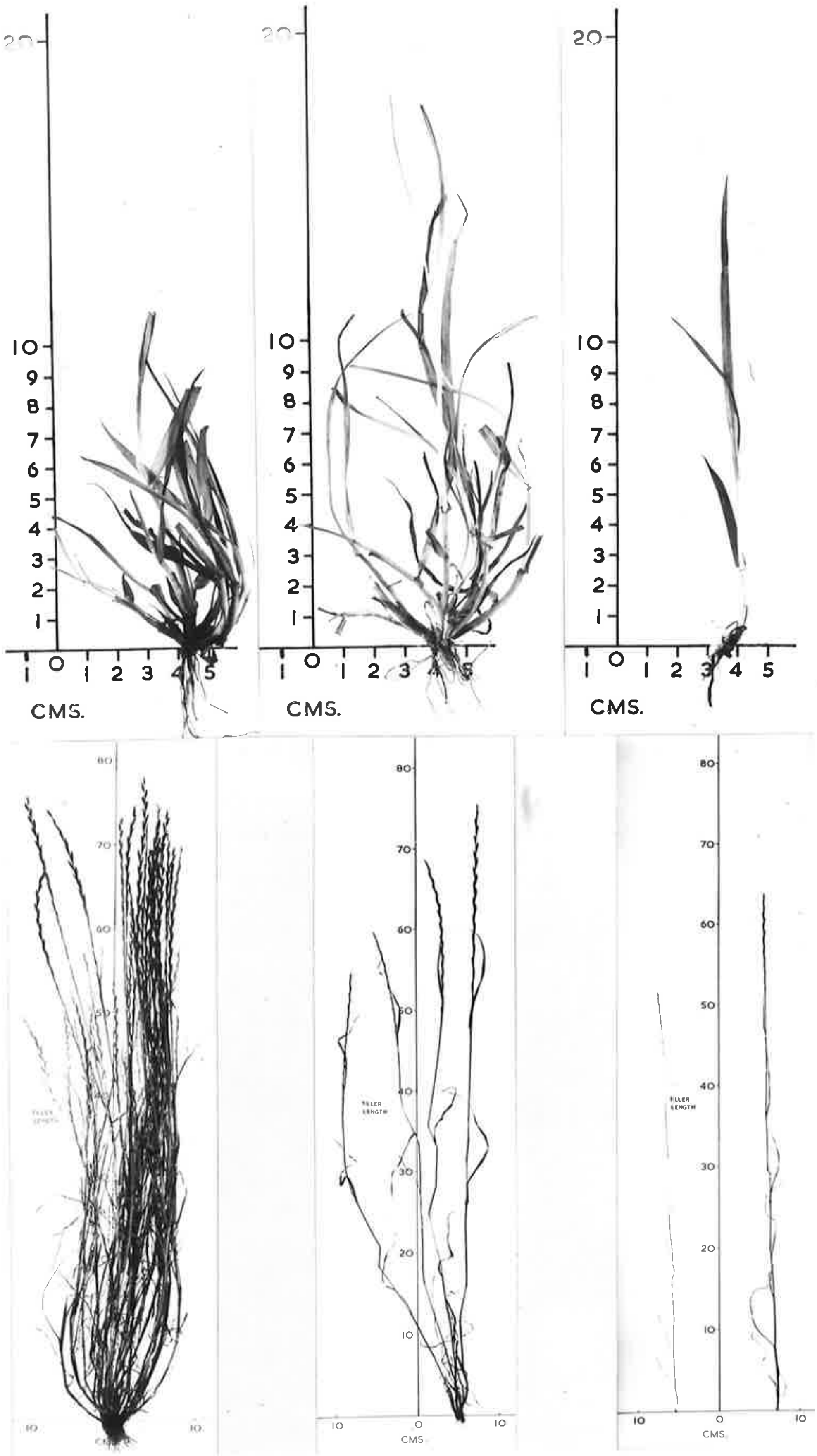
(b) Bottom: H_5 (December 15th)

Left: seeding rate 1 kg ha^{-1}

Centre: seeding rate 32 kg ha^{-1}

Right seeding rate 1024 kg ha^{-1}

All plants are shown in position for tiller length measurements.


CMS.
CMS.
CMS.
TILLER LENGTH
CMS
TILLER LENGTH
CMS

16 kg ha^{-1} in grazed plots that plant number per unit area remained relatively constant during the experiment and large increases in tiller numbers per unit area occurred (Appendix Table 19). This increased tiller production at the 16 kg ha^{-1} seeding rate occurred too late in the growing season (Figure 35) for this treatment to produce maximum plant and animal output ha^{-1} (Section 5.4.2).

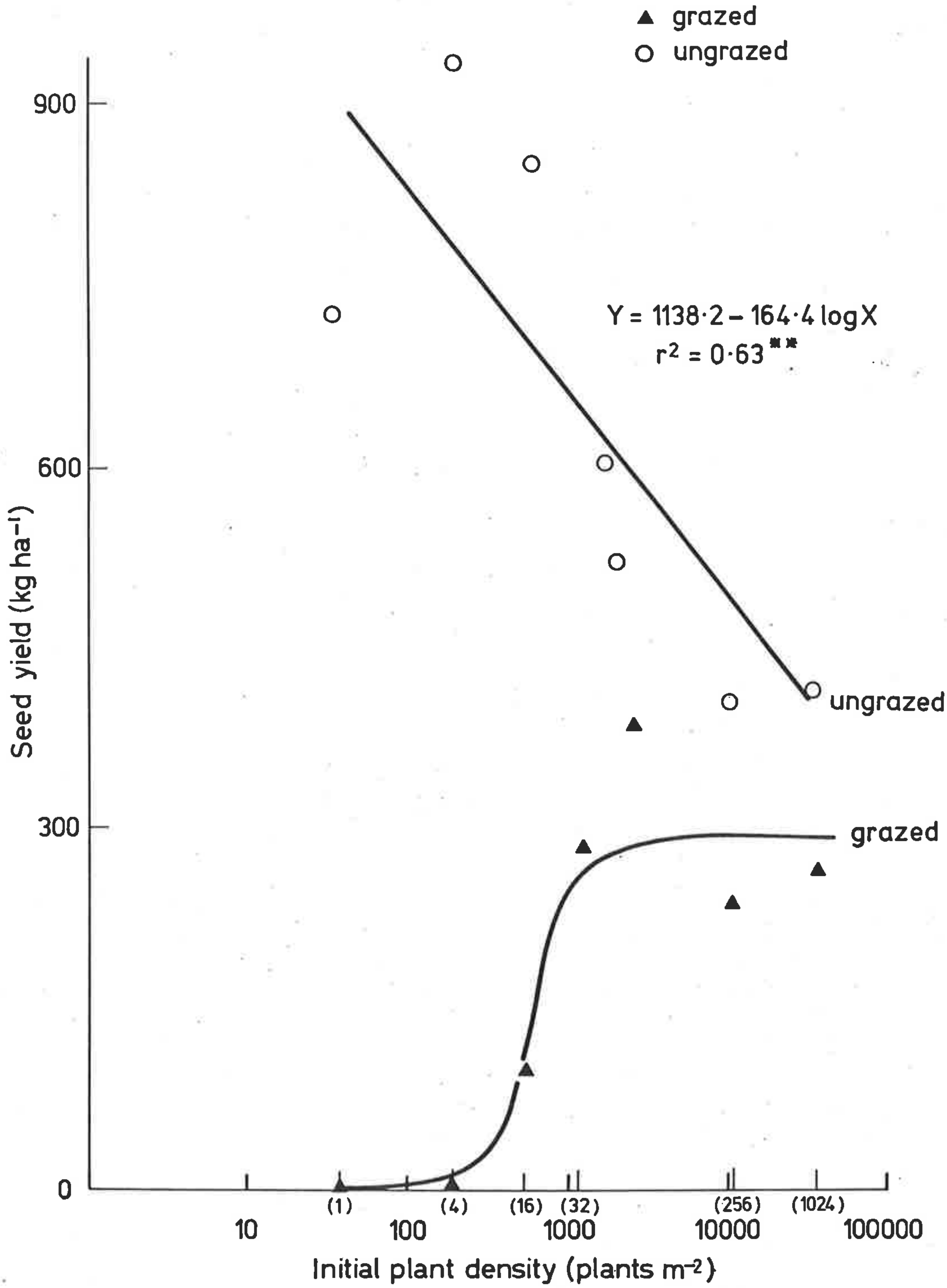
The higher the plant density the more similar were grazed and ungrazed swards in terms of plant and tiller population dynamics.

Correlations coefficients between sward characteristics and herbage growth rate in grazed and ungrazed swards are presented in Appendix Tables 21 and 26. In both grazed and ungrazed swards, at harvest 1, tiller length and plant density were highly correlated with growth rate. At later harvests plant weight became more important.

(e) Seed yield and seeding rate

Figure 36 illustrates the relations between seed yield and seeding rate for grazed and ungrazed pastures. The lowest density grazed sward (seeding rate 1 kg ha^{-1}) produced no seed at the final harvest. Presumably, the sheep consumed the few seedheads produced in this treatment. Seed yield increased up to a maximum at the 32 kg ha^{-1} treatment in grazed swards and thereafter remained constant, whereas in ungrazed swards, seed yield was greatest from the low density swards being reduced by 50% as the seeding rate increased from 1 to 1024 kg ha^{-1}.

Figure 36. The relation of seed yield to initial plant density (on a logarithmic scale) for grazed and ungrazed swards. A selected range of seeding rates are shown in parentheses.



▲ grazed
○ ungrazed
Y = 1138·2 – 164·4 log X
r² = 0·63**
ungrazed
grazed
Seed yield (kg ha⁻¹)
900
600
300
0
(1)
(4)
(16)
(32)
(256)
(1024)
10
100
1000
10000
100000
Initial plant density (plants m⁻²)

At all densities, grazing compared to no grazing caused a significant reduction in seed yield (Table 29). More seed was produced compared to the amount sown in ungrazed plots sown at seeding rates from 1 to 256 kg ha^{-1} and in grazed pastures sown at seeding rates from 16 to 64 kg ha^{-1} (Table 29).

Thus, a minimum seeding rate of 16 kg ha^{-1} was required in grazed pastures to provide at least 32 kg ha^{-1} of seed. This was the level needed for maximum plant and animal production in this experiment.

(f) Economic returns from the different seeding rate treatments

Crude gross margins were calculated from the values of seed and/or wool produced less the cost of seed sown and are presented in Figure 37. Since seeding rate was the only management variable, it was assumed that all other costs would be similar within a wool or seed growing enterprise. Clean wool was valued at $A2.50 per kg. This was the Australian floor (reserve) price for 21 micron wool in 1975-76 (Australian Wool Corporation 1976). Annual ryegrass seed was valued at 25 cents per kg retail price and 20 cents per kg to the grower (Wright Stephenson personal communication).

The highest crude gross margin was from the seed growing enterprise from ungrazed swards sown at seeding rates of 1 to 16 kg ha^{-1} (Figure 37). The maximum crude gross margin for wool plus seed production occurred on swards sown at seeding rates of 32 kg ha^{-1}.

Table 29. Analysis of variance and means of the seed yield (kg ha^{-1}) of grazed and ungrazed swards (using the different density treatments as replicates).

Source of variation	DF	Mean square	F	Probability
Density	6	40291.1	0.2	1.0 n.s.
Density X defol.	6	770017.0		
Defol. (grazed vs ungrazed)	1	3744238.0	13.6	0.010*
Residual	6	274314.0		

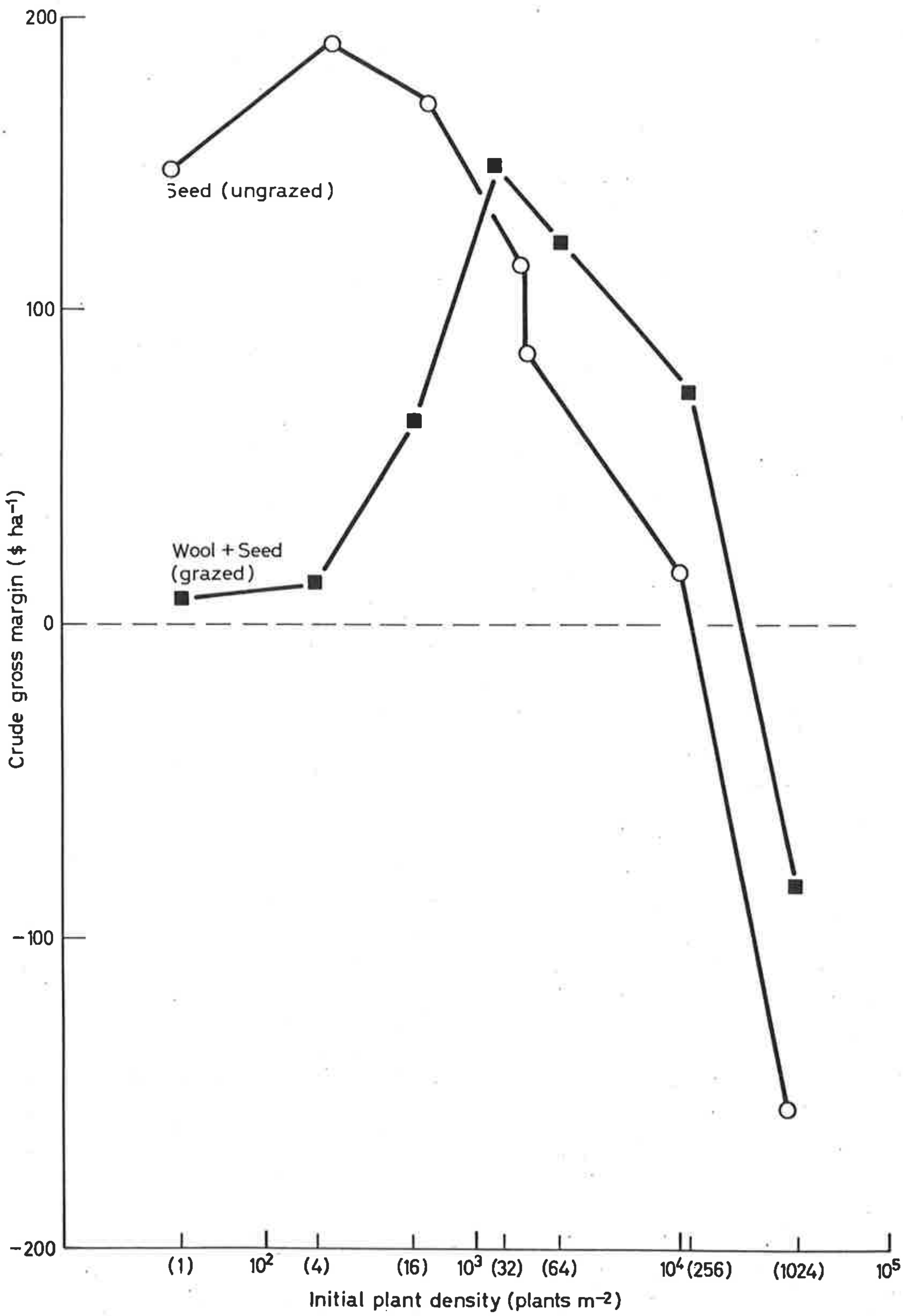
Means

	Seeding rates (kg ha^{-1})							
	1	4	16	32	64	256	1024	Grand Mean*
Seed yield (kg ha^{-1})	Seed yield (kg ha^{-1})							
Grazed	0	1	100	282	383	234	261	180a
Ungrazed	724	932	848	601	516	404	412	634b
	kg seed set per kg seed sown							
Grazed	0.0	0.3	53.0	21.0	8.0	1.0	0.4	0.9
Ungrazed	724.0	233.0	6.2	8.8	5.2	0.7	0.3	3.2

* LSD at $P < 0.05$ = 125 kg ha^{-1}, means with different subscripts differ significantly at $P < 0.05$.

Figure 37. Effects of increasing initial plant density on the crude gross margins from the seed and wool growing enterprises.

A selected range of seeding rates are shown in parentheses.



200
100
0
−100
−200
Seed (ungrazed)
Wool + Seed
(grazed)
Crude gross margin ($ ha⁻¹)
(1)
10²
(4)
(16)
10³
(32)
(64)
10⁴
(256)
(1024)
10⁵
Initial plant density (plants m⁻²)

5.5 Discussion of Experiment 2

The one thousand-fold range in seeding rates produced swards with a 950-fold range in plant density, 53 days after sowing. These seeding rates and initial plant populations cover the wide range of densities, in terms of both the numbers of viable seeds and seedlings surviving, that have been observed in grazed annual pastures over a number of years (Willoughby 1954, 1958; Sharkey *et al.* 1964; Smith 1968c; Smith *et al.* 1972; Gramshaw and Stern 1977a; Squires 1978). Thus, in the one year there was available for comparison a range of seeding rates and plant populations which might be expected to occur over a number of years in annual pastures. Many grazing experiments have recorded the impact of varying the number of sheep on pastures of initially similar density. The current work has shown that variations in the number of plants per sheep have a substantial influence on plant and animal production from newly sown, annual pastures in the year of establishment.

There was more than a five-fold increase in herbage, seed and wool production per hectare in grazed swards as the seeding rate of Wimmera ryegrass was increased from 1 to 32 kg ha^{-1}, with little further increase in total productivity at higher seeding rates. The eleven seeding rate treatments were found to fall into three distinct categories: low, medium and high - based on sheep live weight and survival in time. Swards could also be termed stable or unstable on the basis of animal performance.

The three categories are:

(i) Low density swards (unstable) - seeding rates of $1 - 16$ kg ha^{-1}; IPD of 38 - 495 plants m^{-2},

(ii) Medium density swards (stable) - seeding rates of $32 - 64$ kg ha^{-1}; IPD of 1124 - 2444 plants m^{-2},

(iii) High density swards (stable) - seeding rates of $128 - 1024$ kg ha^{-1}; IPD of 5750 - 35993 plants m^{-2}.

It is emphasized that the classification of pasture stability is based on animal survival and production when animals grazed at the stocking rate selected in the current experiment. At other stocking rates, times of grazing and with different seasonal conditions, instability might occur at different sward densities (Sharkey et al. 1964; Morley 1966a; McKeown and Smith 1970). The term is useful for presentation and discussion of results.

On swards of low density sheep were unable to maintain their initial live weight, except for sheep on the 16 kg ha^{-1} treatment which gained weight for a brief period in the spring. Thus, the fleece-free live weights of sheep on low density swards at the end of the experiment ranged from 25 to 50 kg and were substantially less than those of sheep grazing higher density pastures (the latter sheep weighed 63 kg). Sheep mortality occurred at the low seeding rates, ranging from 100 per cent losses at 1 kg ha^{-1} to 40 per cent deaths at 16 kg ha^{-1}. Such instability of the grazing system (or "crash points" as defined by Morley 1966a) commonly occurs in annual pastures during early growth after periods of drought or false breaks of the grazing season (Donald and Allden 1959; McKeown and Smith 1970) and producers have to sell livestock or feed a supplement if such conditions are prolonged. Monitoring the annual carryover of seed reserves and plant density present could provide an advance indication of the onset of periods of instability in grazing systems.

Swards of medium density (stable swards) carried sheep without loss and although live weights fell through the winter months, the animals compensated for this loss of production during the spring period. Live weight of these animals at the end of the experiment did not differ from those grazing higher density swards where sheep gained weight throughout the experiment. These patterns of animal growth and survival can be expected to occur in a good rainfall year on dense swards of annual pastures grazed at moderate stocking rates (e.g. Carter and Day 1970; Brown 1976, 1977b).

The animal responses recorded suggest that the sheep producer should manage pastures for high seed production. Smith (1968c), on the basis of results from cutting experiments, concluded that the grazier must manage annual pastures for maximum seed set; in order to minimize the effects of variations in the time and nature of the break of the growing season.

In the present work there was a rapid transition from unstable, unproductive to stable, productive pastures when the seeding rate was doubled from 16 to 32 kg ha^{-1}. Such results indicate that plant density should be considered in annual species evaluation experiments. Annual species should be compared at similar densities in order to avoid confounding density and species effects. This may also be necessary in the evaluation of perennial species (Lazenby and Rogers 1962; Harris and Brougham 1970; Harris 1973). Also, the response in plant number and weight, and seed set of a given species to low and high grazing pressure may ultimately determine its survival and the botanical composition of annual pasture.

The most significant aspect of the herbage yield data was that the time to produce maximum herbage yield increased as the seeding rate decreased. In terms of herbage availability, the initial 270-fold difference in herbage availability between pastures of different densities persisted throughout the experiment. A minimum herbage availability ranging from 670 to 2000 kg DM ha^{-1} is required for maximum animal production from annual pastures (Willoughby 1959; Scott Young 1960; Arnold 1964a; Arnold and Dudzinski 1967b; Allden and Whittaker 1970). Since herbage availability on low density swards was always less than 500 kg DM ha^{-1}, limited herbage availability restricted the attainment of maximum animal production from low density swards.

It is interesting to note that the transition from stable to unstable swards occurred as the IPD was reduced from 1126 to 495 plants m^{-2}. Sharkey *et al.* (1964) also found that between 2225 and 275 plants m^{-2} the 'crash point' as defined by Morley (1966b) was reached. Thus the minimum plant population in annual pastures needed to sustain high levels of animal production may be similar in different grazing situations in Mediterranean environments.

Certain compensatory mechanisms which operated in dense, stable pastures to maintain maximum total herbage yield and availability were not fully effective in low density, unstable swards. For example, in medium and high density stable swards any deficiencies in plant numbers were fully compensated for by increases in individual plant weight (at harvests 3 to 5) in the spring period so that total herbage yield and availability were maximised. In contrast, in low density swards deficiencies in plant numbers were not fully compensated for by increases in plant weight or in the components of plant weight - tiller weight and tiller number per plant so that availability and total yield were greatly reduced compared to that of higher density swards. Presumably animal demand was equal to or greater than plant growth in low density swards during most of the experiment and this high grazing pressure restricted increases in plant and tiller weight compared to that recorded in ungrazed swards of comparable density. Although in the 16 kg ha^{-1} seeding rate treatment, the grazed sward produced more tillers compared to the ungrazed sward of similar density, this increase was inadequate and occurred too late in the growing season to compensate fully for the deficiency of plant numbers. Thus the time and duration of favourable environmental conditions for plant growth are likely to have substantial effects on density/yield relationships in grazed annual pastures. In swards protected from grazing, any deficiencies in plant numbers were fully compensated for by increases in plant weight over the full range of seeding rates studied so that final yield was independent of seeding rate. The thousand-fold range in initial plant density in ungrazed swards generated at harvest 5 a 136-fold range in individual plant weight. Whereas, in grazed swards there was only a 22-fold range in plant weight. The ingestion of herbage by the grazing animal was a major factor causing plant size and weight to be greatly reduced in all grazed compared to ungrazed plots of comparable density throughout the experiment.

Furthermore, by varying the number of plants per sheep the full range of responses of plant yield to defoliation as observed in cutting experiments as reviewed by Humphreys (1966) and Davidson (1969) and in grazing experiments (Hutchinson 1969; Carter and Day 1970; Vickery 1972; Langlands and Bennett 1973a) were produced. For example, over the relatively narrow range of 1 to 32 kg ha^{-1} in seeding rate the yield differences were changed greatly. At the lowest seeding rate of 1 kg ha^{-1}, there was a twelve-fold difference in total herbage yield in favour of the ungrazed swards; while at a seeding rate of 16 kg ha^{-1}, total yield from grazed and ungrazed swards was similar. At seeding rates of 32 kg ha^{-1} and above total yield was 17 per cent greater in grazed compared to ungrazed swards. Some of these differences may have been due to the different methods used to assess herbage yield in grazed (open and closed quadrat method of McIntyre 1951) and ungrazed (visual method of Morley _et al._ 1964) swards.

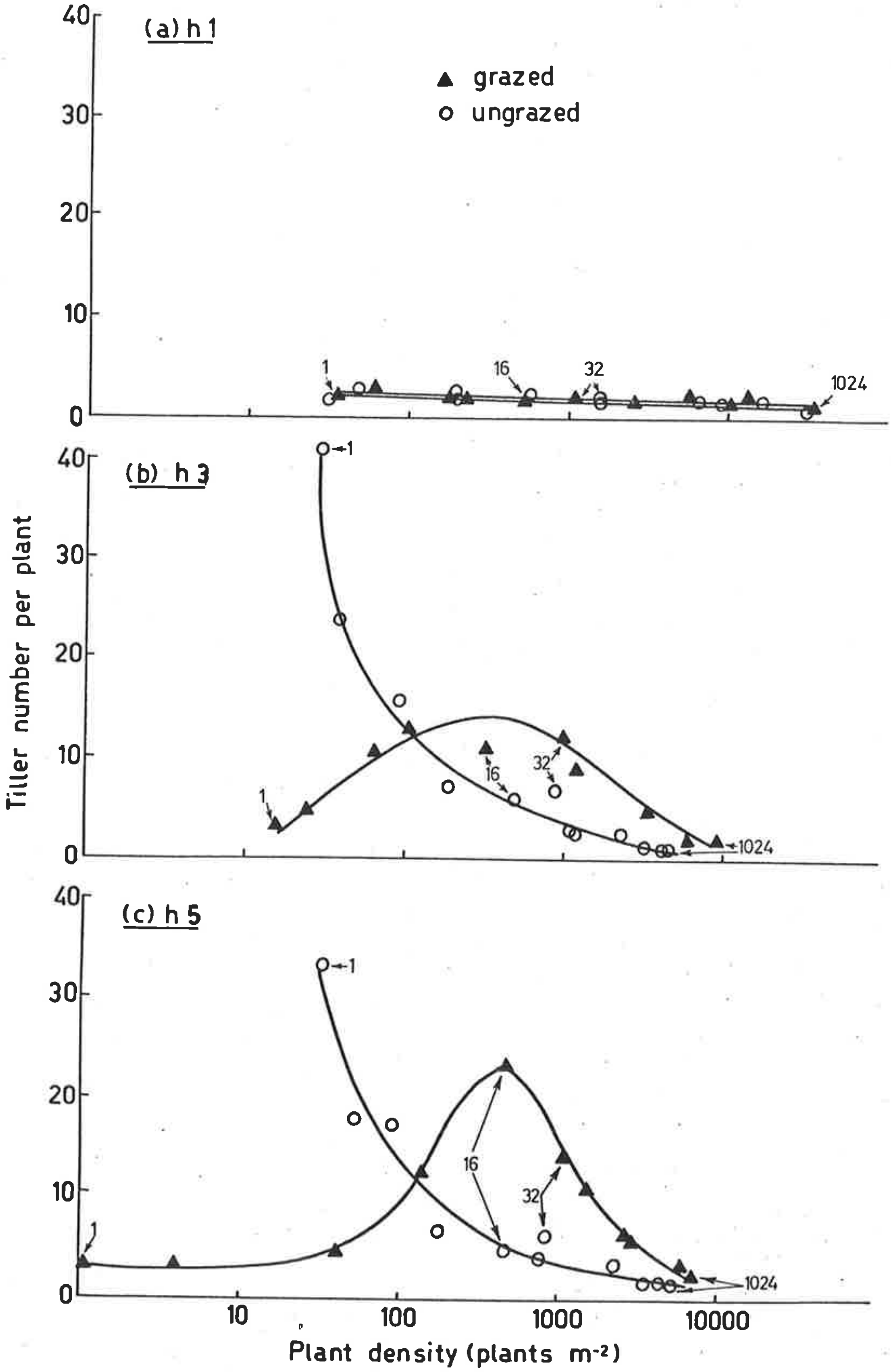
The presence or absence of the grazing animal also influenced the tillering capacity of swards. Figure 38 illustrates tiller numbers per plant at harvests 1, 3 and 5 in relation to

FIGURE 38: The relations between the number of tillers per plant and initial plant density in grazed and ungrazed swards at harvests 1 (Top), 3 (Centre) and 5 (Bottom).

All lines are fitted by eye.

The seeding rate treatments 1, 16, 32 and 1024 kg ha^{-1} are shown for each harvest.

Tiller number per plant data for individual grazed and ungrazed plots at 5 harvests are presented in Appendix Table 18.


(a) h 1
grazed
ungrazed
(b) h 3
(c) h 5
Tiller number per plant
Plant density (plants m-2)
10
100
1000
10000
0
10
20
30
40
1
16
32
1024

plant density for grazed and ungrazed plots. No grazing had taken place at harvest 1, so values for the two treatments were similar. It can be seen that the tillering capacity of plants was either reduced, increased or unaffected in grazed compared to ungrazed swards over a similar range in plant density.

The three responses observed at harvests 3 and 5 were:

(i) Reduced tillering

In swards of low density the number of tillers per plant was far less in grazed compared to ungrazed swards at all harvests when less than c. 100 plants m^{-2} were present. Continuous grazing inhibited tiller growth and development. At harvest 3, single plants in ungrazed plots at the lowest seeding rate had 40 tillers per plant, whereas, at the corresponding seeding rate grazed plants had an average of 3 tillers per plant.

Reduction in plant productivity on the very low density swards (1 - 4 kg ha^{-1}) as a result of frequent defoliation by the grazing animal was presumably caused by a reduction in the rate at which tillers grew and a decline in the number of tillers per plant. This decline in the rate of tiller initiation, growth and development under high grazing pressures was probably due to reduced carbohydrate levels within the bases of expanding leaves, as demonstrated by Davidson and Milthorpe (1966b). Carbohydrate levels would be reduced because of insufficient time between defoliations to allow replenishment from the current products of photosynthesis.

(ii) Increased tillering

There were substantial increases in tiller numbers per plant in grazed compared to ungrazed swards sown at seeding rates of 16 to 64 kg ha^{-1} at harvests 3 to 5 when there were from 200 to 2000 plants m^{-2} present. The importance of the time sequence of tiller production in annual swards is further shown by the fact that although the grazed sward sown at 16 kg ha^{-1} produced the most tillers per plant of any grazed sward (24) - this occurred too late in the growing season to compensate (in terms of total plant and animal production) for a reduced plant population in this experiment. Hill (1971) and Hill and Watkin (1975) have ascribed this type of plant response to the fact that when animals remove tiller parts and apical meristems from pastures of moderate density, this may stimulate increased tillering.

(iii) Similar tillering

Grazing had little effect on the numbers of tillers per plant in all high density swards (seeding rates of 128 to 1024 kg ha^{-1}). It is evident that the major factor affecting tiller numbers per plant in these swards was high density (Donald 1951, 1954). Thus, grazed and ungrazed pastures behaved most similarly in high density situations. The lower the plant density the greater was the disparity. By varying the number of plants per sheep it was possible in the one grazing experiment to produce the full range of responses of tillering to defoliation observed in ungrazed, cutting experiments (Silsbury 1965, 1966; Davies 1969; Knight 1970a, b; Hill 1971; Wilman et al. 1976) and grazing experiments (Hutchinson 1969).

The results point to the danger of making extrapolations from the herbage yield and tillering responses obtained in ungrazed, small plot studies to grazing situations. The results may only be applicable at one time, or at one plant density subject to the conditions of the original experiment. This emphasizes the need to define the extent and frequency of defoliation of individual plants, by the grazing animal, and compensatory mechanisms operating in normal grazing systems. Such measurements may provide indices or advance warning of periods of low productivity and instability in annual pastures so that management methods can be adopted to help alleviate such stress periods. For example, removing and/or reducing stock numbers from low density swards in the spring to permit adequate tiller growth and development to promote seed set and the attainment of a dense, productive pasture in the following year.

Grazing animals were found to exhibit compensatory mechanisms in an attempt to maintain their nutrient intake on different pastures. At harvest 1, both intake and rate of intake increased over the full range of plant density treatments. When herbage availability was less than c. 1000 kg DM ha^{-1} although sheep increased their grazing time, this was inadequate to fully compensate for a greatly reduced rate of intake and total intake declined.

As time progressed, the relationships between intake, rate of intake and plant density (and indirectly availability) changed from exponential form at harvest 1 to asymptotic at harvests 2, 3 and 5 to quadratic at harvest 4. At harvests 3, 4 and 5, a minimum seeding rate of 32 kg ha^{-1} was required for maximum intake and rate of intake. This was also the minimum seeding rate treatment for maximum animal production and survival. Thus, the previous nutrition of the sheep influenced their current response to plant density and herbage availability. An asymptotic intake/availability relationship was obtained before and after animals had exhibited compensatory intake and growth at harvest 4. The previous nutritional experience is likely to interact with the effects of current herbage availability influencing sheep intake at different times (Arnold 1964b; Arnold and Dudzinski 1967b; Allden and Whittaker 1970; Curll 1976). Also plant and tiller characteristics (e.g. plant number and weight, tiller length and tiller numbers per plant) of the swards were found to fluctuate widely over time, with density, and with grazing. These factors may also affect sheep intake and liveweight gain (Arnold and Dudzinski 1967b, c; Allden and Whittaker 1970; Smith et al. 1972.). It is unlikely and unrealistic to expect there will ever be one general intake/ availability relationship developed. In the current work, plant density and tiller length of swards were highly correlated with plant growth rate and sheep intake early in the growing season. In the latter half of the experiment, plant weight became more important.

Other interactions between animals and plants differed markedly over time. Sheep maintained a live weight of 45 kg in the first half of the experiment on swards providing 2972 plants m^{-2}, whereas in the second half, 230 plants m^{-2} achieved this. Presumably the substantial increase in plant weight over time in swards of intermediate density was associated with the patterns of compensatory intake and growth of sheep observed in the second half of the experiment (spring). Wool growth, however, was linearly related to the logarithm of initial plant density in a similar fashion in both periods. There was a trend for wool production, both per sheep and per hectare to increase as the seeding rate increased from 1 up to 512 kg ha^{-1} (Figure 18 and Appendix Table 12).

The experiment also provided an opportunity to compare the daily intake of herbage determined indirectly by a herbage cutting technique with estimates assessed from a faecal collection method. These two estimates of intake were used in the computation of herbage crude utilization (CU) as defined by Carter and Day (1970) and results are shown in Table 30. Herbage intake as assessed from herbage cutting techniques is a measure of herbage disappearance, much of which may be attributable to senescence and soil flora and fauna decomposing herbage, in addition to herbage ingested by sheep. Crude utilisations of herbage ranged from 75 to 99 per cent, or 30 to 51 per cent when intake was estimated from herbage cutting and faecal collection techniques, respectively. Thus, there were big differences in intake estimated by the two methods. However, part of these differences could be due to the problems of measuring herbage production accurately (Langlands and Bennett 1973a). When liveweight responses and wool growth by sheep were related to energy intake, there was a large discrepancy between the two methods. Intake estimated by the faecal collection method gave good agreement with values reported in the literature for maintenance, gain and wool growth. However, the herbage cutting method overestimated these production criteria by a factor of two. These results suggest that the faecal collection method is a more accurate estimate of the herbage intake of sheep grazing annual pastures.

Table 30: Estimates of herbage consumption and crude utilization when intake is estimated by two methods for swards sown at different seeding rates.

Seeding rate (kg ha^{-1})	Total dry matter grown (kg ha^{-1}) (1)	Dry matter consumption (kg ha^{-1})		Herbage crude utilization (CU) (%)	
		(a) Herbage cutting technique (2)	(b) Faecal collection method (3)	* (a) Herbage cutting technique (2/1)	+ (b) Faecal collection method (3/1)
1	713	709	n.a.	99.4	n.a.
2	1706	1685	555	98.7	32.5
4	3197	3141	n.a.	98.2	n.a.
8	5032	4928	1494	97.9	29.6
16	6801	5087	2298	74.7	33.7
32	9653	7445	3391	77.1	35.1
64	9741	7874	3566	80.8	36.6
128	9976	7762	3689	77.8	36.9
256	8283	6890	4113	83.1	49.6
512	9238	6983	4688	75.6	50.7
1024	9851	8277	4530	84.0	45.9

* CU = 2/1 (where intake was estimated by a herbage cutting technique).

\+ CU = 3/1 (where intake was estimated using a faecal collection method).

n.a. = not available as all original sheep died on these treatments.

The herbage cutting technique of estimating intake has been discredited elsewhere in the literature (Raymond 1969; Ulyatt et al. 1974). Also other workers have shown that a 6-week cutting interval overestimates pasture growth (McIntyre 1951; Raymond 1969), and overestimation may still occur even when plots are cut before and after a 3 day grazing period (Ulyatt et al. 1974). The latter authors also suggested that the method overestimates the intake of grazing animals, especially if plant growth is high during the period of observation. In view of these and the discrepancies of the herbage cutting technique recorded in the current work, intake values as estimated by the faecal collection method are preferred in the computation of crude utilisation of herbage. Using this method a maximum of approximately half the herbage grown was consumed by the grazing animal. A figure very close to that recorded by Rossiter (1958), when intake was assessed by a faecal nitrogen index technique for sheep grazing at 10 ha^{-1} on annual pastures in Western Australia. Furthermore, the patterns of herbage production and consumption on high density swards were the most favourable to ensure the maximum crude utilization of herbage (Table 30) and wool production (Figure 18 and Appendix Table 12).

A useful preliminary comparison of the profitability of seed-growing and grazing enterprises was possible (Figure 37). However, other variable costs such as investment in equipment or livestock capital would need to be considered to permit a comprehensive comparison of the profitability of the different enterprises. Pastures sown at seeding rates of 1 to 16 kg ha^{-1} produced the highest economic returns (from seed production) in ungrazed situations, but they did not produce acceptable levels of seed and wool production when stocked heavily in the year of establishment. However, estimated profits from wool and seed production from grazed pastures increased up to a seeding rate of 32 kg ha^{-1} and were greatly reduced at higher seeding rates. At seeding rates of 256 kg ha^{-1} and greater, the cost of seed became prohibitive, relative to the value of saleable products produced.

In this experiment, grazed annual pastures were capable of supporting several thousand plants m^{-2} during the growing season and plant populations of above 1000 plants m^{-2} were essential to maintain stable and high levels of plant and animal production per hectare. Annual pastures which fell into the high density category (as outlined earlier) offer the sheep producer the most desirable production situation. Plant and tiller numbers m^{-2} in these high density, grazed swards stabilised at harvests 3 to 5 at approximately 5130 and 12920, respectively. These populations were equivalent to sowing 128 kg ryegrass seed ha^{-1}. However, in ungrazed swards sown at the same seeding rates, stable populations of approximately 3540 plants m^{-2} and 5660 tillers m^{-2} were present at harvests 3 to 5 (Appendix Tables 15 and 18).

The results emphasize that the amount of viable seed present in autumn and the number of seedlings surviving is a key to the maintenance of highly productive and stable grazing systems from annual pastures in Mediterranean environments. However, the relationship between seed production in spring and annual carryover of seed during summer has not been studied in this experiment.

Therefore, quantitative estimates of the annual carryover of seed reserves is not possible. When sheep eat maturing seedheads, seed yield may be reduced by as much as 70 per cent under heavy grazing (Anon. 1971; Williams and Boyce 1978). Reeves and Smith (1975) demonstrated the value of heavy grazing over the spring/summer period in decreasing ryegrass density and increasing yield in a subsequent wheat crop. This may also be desirable in areas where annual ryegrass toxicity is a problem (Michelmore and Mackie 1977). Gramshaw and Stern (1977a) estimated that intensive grazing over summer reduced seed numbers by 20 per cent, on sandy soils in Western Australia. On hard clay soils of the Riverina, where subclover burr burial is negligible (Myers and Squires 1968), losses may be higher (Squires 1978).

Ant theft, dessication, fire, dormancy mechanisms (Gramshaw and Stern 1977b) and climatic factors may play an important role in influencing the annual carryover of seed reserves and seed flows in annual pastures. The current work relates to newly sown pastures in the year of establishment. Further work is required to examine the dynamics of long term seed flows in self regenerating annual pastures. This may provide answers to the widespread problems encountered in the establishment and maintenance of annual legumes as important components of grazed annual swards (Smith 1977). Brooks (1977) has initiated long term investigations in the wheat-sheep zone of South Australia to determine a satisfactory level of seed reserves required for pasture regeneration, and the situations when pasture resowing is necessary.

Management strategies such as the use of low seeding rates (1 - 10 kg ha^{-1}) combined with reduced stock numbers per unit land area or closing up these pastures in the spring may be desirable in certain situations (Watson *et al.* 1976). Lighter seeding rates might suffice if the sown pasture is not required for grazing for 6-12 months, if weeds are not a problem and if moisture and nutrients are in short supply.

If a pasture is needed for grazing soon after sowing, moisture and nutrients are adequate and weeds may be a problem, then much higher seeding rates (e.g. 32 kg ha^{-1} or more) could be used to support similar numbers of stock as in the present study. There is little point in establishing dense pastures if high stocking rates are not employed. Otherwise, the pasture produced is unlikely to be harvested by the grazing animal.

6. SUMMARY DISCUSSION

In Mediterranean environments the sheep producer at the same time, in different years, is faced with situations ranging from feed scarcity, adequacy or abundance for periods of weeks, months or even years. This poses special problems in feeding a relatively constant number of livestock from a fixed land area.

The two experiments reported in this thesis have examined in a given year the impact on the plant and animal population of a range of different pasture situations which are likely to be encountered by grazing animals in southern Australia (see Plates 4 to 7 in Appendix).

Herbage availability was found to have a major influence on lamb intake and growth rate in the short term. Situations have been described in which it is possible to apportion herbage to the lamb and/or ewe depending on the feed supply to maximise lamb growth. Seeding rate and consequently the number of plants per sheep were found to be major determinants of plant and animal production and stability of the grazing system in newly sown annual swards in the year of establishment.

The investigations were carried out in short term studies which permitted intensive study of both the plant and animal community, concurrently. Such experiments are unlikely to provide a complete answer to any one problem, but have proved valuable in the analysis of grazing systems. This work presents much evidence to show the importance of herbage availability and plant density to animal performance from annual pastures. Provided the results of these short term studies are viewed within the context of the designs, they are valuable in the analysis of grazing systems, especially in permitting close examination of many of the processes operating at the plant/animal interface. Such analyses are needed to identify the next step which requires evaluation.

Further work is required to examine the effects of such factors as changes in stocking rates, times of initiation of grazing and length of the pasture growing season on the responses of the plant and animal communities to weaning management and plant density as found in these studies.

7. APPENDICES

Table 1. Mean herbage dry matter present (kg ha^{-1}) and tiller length (cm) of swards of five availabilities, each grazed by either weaned lambs, lactating ewes + sucking lambs or dry ewes.

Avail-ability	Grazing treat-ment	Harvest 1			Harvest 2			Harvest 3			Harvest 4		
		DM*	PDM≁	TL	DM	PDM	TL	DM	PDM	TL	DM	PDM	TL
1.	L	390	732	3.3	689	1332	3.4	635	893	2.9	237	1146	2.1
	EL	662	732	4.1	681	1332	3.2	603	893	2.5	253	1146	2.0
	E	406	732	3.0	509	1332	2.8	371	893	2.0	145	1146	1.7
2.	L	1747	1116	8.1	1264	1323	7.8	1720	1116	6.1	810	1146	3.9
	EL	1601	1345	6.8	1087	1048	5.2	743	1402	3.7	664	1146	2.9
	E	1308	987	6.6	1039	844	4.3	452	987	3.3	576	1146	3.1
3.	L	2694	2849	12.2	2591	3099	14.6	2849	2675	11.3	1181	1237	7.2
	EL	2963	2459	12.8	1607	1570	9.3	2377	1564	7.4	1264	1413	7.7
	E	2681	2212	10.8	1572	1057	6.3	2212	1071	4.4	1176	1311	5.8
4.	L	3262	4704	25.8	4260	5308	22.7	3921	4704	29.1	5705	6095	38.0
	EL	2554	4269	22.1	3541	4210	17.4	2858	4338	14.6	4454	6469	20.7
	E	4010	4823	25.6	3776	4659	20.0	2675	4823	13.2	4967	5894	32.0
5.	L	5248	5613	53.8	6849	6383	53.0	5468	5613	49.8	7782	4520	62.3
	EL	4992	5652	48.0	5772	5758	44.0	5753	5650	35.9	5918	6394	45.6
	E	5584	5563	50.0	6345	4659	35.2	5226	5563	33.1	6881	5806	47.2

* DM = the amount of herbage present assessed by the visual method of Morley et al. (1964).

≁ PDM = the amount of herbage present assessed by the electronic capacitance probe (Back et al. 1969).

TL = tiller length (cm)

L = weaned lambs

EL = lactating ewes + sucking lambs

E = dry ewes

Simple correlation coefficients relating TL to DM at each harvest

Harvest 1	Harvest 2	Harvest 3	Harvest 4	Mean
0.94***	0.97***	0.92***	0.98***	0.95***

*** $P < 0.001 \simeq 0.88$

Table 2. Plot mean live weight (kg) of lambs and ewes grazing swards of different availability. The lamb weight data was adjusted by covariance analysis to equal ages (days)

(a) Lambs

Availability	Class of lamb	Date of weighing 28/9* (42)	5/10⁄ (49)	12/10 (56)	21/10 (64)	6/11 (81)
1	W	20.2	22.9	20.8	20.3	18.1
	S	20.5	23.5	23.8	24.4	25.0
2	W	21.7	23.8	24.1	25.4	27.9
	S	21.6	24.7	25.9	27.1	30.3
3	W	21.7	23.2	24.4	26.6	30.5
	S	18.2	21.7	24.2	26.8	31.8
4	W	21.0	22.1	24.1	25.4	28.7
	S	20.7	23.7	26.7	28.6	33.2
5	W	21.3	23.0	23.9	25.9	28.4
	S	19.2	22.1	24.7	27.2	31.0

(b) Ewes

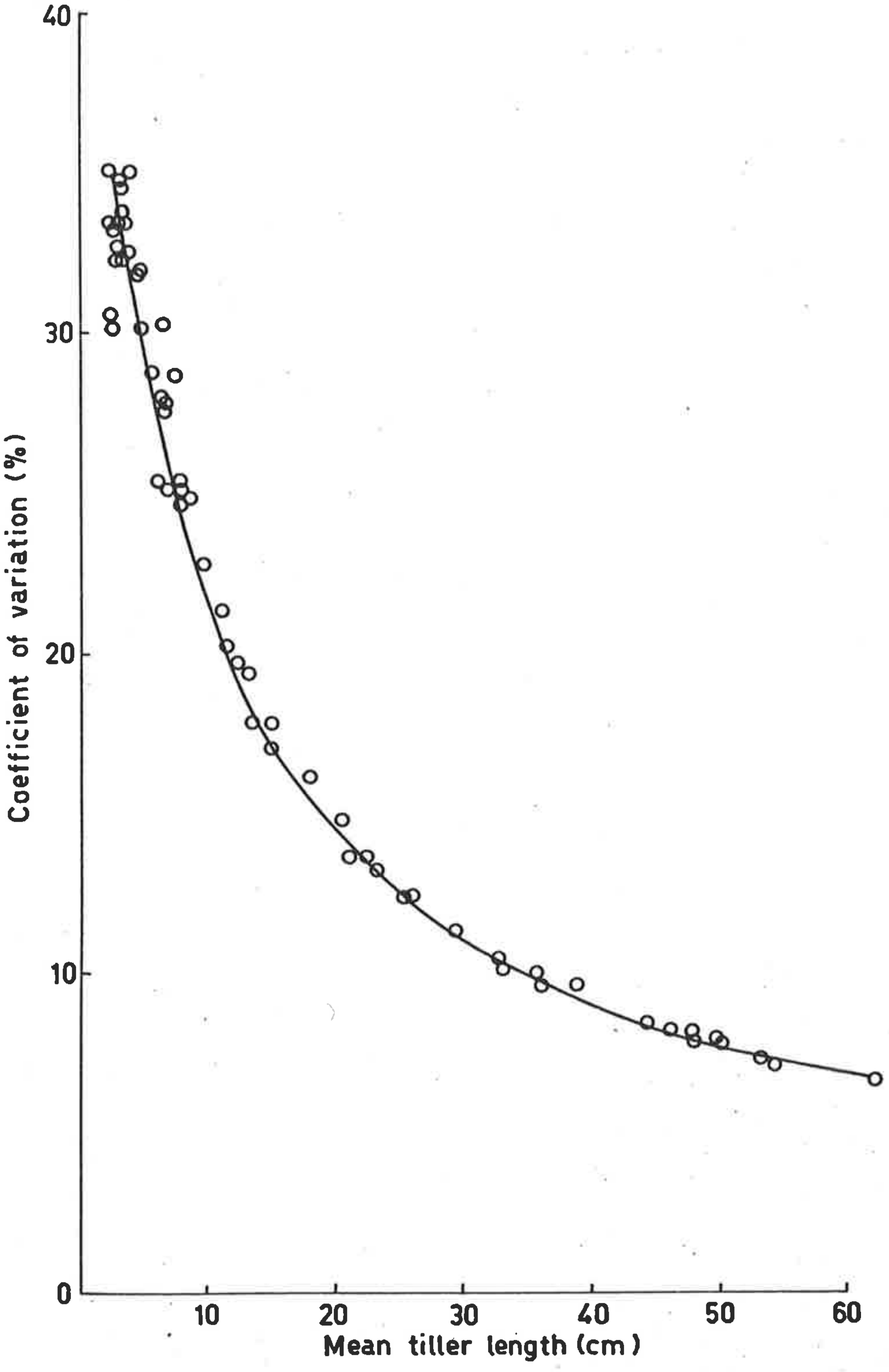
Availability	Class of ewe	Date of weighing 28/9	5/10	12/10	21/10	6/11
1	D	67.9	72.2	64.3	59.8	56.9
	L	69.8	74.1	64.6	59.3	53.6
2	D	70.1	73.1	69.5	66.7	65.9
	L	70.3	72.9	67.8	67.1	61.4
3	D	67.8	70.2	68.2	67.2	71.2
	L	69.9	73.2	73.5	73.8	73.8
4	D	70.1	76.0	77.2	77.6	81.0
	L	68.3	71.8	75.6	74.7	76.7
5	D	71.7	76.0	77.0	77.3	78.5
	L	66.1	70.9	72.5	73.0	74.3

* Day of weaning. ⁄ Beginning of the experiment.

W = weaned, S = sucking lambs; D = dry, L = lactating ewes.

The age of lambs in days is shown in parentheses.

Figure 1. Coefficients of variation of the means of swards of different tiller lengths. All means are based on 100 observations and the data from the four harvests in Experiment 1 are presented.



Coefficient of variation (%)
0
10
20
30
40
10
20
30
40
50
60
Mean tiller length (cm)

Table 3. Equations relating intake and the components of intake to tiller length of swards.

(a) Daily herbage DE intake (Figure 8)

Regression analysis was used to relate TL (X, cm) to herbage DE intake (Y, kJ $kg^{-1}W^{0.75}$ day^{-1}). The model used was as described in Section 4.3,

$$Y = A + BX + C\sqrt{X} + DX^2$$

(1) Weaned lambs, phase 1:

$Y = -2270.41 - 291.56X + 1922.03\sqrt{X} + 1.71X^2$. ($r^2 = 0.80$)

(2) Weaned lambs, phase 2:

$Y = -1952.52 - 301.21X + 2031.63\sqrt{X} + 1.39X^2$. ($r^2 = 0.71$)

(3) Sucking lambs, phase 1:

$Y = -57.65 + 63.72X - 38.29\sqrt{X} - 1.06X^2$. ($r^2 = 0.69$)

(4) Sucking lambs, phase 2:

$Y = -523.41 - 94.98X + 66.26\sqrt{X} + 0.49X^2$. ($r^2 = 0.79$)

(b) Total daily DE intake (Figure 9)

Regression analysis was used to relate TL (X, cm) to total DE intake (Y, kJ $kg^{-1}W^{0.75}$ day^{-1}).

(1,2) Weaned lambs in phases 1 and 2 as above.

(5) Sucking lambs, phase 1:

$Y = -2167.73 - 395.10X + 2283.74\sqrt{X} + 2.79X^2$. ($r^2 = 0.59$)

(6) Sucking lambs, phase 2:

$Y = -701.82 - 203.69X + 1184.60\sqrt{X} + 1.40X^2$. ($r^2 = 0.65$)

(c) Total daily herbage intake (Figure 11a)

Regression analysis was used to relate TL (X, cm) to total herbage OM intake (Y, gOM day^{-1}).

(7) Weaned lambs:

$Y = -1661.18 - 219.04X + 1408.51\sqrt{X} + 1.34X^2$. ($r^2 = 0.62$)

(8) Sucking lambs:

$Y = 100.23 + 53.45X - 65.01\sqrt{X} - 0.86X^2$. ($r^2 = 0.50$)

(d) Grazing time (Figure 11b)

Curvilinear regression model:

$$Y = A + \frac{B}{X + C}$$

where Y = total grazing time (min day^{-1}) and X = tiller length (cm).

Table 3 (continued).

(9) Weaned lambs:

$$Y = 7.63 + \frac{36.41}{X + 7.57}$$

(10) Sucking lambs:

$$Y = 7.00 + \frac{12.06}{X + 0.26}$$

(e) Potential rate of herbage intake (Figure 11c)

Model: $Y = A + BX + C\sqrt{X}$

where Y = potential rate of herbage intake (g OM min^{-1} $lamb^{-1}$)
and X = tiller length (cm).

(13) Weaned lambs:

$Y = -3.31 - 0.22X + 2.61\sqrt{X}$. ($r^2 = 0.80$)

(14) Sucking lambs:

$Y = -3.35 - 0.27X + 2.64\sqrt{X}$ ($r^2 = 0.63$)

(f) Daily rate of herbage intake (Figure 11d)

Regression analysis was used to relate the mean rate of herbage intake (Y, g OM min^{-1} $lamb^{-1}$) and tiller length (X, cm).

Model: $Y = A + BX + C\sqrt{X}$

(11) Weaned lambs:

$Y = 1.23 - 0.09X + 1.04\sqrt{X}$ ($r^2 = 0.66$)

(12) Sucking lambs:

$Y = 1.17 - 0.09X + 0.91\sqrt{X}$ ($r^2 = 0.60$)

(g) Potential rate of herbage intake (Figure 13)

Regression analysis was used to relate TL (X, cm) to potential rate of herbage intake (g DM min^{-1} $sheep^{-1}$).

(15) Weaned lambs, phase 1:

$Y = -3.27 - 0.24X + 2.82\sqrt{X}$ ($r^2 = 0.77$)

(16) Sucking lambs, phase 1:

$Y = -3.37 - 0.29X + 2.84\sqrt{X}$ ($r^2 = 0.58$)

(17) Weaned lambs (25 kg in live weight), (Allden and Whittaker 1970):

$Y = -3.21 - 0.20X + 2.58\sqrt{X}$ ($r^2 = 0.99$)

(18) Yearlings (43 kg in live weight), (Allden and Whittaker 1970):

$Y = -8.85 - 0.42X + 5.36\sqrt{X}$ ($r^2 = 0.94$)

Table 4. Mean intakes of organic matter as herbage (OMIh, g day^{-1}) and milk (OMIm, g day^{-1}) by sucking lambs and herbage intakes of weaned lambs (OMIh, g day^{-1}) grazing swards of different availabilities at phase 1. These intakes are also expressed in terms of digestible organic matter (DOMI) and digestible energy (DE).

Class of lamb	Nominal availability 1	2	3	4	5
(a) OMI					
Weaned, OMIh	210.3	644.1	822.5	761.4	747.7
Sucking, OMIh	113.2	279.5	268.8	513.9	351.2
Sucking, OMIm	180.1	301.4	355.0	249.5	187.4
Sucking, OMIt*	293.3	580.9	623.8	763.4	538.6
Sucking, OMIh/OMIt	39	48	43	67	65
Sucking, OMIh/Weaned OMIh	54	43	33	68	50
(b) DOMI					
Weaned, DOMIh	160.5	512.1	685.1	631.2	598.9
Sucking, DOMIh	85.4	217.0	222.8	429.6	282.3
Sucking, DOMIm	176.5	295.4	347.9	244.5	183.7
Sucking, DOMIt	261.9	512.4	570.7	674.1	466.0
Sucking, DOMIh/DOMIt	33	42	39	64	61
Sucking, DOMIh/Weaned DOMIh	53	42	33	68	47
(c) DE					
Weaned, DEh	310	901	1213	1133	1061
Sucking, DEh	141	281	326	705	500
Sucking, DEm	511	762	862	637	685
Sucking, DEt	652	1043	1188	1342	1185
Sucking DEh/Sucking DEt	22	27	27	53	42
Sucking DEh/Weaned DEh	45	31	27	62	47

* t = the total intake of herbage plus milk.

Table 5. Mean intakes of organic matter as herbage (OMIh, g day^{-1}) and milk (OMIm, g day^{-1}) by sucking lambs and herbage intakes of weaned lambs (OMIh, g day^{-1}) grazing pastures of different availabilities at phase 2. These intakes are also expressed in terms of digestible organic matter (DOMI) and digestible energy (DE).

Class of lamb	Nominal availability 1	2	3	4	5
(a) OMI					
Weaned, OMIh	157.6	864.6	1012.9	878.2	645.8
Sucking, OMIh	110.6	394.4	481.7	677.0	552.2
Sucking, OMIm	137.0	153.5	226.4	160.9	127.4
Sucking, OMIt*	247.6	544.9	708.1	837.9	679.6
Sucking, OMIh/Sucking, OMIt	45	72	68	81	81
Sucking, OMIh/Weaned, OMIh	70	45	48	77	86
(b) DOMI					
Weaned, DOMIh	114.7	704.6	843.7	645.6	460.5
Sucking, DOMIh	81.5	300.2	384.4	522.6	419.7
Sucking, DOMIm	108.4	150.4	221.9	157.7	124.9
Sucking, DOMIt	189.9	450.6	606.3	680.3	544.6
Sucking, DOMIh/Sucking, DOMIt	43	67	63	77	77
Sucking, DOMIh/Sucking, DOMIh	71	43	46	81	91
(c) DE					
Weaned, DEh	254	1137	1274	1150	717
Sucking, DEh	140	459	538	746	628
Sucking, DEm	385	347	507	335	285
Sucking, DEt	525	806	1045	1081	913
Sucking, DEh/Sucking DEt	27	57	51	69	69
Sucking, DEh/Weaned, DEh	55	40	42	65	88

* t = the total intake of herbage plus milk.

Table 6. Plot mean values for the potential rate of herbage intake (g DM and g OM min^{-1}), daily rate of intake (g OM min^{-1}), total intake (g OM day^{-1}) and total grazing time (min day^{-1}) for each treatment in phase 1.

Availability	Class of lamb	Potential rate of herbage intake ($gDMmin^{-1}$)	($gOMmin^{-1}$)	Daily rate + of herbage intake (gOM min^{-1})	Total intake (gOM day^{-1})	Grazing time (min day^{-1})
1	W*	0.95	0.67	0.33	210.3	648
	S*	0.56	0.41	0.18	113.2	618
2	W	2.96	2.33	1.03	644.1	624
	S	1.95	1.51	0.47	279.5	594
3	W	4.00	3.46	1.40	822.5	570
	S	2.37	2.01	0.60	268.8	450
4	W	4.43	3.89	1.55	761.4	492
	S	3.37	3.01	1.10	513.9	468
5	W	4.38	3.81	1.48	747.7	504
	S	2.55	2.25	0.79	351.2	444

* W = weaned and S = sucking lamb

\+ Derived from total intake for the day divided by total grazing time for the day

Table 7. Analysis of variance and means of the live weight (kg) of lambs on October 12th, one week after the start of the experiment.

Source of variation	DF	Mean square	F	Probability
Availability	4	11.6	0.4	n.s.
Class of stock (weaned vs sucking)	1	25.3	1.0	n.s.
Availability X class	4	3.5	0.1	n.s.
Residual	30	25.9		

Means

Nominal availability

1	2	3	4	5	LSD
22.3	25.0	24.3	25.4	24.3	n.s.

Class of lamb

Weaned	Sucking	LSD
23.5	25.1	n.s.

n.s. = not significant.

Table 8. Analysis of variance and means of the *in vitro* OMD of herbage extrusa samples from O.F. lambs in phage 2 (simple randomised block analysis).

Source of variation	DF	Mean square	F	Probability
Class (weaned vs sucking)	1	4.4	1.51	n.s.
Availability	4	51.7	17.78	***
Availability X class	4	14.4	5.0	*
Residual	10	2.9		

n.s. = not significant *P < 0.5 ***P < 0.001

Means

Nominal availability					
1	2	3	4	5	LSD
73.3a*	79.1b	81.6b	78.2b	73.7a	2.6

Class of lamb		
Weaned	Sucking	LSD
77.6a	76.7a	n.s.

* Means with different subscripts within rows are significantly different at P < 0.05.

Treatment means

Phase	Class of lamb	Nominal availability 1	2	3	4	5	Means
1	Weaned	76.3	79.5	83.3	82.9	80.1	80.4
1	Sucking	75.4	77.6	82.1	83.6	80.4	79.8
2	Weaned	72.8	81.5	83.3	79.2	71.3	77.6
2	Sucking	73.7	76.7	79.8	77.2	76.0	76.7

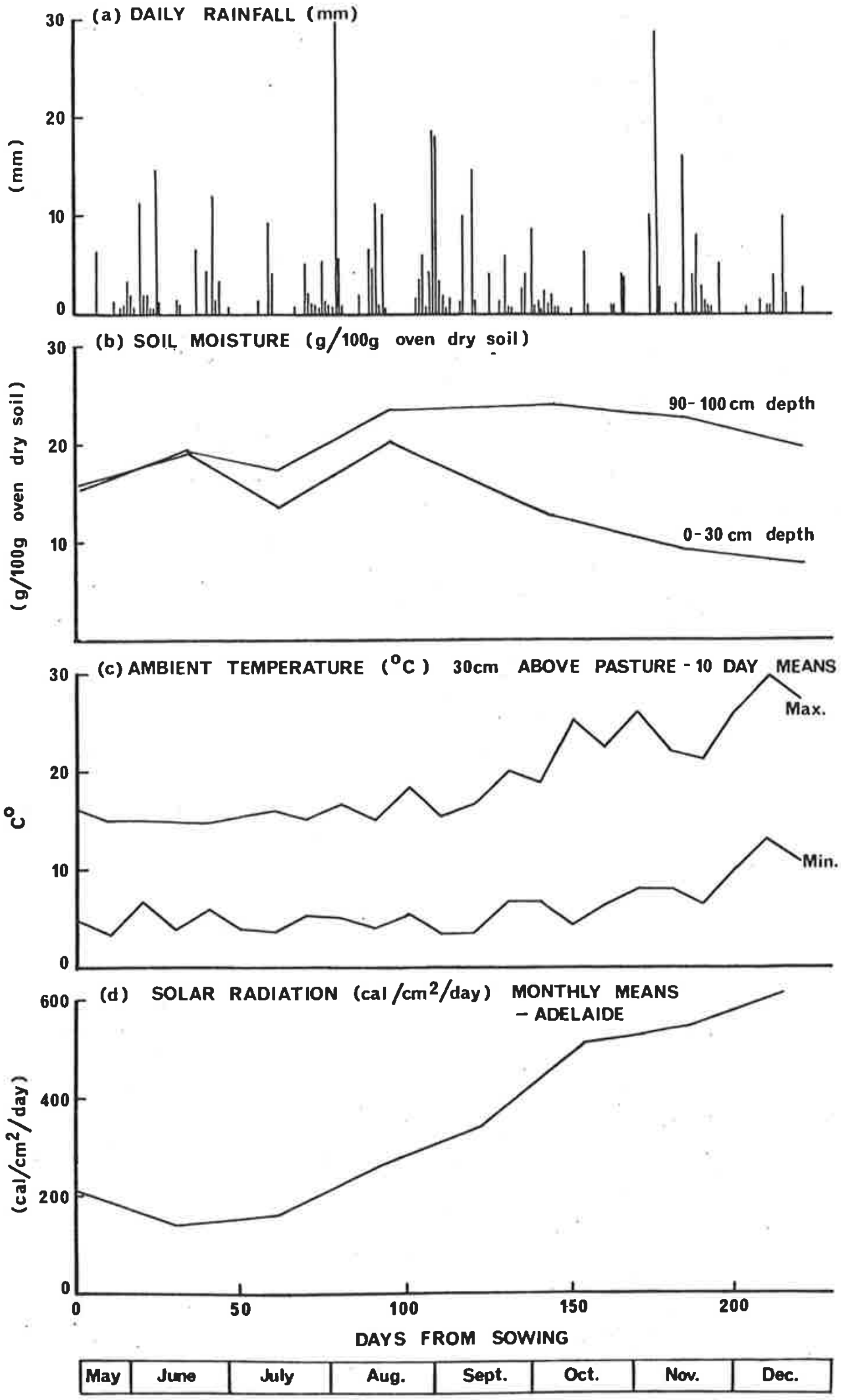
Figure 2. Meteorological data for Experiment 2 in 1971.

(a) Daily rainfall (mm) was recorded from meteorological equipment located adjacent to the site as shown in Figure 14.

(b) Soil moisture was recorded on seven occasions during the experiment from five auger samples taken at random from the 32 kg ha^{-1} seeding rate plot. Soil samples were oven dried at $80^{o}C$ for 24 hours and the percentage water content determined.

(c) Mean ten-day values for maximum and minimum temperatures recorded daily at the site during the experiment.

(d) Monthly mean incoming solar radiation recorded at the Waite Agricultural Research Institute, Adelaide.



(a) DAILY RAINFALL (mm)
(mm)
30
20
10
0
(b) SOIL MOISTURE (g/100g oven dry soil)
(g/100g oven dry soil)
90-100 cm depth
0-30 cm depth
(c) AMBIENT TEMPERATURE (°C) 30cm ABOVE PASTURE - 10 DAY MEANS
C°
Max.
Min.
(d) SOLAR RADIATION (cal/cm²/day) MONTHLY MEANS - ADELAIDE
(cal/cm²/day)
600
400
200
0
50
100
150
200
DAYS FROM SOWING
May
June
July
Aug.
Sept.
Oct.
Nov.
Dec.

Table 9. Total sheep mortality (original + replacement animals) in time on swards sown at different seeding rates.

Seeding rate ($kg\ ha^{-1}$)	Sheep mortality: Days from the initial set stocking of plots till death					
	25	50	75	100	125	Total
1	0	5	2	0	1	8
2	0	0	3	3	0	6
4	0	2	2	1	2	7
8	0	0	3	0	0	3
16	0	1	0	1	0	2
32-1024	0	0	0	0	0	0

Table 10. Analysis of variance and means of the fleece-free live weight (kg) of sheep grazing pastures of different densities at different harvest occasions.

(a) Harvest one (July 5th), the day that the grazing of plots began

Source of variation	DF	MS	F	Probability
Densities	8	5.9	0.2	n.s.
Between sheep within a density	2	23.7	0.9	n.s.
Residual	8	26.9		

Means

Densities≠

2	4	5	6	7	8	9	10	11	LSD
49.3	48.8	48.7	45.6	45.7	46.1	45.0	48.9	47.7	n.s.

≠ All original sheep died on density treatments 1 and 3 before the end of the experiment.

(b) Harvest two (August 16th)

Source of variation	DF	MS	F	Probability
Densities	8	150.5	8.5	***
Between sheep within a density	2	17.5	1.0	n.s.
Residual	8	23.7		

Means

Densities

2	4	5	6	7	8	9	10	11	LSD
41.6a*	33.6b	35.3b	37.8a	39.5a	48.0ac	50.8c	56.8c	51.0c	7.8

(c) Harvest three (September 27th)

Source of variation	DF	MS	F	Probability
Densities	8	648.2	10.8	***
Between sheep within a density	2	16.3	0.3	n.s.
Residual	8	60.1		

Means

Densities

2	4	5	6	7	8	9	10	11	LSD
33.1a	31.3a	32.5a	46.1b	46.1b	50.0b	52.6b	60.6c	60.0c	6.9

Table 10 (continued).

(d) Harvest four (November 15th)

Source of variation	DF	MS	F	Probability
Densities	8	204.6	2.83	*
Between sheep within a density	2	65.8	1.9	n.s.
Residual	8	108.1		

Means

Densities

2	4	5	6	7	8	9	10	11	LSD
31.4a	37.9a	43.7b	57.7c	56.3c	61.0c	60.4c	63.3c	63.1c	9.1

(e) Harvest five (December 21st)

Source of variation	DF	MS	F	Probability
Densities	8	273.6	2.7	*
Between sheep within a density	2	108.9	1.8	n.s.
Residual	8	102.0		

Means

Densities

2	4	5	6	7	8	9	10	11	LSD
25.1a	31.8a	50.6b	60.6c	60.7c	63.4c	63.2c	64.0c	64.1c	8.2

* Means with different subscripts are significantly different at P < 0.05.

n.s. = not significant, *P < 0.05, **P < 0.01, ***P < 0.001.

Table 11. Mean daily intake of herbage (in terms of both DE intake, kJ $kg^{-1}W^{0.75}$ $sheep^{-1}$ and OM intake, g OM $sheep^{-1}$) and the components of intake - rate of intake (RI, g OM min^{-1}) and grazing time (GT, min day^{-1}) of sheep grazing swards sown at different seeding rates at 5 harvests.

Harvest	Variable	(i) Low			(ii) Medium					(iii) High		
		Seeding rates (kg ha^{-1})										
		1	2	4	8	16	32	64	128	256	512	1024
1	DE	103	140	201	218	354	503	520	796	931	1013	1112
	OMI	104	137	253	312	333	631	509	812	1008	1089	1211
	RI	0.21	0.24	0.52	0.50	0.61	0.88	1.18	1.61	2.24	2.30	2.88
	GT	498	576	490	630	548	714	432	504	450	474	420
2	DE	76	119	91	292	194	360	337	476	666	1239	1344
	OMI	71	114	97	235	176	320	235	464	631	1275	1055
	RI	0.71	0.17	0.16	0.46	0.41	0.64	0.48	1.03	1.28	2.76	2.19
	GT	640	672	600	516	432	502	492	450	492	462	482
3	DE	47	125	99	481	697	1096	1064	917	826	1090	842
	OMI	23	87	85	190	350	986	993	1003	796	1066	894
	RI	0.03	0.12	0.14	0.26	0.52	1.38	1.61	.161	1.47	1.74	1.28
	GT	670	726	624	738	670	714	618	624	540	612	696
4	DE	n.a.	316*	n.a.	1104	1567	1933	2173	1924	1734	901	1303
	OMI	n.a.	129	n.a.	899	1276	2285	2373	2534	2397	1648	1632
	RI	n.a.	0.24	n.a.	1.68	2.36	4.53	4.49	5.71	4.76	4.50	4.32
	GT	n.a.	540	n.a.	534	540	504	528	444	504	366	378
5	DE	n.a.	103*	n.a.	186	1021	722	884	766	768	905	786
	OMI	n.a.	25	n.a.	215	1347	998	1354	1185	1154	1378	1232
	RI	n.a.	0.12	n.a.	0.53	2.81	2.52	3.37	3.46	2.90	3.59	3.31
	GT	n.a.	210	n.a.	408	480	396	402	342	398	384	372

Density categories: (i) Low; (ii) Medium; (iii) High.

n.a. Data not available as all original sheep had died on these treatments.

* Data for the one surviving animal presented.

Table 12. Mean clean oven dry (a) wool growth (g day^{-1}) and (b) cumulative wool production (kg ha^{-1}) from sheep grazing swards sown at different seeding rates.

Period						Density categories					
	(i) Low					(ii) Medium			(iii) High		
	Seeding rates (kg ha^{-1})										
	1	2	4	8	16	32	64	128	256	512	1024
(a) Daily wool growth (g day^{-1})											
h_1-h_2	4.4	3.7	5.0	4.7	6.7	10.6	7.3	13.1	13.6	18.6	18.9
h_2-h_3	(0.9)	2.0	(1.5)	3.4	3.5	12.0	9.5	13.0	13.1	17.0	17.5
h_3-h_4	(1.0)	1.6	(2.2)	7.1	12.5	18.8	12.7	11.7	7.0	18.6	12.7
h_4-h_5	n.a.	2.3	n.a.	5.1	9.7	14.4	12.0	13.4	11.6	12.3	13.4
(b) Cumulative wool production (kg ha^{-1})											
h_1-h_2	3.1	2.6	3.5	3.3	4.7	7.4	5.1	9.2	9.5	13.0	13.2
h_1-h_3	(4.0)	4.9	(5.0)	6.9	7.1	19.2	14.4	21.9	22.3	29.7	30.3
h_1-h_4	(4.5)	5.7	(6.1)	10.5	13.4	28.7	20.8	27.8	28.3	39.1	36.7
h_1-h_5	n.a.	6.7	n.a.	12.7	17.6	34.9	26.0	33.6	33.3	44.4	42.5

n.a. Data not available since all original sheep had died on these treatments.

Figures in parentheses refer to wool growth and production of sheep from the start of a harvest to the time of death.

Table 13. Cumulative herbage DM yield (kg ha^{-1}) at five harvest occasions of grazed and ungrazed swards sown at different seeding rates.

Means

Seeding rate (kg ha^{-1})	Grazed					Ungrazed				
	Date of harvests									
	5/7	9/8	27/9	8/11	13/12	6/7	10/8	28/9	9/11	14/12
1	8	248	576	678	713	9	280	5176	8518	7851
2	14	471	1391	1658	1706	13	310	4022	8239	8340
4	43	762	2457	2936	3197	39	569	5249	8206	7737
8	83	807	2914	4287	5032	116	927	5692	8244	7735
16	113	888	3296	5142	6801	136	1318	7747	7937	7952
32	237	1502	5086	8442	9653	254	1606	6582	8435	7699
64	167	1232	4914	9012	9741	150	1664	6504	8357	7059
128	595	2602	6012	8574	9976	574	3019	8645	8395	8420
256	815	2713	5172	6940	8283	785	2462	6815	8230	8671
512	1507	3700	6321	8488	9238	1518	3921	7681	8127	8319
1024	1620	3886	6843	9206	9851	1600	3599	7286	8096	8617

Table 14. Herbage yield present (kg DM ha^{-1}) at five harvest occasions in grazed and ungrazed swards sown at different seeding rates.

Means

Seeding rate (kg ha^{-1})	Grazed					Ungrazed				
	Date of harvests									
	6/7	10/8	28/9	9/11	14/12	6/7	10/8	28/9	9/11	14/12
1	8	7	16	1	1	8	280	5176	8518	7851
2	6	3	4	2	1	13	310	4022	8239	8340
4	31	13	71	15	1	39	569	5249	8206	7737
8	55	24	100	200	40	116	927	5692	8244	7735
16	105	54	331	500	460	136	1318	7747	7937	7952
32	211	301	749	1893	1424	254	1606	6582	8435	7699
64	159	117	588	2198	1222	150	1664	6504	8357	7059
128	641	560	979	1942	1404	574	3019	8645	8395	8420
256	806	719	726	1141	932	785	2462	6815	8230	8671
512	1486	1570	968	1736	1748	1518	3921	7681	8127	8319
1024	1608	1550	897	1601	1187	1600	3599	7286	8096	8617

Table 15. Plant number (plants m^{-2}) at five harvest occasions in grazed and ungrazed swards sown at different seeding rates.

Means

Seeding rate ($kg\ ha^{-1}$)	Grazed					Ungrazed				
	Date of harvests									
	7/7	11/8	30/9	10/11	15/12	7/7	11/8	30/9	10/11	15/12
1	38	18	24	9	4	34	30	28	29	32
2	58	60	16	5	1	47	42	39	51	32
4	165	130	62	46	40	185	110	91	91	88
8	243	241	120	114	131	202	181	189	156	170
16	495	396	328	315	515	581	410	501	456	473
32	1126	766	1406	804	1123	1580	843	900	853	810
64	2444	1366	1106	915	1500	2103	1055	1057	916	802
128	5750	6624	3417	5566	2632	6568	2283	2264	1747	2216
256	10543	3927	3496	4160	2838	9253	4561	3263	3780	4401
512	13763	6521	5936	4100	5298	15982	6705	4339	3305	3511
1024	35993	8814	8230	8133	6868	32694	6136	4659	4152	4789

Table 16. Absolute and relative[+] numbers of plants present in (a) grazed and (b) ungrazed swards at establishment (h_1) and maturity (h_5), and the percentage plant survival over this period.

(a) Grazed swards

Density category	Seeding rate (kg ha^{-1})	Establishment counts (h_1) Plant no. (plants m^{-2}) A	Establishment counts (h_1) Relative plant no.	Maturity counts (h_5) Plant no. (plants m^{-2}) B	Maturity counts (h_5) Relative plant no.	Survival (%) B/Ax100
(i) Low	1	38	1	4	0.1	11
	2	58	2	1	0.02	2
	4	165	5	40	1	24
	8	243	7	131	4	54
	16	495	15	515	15	100
(ii) Medium	32	1126	33	1130	33	100
	64	2444	72	1500	44	62
(iii) High	128	5750	169	2632	77	46
	256	10543	310	2838	84	27
	512	13763	417	6045	178	42
	1024	35993	1060	6964	205	19

(b) Ungrazed swards

Density category	Seeding rate (kg ha^{-1})	Establishment counts (h_1) Plant no. (plants m^{-2}) A	Establishment counts (h_1) Relative plant no.	Maturity counts (h_5) Plant no. (plants m^{-2}) B	Maturity counts (h_5) Relative plant no.	Survival (%) B/Ax100
(i) Low	1	34	1	32	1	94
	2	47	1	50	1	100
	4	185	5	88	2	48
	8	202	5	170	5	84
	16	581	15	473	12	81
(ii) Medium	32	1580	42	810	21	51
	64	2103	55	802	21	38
(iii) High	128	6568	173	2216	58	34
	256	9253	244	4401	116	48
	512	15982	421	3511	92	22
	1024	32694	860	4789	126	15

+ Relative plant number calculations based on 38 plants m^{-2} = 1.0.

Table 17. The dry weight of individual plants (g) at five harvest occasions in grazed and ungrazed swards sown at different seeding rates.

Means

Seeding rate (kg ha^{-1})	Grazed					Ungrazed				
	Date of harvests									
	7/7	11/8	29/9	10/11	15/12	7/7	11/8	29/9	10/11	15/12
1	.010	.006	.014	.015	.010	.011	.940	21.171	28.150	24.500
2	.008	.003	.012	.018	.011	.010	.740	10.421	19.006	17.050
4	.008	.006	.026	.028	.020	.015	.518	11.576	9.056	8.960
8	.009	.008	.037	.116	.050	.007	.514	3.010	5.106	4.560
16	.007	.010	.032	.221	.186	.010	.322	1.547	1.800	1.680
32	.006	.019	.070	.264	.217	.005	.191	.731	.980	.950
64	.007	.016	.116	.263	.198	.007	.158	.615	.917	.880
128	.009	.013	.062	.044	.069	.008	.132	.382	.471	.380
256	.007	.017	.027	.036	.050	.007	.054	.209	.215	.197
512	.012	.017	.028	.045	.030	.008	.059	.177	.245	.237
1024	.004	.017	.021	.027	.022	.004	.059	.147	.195	.180

Table 18. The number of tillers per plant at five harvest occasions in grazed and ungrazed swards sown at different seeding rates.

Means

Seeding rate (kg ha^{-1})	Grazed					Ungrazed				
	Date of harvests									
	7/7	11/8	29/9	10/11	15/12	7/7	11/8	29/9	10/11	15/12
1	3.0	2.7	2.9	6.9	3.6	1.4	8.1	40.4	42.0	32.8
2	2.1	2.4	4.1	6.4	3.0	2.5	9.6	24.4	17.4	17.4
4	2.1	3.7	10.6	6.4	4.5	2.5	10.4	15.9	17.6	17.6
8	2.3	5.3	12.8	17.3	12.6	1.7	8.9	7.5	6.6	6.6
16	1.7	5.2	10.9	15.3	23.5	2.3	6.1	6.1	4.1	4.9
32	1.9	6.7	8.7	14.1	13.9	1.5	5.3	7.0	5.0	4.4
64	1.2	7.7	12.0	11.1	15.7	1.8	5.0	3.9	4.0	7.0
128	2.1	3.1	4.4	1.6	5.3	1.8	3.7	2.5	2.8	3.8
256	1.4	2.9	4.6	1.9	3.5	1.5	1.8	1.3	1.9	1.5
512	2.3	2.5	2.5	1.7	2.3	1.4	1.6	1.0	1.9	1.4
1024	1.0	1.8	2.0	1.3	2.5	1.0	1.8	1.1	1.1	1.2

Table 19a, b. Absolute and relative[+] numbers of tillers present in (a) grazed and (b) ungrazed swards at establishment and maturity (tillers m^{-2}) and the percentage of original tillers present over this period.

(a) Grazed swards

Density category	Seeding rate ($kg\ ha^{-1}$)	Establishment counts: Tiller no. (tillers m^{-2}) A	Establishment counts: Relative tiller no.[+]	Maturity counts: Tiller no. (tillers m^{-2}) B	Maturity counts: Relative tiller no.[+]	Percentage of original tillers present B/Ax100 (%)
(i) Low	1	115	1	14	1	12
	2	123	1	3	1	2
	4	347	3	178	1	51
	8	558	5	1656	11	297
	16	841	7	12093	84	1438
(ii) Medium	32	2139	19	15610	108	730
	64	2933	26	13540	94	462
(iii) High	128	12074	105	13948	97	116
	256	14760	128	9934	69	67
	512	22760	198	13904	96	61
	1024	35994	312	17409	120	48

(b) Ungrazed swards

Density category	Seeding rate ($kg\ ha^{-1}$)	Establishment counts: Tiller no. (tillers m^{-2}) A	Establishment counts: Relative tiller no.[+]	Maturity counts: Tiller no. (tiller m^{-2}) B	Maturity counts: Relative tiller no.[+]	Percentage of original tillers present B/Ax100 (%)
(i) Low	1	48	<1	1050	9	2190
	2	118	1	870	8	737
	4	463	4	1549	14	335
	8	343	3	1122	10	327
	16	1336	12	2303	20	172
(ii) Medium	32	2370	21	3564	31	150
	64	3785	33	5614	49	148
(iii) High	128	11822	103	8421	73	71
	256	13880	121	6602	57	48
	512	22375	195	4915	43	22
	1024	32694	284	5747	50	18

+ Relative tiller number calculations based on 115 tillers m^{-2} = 1.0.

Table 20. Tiller length (TL, cm) at five harvest occasions in grazed and ungrazed swards sown at different seeding rates.

Means

Seeding rate (kg ha^{-1})	Grazed					Ungrazed				
	Date of harvests									
	7/7	11/8	29/9	10/11	15/12	7/7	11/8	29/9	10/11	15/12
1	3.2	2.0	3.0	2.8	2.9	5	11	39	79	55
2	3.3	1.5	2.5	2.1	3.0	5	12	37	75	59
4	3.7	2.2	4.0	2.6	2.4	5	14	33	82	50
8	4.4	2.8	3.9	4.8	3.9	5	14	33	79	55
16	4.4	2.9	4.4	5.9	6.5	5	13	44	86	45
32	4.1	4.3	7.1	8.9	8.0	5	14	43	85	46
64	5.7	3.9	7.3	11.5	8.7	6	14	49	71	33
128	6.6	4.6	6.5	6.6	8.5	5	18	56	84	38
256	7.9	4.8	5.9	6.8	6.5	7	15	40	61	37
512	8.5	5.7	5.2	8.7	8.1	8	18	47	71	35
1024	7.6	6.5	5.5	7.2	6.0	8	19	42	63	47

Table 21. Matrix of simple correlation coefficients between sward characteristics and plant growth rate and sheep intake in grazed swards on three harvest occasions.

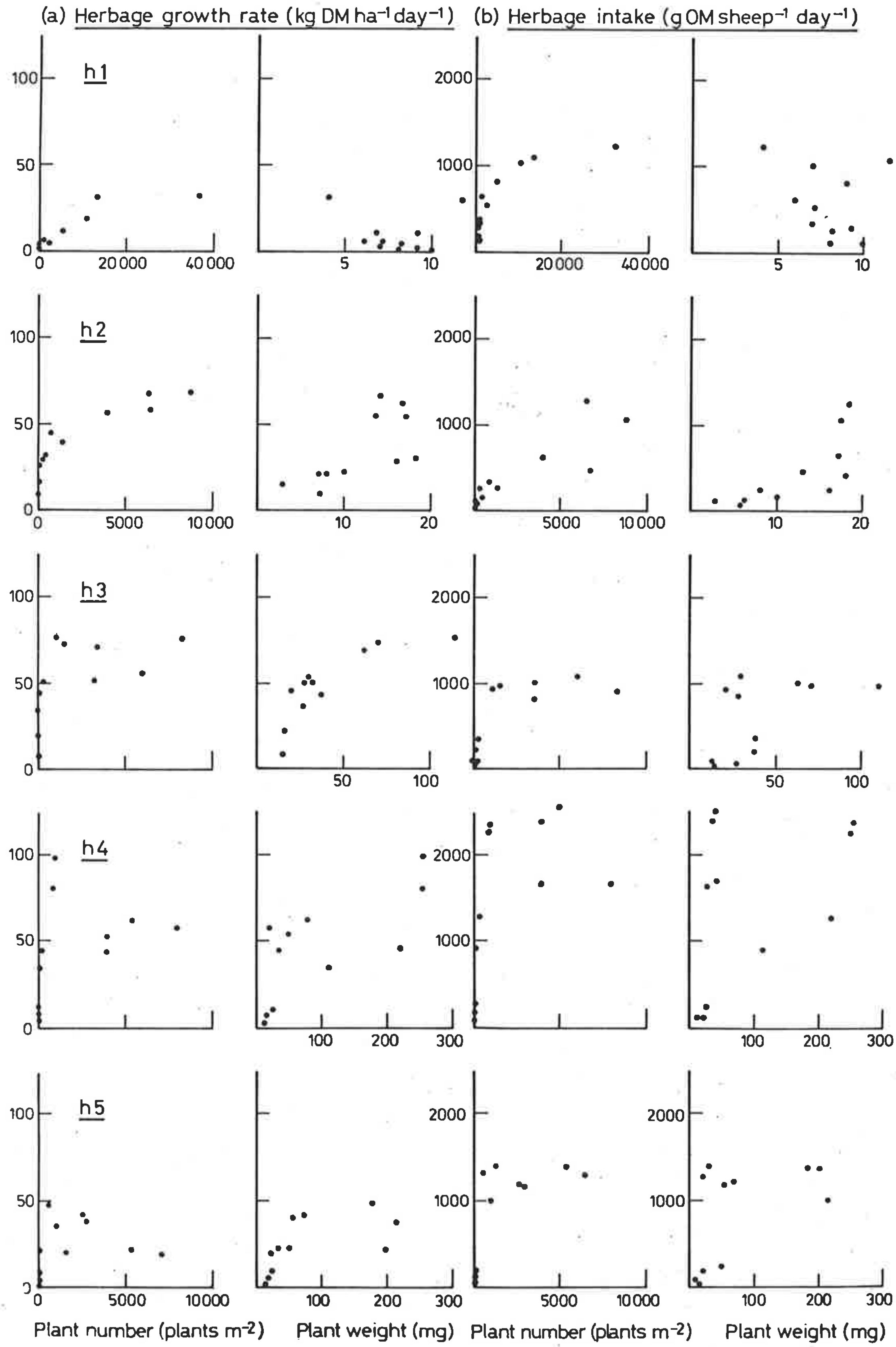
Variable	Harvest	TL	PNO	PWT	TP	OMD	GR	OMI
	1	0.90	0.90	n.s.	n.s.	n.s.	n.a.	0.93
DM	3	0.80	0.81	n.s.	n.s.	0.84	0.74	0.94
	5	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	0.72
	1		0.72	n.s.	n.s.	0.68	0.89	0.94
TL	3		n.s.	n.s.	n.s.	0.81	0.94	0.88
	5		n.s.	n.s.	n.s.	n.s.	0.71	0.86
	1			n.s.	n.s.	n.s.	0.90	0.80
PNO	3			n.s.	n.s.	n.s.	n.s.	0.62
	5			n.s.	n.s.	n.s.	n.s.	n.s.
	1				0.78	n.s.	0.60	n.s.
PWT	3				n.s.	n.s.	0.80	n.s.
	5				0.85	n.s.	0.60	n.s.
	1					0.66	n.s.	n.s.
TP	3					n.s.	n.s.	n.s.
	5					n.s.	n.s.	n.s.
	1						n.s.	0.73
OMD	3						0.89	0.87
	5						0.82	0.78
	1							0.93
GR	3							0.79
	5							0.60

n.s. = not significant, n.a. = not applicable.

$P < 0.05 \simeq 0.60$, $P < 0.01 \simeq 0.74$, $P < 0.001 \simeq 0.85$

DM = total herbage yield present (kg DMha^{-1})
TL = tiller length (cm)
PNO = plant density (plants m^{-2})
PWT = plant weight (g)
GR = plant growth rate (kg DM ha^{-1}day^{-1})
TP = tillers per plant
OMD = organic matter digestibility (%) (O.F. samples)
OMI = daily organic matter intake (g OM sheep^{-1})

Figure 3. The relations between (a) (Left) herbage growth rate, (b) (Right) herbage intake to plant number and weight in grazed swards on five harvest occasions.



(a) Herbage growth rate (kg DM ha⁻¹ day⁻¹)
(b) Herbage intake (g OM sheep⁻¹ day⁻¹)
h1
h2
h3
h4
h5
Plant number (plants m⁻²)
Plant weight (mg)
Plant number (plants m⁻²)
Plant weight (mg)

Table 22. Analysis of variance of regression lines and t tests for the difference between the slopes and displacements of the two regression lines relating the DE intake (X, kJ $kg^{-1}W^{0.75}day^{-1}$) to (a) sheep liveweight change and (b) wool growth (Y, g day^{-1}) when intake was assessed by two methods.

(a) Sheep liveweight change

Source of variation	DF	Mean square	F	Probability
Slopes	1	9.4	8.6	**
Displacements	1	88.7	86.3	***
Residual	28	1.1		

t tests
Comparison of individual slopes and displacements

Comparison of two methods of estimating intake	Slopes	Displacements
(i) Herbage cutting technique versus (ii) Faecal collection method	3.0**	9.2***

(b) Wool growth

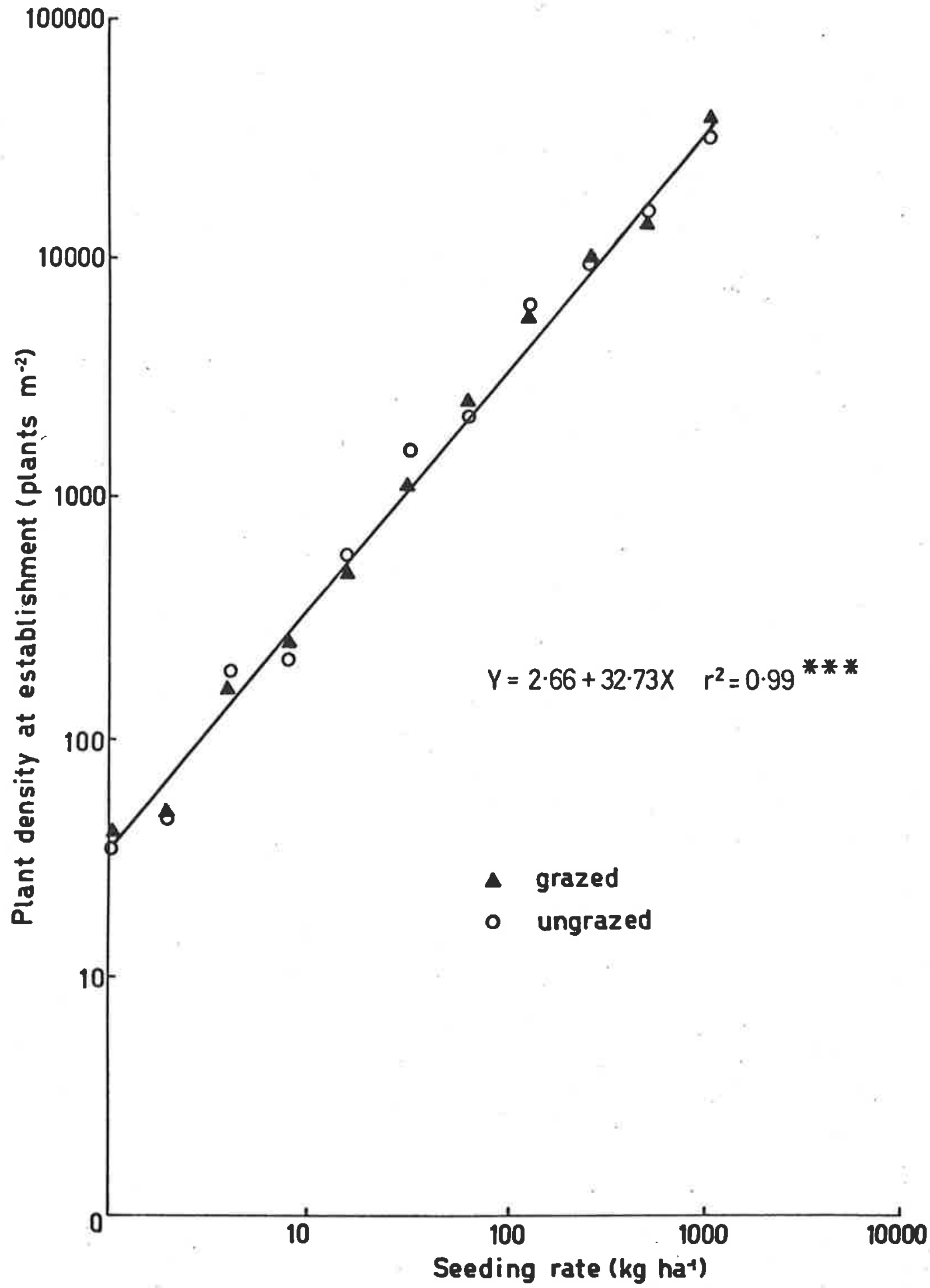
Source of variation	DF	Mean square	F	Probability
Slopes	1	239036.5	6.4	*
Displacements	1	2081326.4	55.9	***
Residual	28	37255.3		

t tests
Comparison of individual slopes and displacements

Comparison of two methods of estimating intake	Slopes	Displacements
(i) Herbage cutting technique versus (ii) Faecal collection method	-2.5*	-7.5***

*P < 0.05, **P < 0.01, ***P < 0.001.

Figure 4. Logarithmic relationship between seeding rate (kg seed ha^{-1}) on May 15th and initial plant density (plants m^{-2}) on July 7th for all grazed and ungrazed swards. The relationship was similar for grazed and ungrazed data (Appendix Table 23).



100000
10000
1000
100
10
0
Plant density at establishment (plants m-2)
Y = 2·66 + 32·73X r2 = 0·99 ***
grazed
ungrazed
10
100
1000
10000
Seeding rate (kg ha-1)

Table 23. Analysis of variance of regression lines and t tests for the difference between the slopes and displacements of the two regression lines relating the log of seeding rate (X, kg seed ha^{-1}) to the log of initial plant density (Y, plants m^{-2}).

Source of variation	DF	Mean square	F	Probability
Slopes	1	0.000495	0.056	n.s.
Displacements	1	0.000113	0.013	n.s.
Residual	18	0.008889		

t tests
Comparisons of individual slopes and intercepts

Comparison	Slopes	Displacements
Grazed versus ungrazed	-0.2 n.s.	-0.1 n.s.

n.s. = not significant

Table 24. A comparison of plant growth rate (kg DM ha^{-1} day^{-1}) of grazed and ungrazed swards sown at different seeding rates.

Means

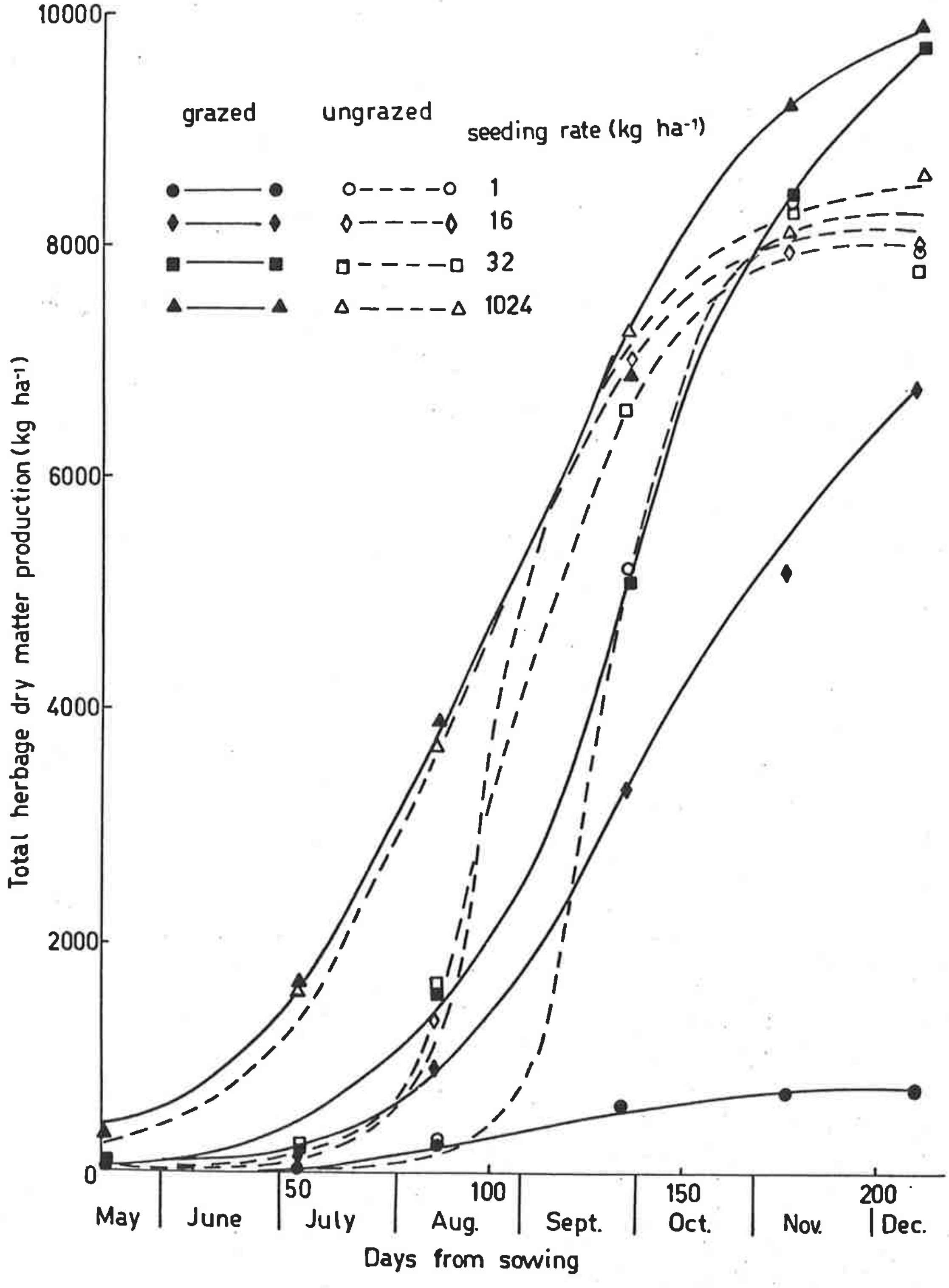
Seeding rate (kg ha^{-1})	Grazed 15/5 to 5/7	Grazed 5/7 to 9/8	Grazed 9/8 to 28/9	Grazed 28/9 to 8/11	Grazed 8/11 to 13/12	Ungrazed 15/5 to 6/7	Ungrazed 6/7 to 10/8	Ungrazed 10/8 to 29/9	Ungrazed 29/9 to 9/11	Ungrazed 9/11 to 14/12
1	0.2	6.8	6.7	2.4	1.0	0.2	7.7	100.0	79.6	20.0
2	0.3	13.1	18.8	6.3	1.4	0.3	8.6	75.8	100.4	2.9
4	0.9	20.5	34.6	11.0	7.5	0.8	5.1	95.5	70.4	-13.4
8	1.6	20.7	43.0	32.7	21.3	2.3	22.3	97.2	60.8	-14.5
16	2.2	22.1	49.2	44.0	47.4	2.7	33.8	131.2	45.0	0.4
32	4.6	36.1	73.2	79.9	34.6	5.0	38.7	101.6	45.2	-21.1
64	3.3	30.4	75.1	97.6	20.8	3.0	43.3	58.0	91.7	-37.1
128	11.7	57.4	69.1	61.0	40.1	11.3	69.9	114.8	59.5	7.0
256	16.0	54.2	50.2	42.1	38.2	15.4	47.9	88.8	33.7	12.6
512	29.6	62.7	53.5	51.6	21.4	29.7	68.7	76.7	10.6	5.5
1024	31.8	65.2	46.6	56.3	18.5	31.4	57.1	75.2	19.0	14.9

Table 25. A comparison of the organic matter digestibility (%) of whole plants from grazed and ungrazed swards sown at different seeding rates.

Means

Seeding rate (kg ha^{-1})	Grazed					Ungrazed				
	Date of harvests									
	5/7	9/8	28/9	8/11	13/12	5/7	9/8	28/9	8/11	13/12
1	82.2	74.9	75.4	77.1	45.4	81.5	76.5	78.2	64.1	55.2
2	78.3	76.9	76.4	76.0	49.1	78.3	76.7	79.2	69.3	52.8
4	81.0	79.6	76.8	77.4	66.6	82.4	84.5	79.8	57.0	47.7
8	82.8	71.4	78.4	80.2	65.0	84.0	75.9	78.3	56.8	48.6
16	81.4	75.0	76.4	81.0	65.7	82.5	85.1	77.4	59.4	47.3
32	82.7	74.0	78.0	78.9	55.8	82.4	85.2	73.7	57.5	47.7
64	79.5	75.1	81.0	80.0	49.9	75.9	83.1	77.4	59.0	54.3
128	78.4	73.4	78.2	71.0	54.3	76.1	84.4	68.6	58.5	45.9
256	75.9	74.6	78.4	72.3	52.2	76.9	87.1	73.4	52.5	43.8
512	80.9	78.3	77.4	72.7	65.1	82.1	83.8	69.9	54.5	52.8
1024	77.2	81.9	74.1	74.1	61.5	80.1	83.0	68.4	54.7	52.1

Figure 5. Accumulation of herbage in time in grazed and ungrazed swards for a selected range of seeding rates.
Curves are fitted logistic functions as described in Section 5.3.6.



grazed
ungrazed
seeding rate (kg ha-1)
1
16
32
1024
Total herbage dry matter production (kg ha-1)
10000
8000
6000
4000
2000
0
50
100
150
200
May
June
July
Aug.
Sept.
Oct.
Nov.
Dec.
Days from sowing

Table 26. Matrix of simple correlation coefficients between sward characteristics and plant growth rate in ungrazed swards on three harvest occasions.

Variable	Harvest	TL	PNO	PWT	TP	OMD	GR
	1	0.93	0.83	n.s.	n.s.	n.s.	n.a.
DM	3	0.78	0.63	-0.72	-0.73	-0.78	n.s.
	5	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	1		0.91	n.s.	0.69	n.s.	0.93
TL	3		n.s.	n.s.	n.s.	0.64	n.s.
	5		n.s.	n.s.	n.s.	n.s.	n.s.
	1			n.s.	0.67	n.s.	0.99
PNO	3			n.s.	-0.63	-0.90	n.s.
	5			n.s.	-0.63	n.s.	n.s.
	1				0.73	n.s.	n.s.
PWT	3				n.s.	0.61	n.s.
	5				0.96	n.s.	n.s.
	1					n.s.	n.s.
TP	3					0.62	n.s.
	5					n.s.	n.s.
	1						n.s.
OMD	3						n.s.
	5						n.s.

n.s. = not significant   n.a. = not applicable.

$P < 0.05 \simeq 0.60$, $P < 0.01 \simeq 0.74$, $P < 0.001 \simeq 0.85$

DM = total herbage yield present (kg DM ha^{-1})
TL = tiller length (cm)
PNO = plant density (plants m^{-2})
GR = plant growth rate (kg DM $ha^{-1} day^{-1}$)
PWT = plant weight (g)
TP = tillers per plant
OMD = organic matter digestibility (%) (whole plant samples)

(a) (Top) A view of a range of seeding rate treatments at harvest 1 (July 5th). The differences in herbage availability and ground cover persisted throughout the experiment (see b, and c below).

Plate 4.

(b) (Centre) A view of a range of the seeding rate treatments at harvest 3 (September 27th). The differences in herbage yield and ground cover are evident.

(c) (Bottom) A view of a range of seeding rate treatments at harvest 5 (December 21st). Note that differences in yield and ground cover are still evident.

(a) (Top) A view of plants and sheep on the 1 kg ha^{-1} treatments at harvest 1 (July 5th) when the grazing of plots began. Note the ungrazed area fenced off in the background.

For a grazed sward of the following characteristics:

(i) herbage availability = 8 (kg DM ha^{-1})

(ii) tiller length = 3.2 (cm)

(iii) plant density = 38 (plants m^{-2})

and

(iv) plant weight = 10 (mg)

sheep intake was 104 (g OM day^{-1}).

(b) (Centre) A view of plants and sheep on the 32 kg ha^{-1} treatment at harvest 1 (July 5th). Note the ungrazed area fenced off in the background.

For a grazed sward of the following characteristics:

(i) herbage availability = 211 (kg DM ha^{-1})

Plate 5.

(ii) tiller length = 4.1 (cm)

(iii) plant number = 1126 (plants m^{-2})

and

(iv) plant weight = 6 (mg)

sheep intake was 631 (g OM day^{-1}).

(c) (Bottom) A view of plants and sheep on the 1024 kg ha^{-1} treatment at harvest 1 (July 5th). Note the ungrazed area fenced off in the background. The sward has formed a closed canopy in less than 51 days after sowing.

For a grazed sward of the following plant characteristics:

(i) herbage availability = 1608 (kg DM ha^{-1})

(ii) tiller length = 7.6 (cm)

(iii) plant number = 35993 (plants m^{-2})

and

(iv) plant weight = 4 (mg)

sheep intake was 1211 (g OM day^{-1}).

Plate 6.

(a) (Top) A view of plants and sheep on the 1 kg ha^{-1} seeding rate treatment at harvest 3 (September 27th). Note all animals are replacements as all original sheep had died by this time. Pasture characteristics of grazed and ungrazed (i.e. fenced off area in background) swards and sheep intake are shown below:

	Grazed	Ungrazed	
Herbage availability	16	5176	(kg DM ha^{-1})
Tiller length	3	39	(cm)
Plant number	24	28	(plants m^{-2})
Plant weight	0.014	21.171	(g)
Sheep intake (replacements)	23		(g OM day^{-1})

(b) (Centre) A view of plants and sheep on the 32 kg ha^{-1} seeding rate treatment at harvest 3 (September 27th). Pasture characteristics of grazed and ungrazed (i.e. the area fenced off in the background) swards and sheep intake are given below:

	Grazed	Ungrazed	
Herbage availability	749	6582	(kg DM ha^{-1})
Tiller length	7	43	(cm)
Plant number	1406	900	(plants m^{-2})
Plant weight	0.700	0.731	(g)
Sheep intake	986		(g OM day^{-1})

(c) (Bottom) A view of plants and sheep on the 1024 kg ha^{-1} seeding rate treatment at harvest 3 (September 27th). Plant characteristics of grazed and ungrazed (i.e. the area fenced off adjacent to the sheep) swards are given below:

	Grazed	Ungrazed	
Herbage availability	897	7286	(kg DM ha^{-1})
Tiller length	6	42	(cm)
Plant number	8230	4659	(plants m^{-2})
Plant weight	0.021	0.147	(g)
Sheep intake	894		(g OM day^{-1})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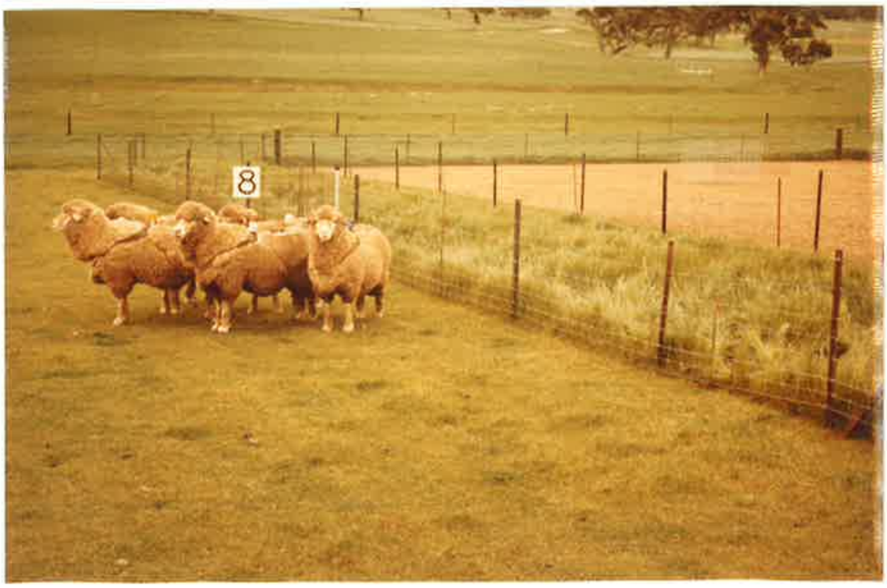
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Plate 7.

(a) (Top) A view of plants and sheep (replacements) on the 1 kg ha^{-1} seeding rate treatment at harvest 5 (December 21st). Pasture characteristics of grazed and ungrazed (i.e. fenced off area adjacent to sheep) swards and sheep intake are given below:

	Grazed	Ungrazed	
Herbage availability	1	7851	(kg DM ha^{-1})
Tiller length	3	55	(cm)
Plant number	4	32	(plants m^{-2})
Plant weight	0.010	24.5	(g)
Sheep intake (replacements)	42 (g OM day^{-1})		

(b) (Centre) A view of plants and sheep on the 32 kg ha^{-1} seeding rate treatment at harvest 5 (December 21st). Pasture characteristics of grazed and ungrazed (i.e. fenced off area adjacent to sheep) swards and sheep intake are given below:

	Grazed	Ungrazed	
Herbage availability	1424	7899	(kg DM ha^{-1})
Tiller length	8	46	(cm)
Plant number	1123	810	(plants m^{-2})
Plant weight	0.217	0.950	(mg)
Sheep intake	998 (g OM day^{-1})		

(c) (Bottom) A view of plants and sheep on the 1024 kg ha^{-1} seeding rate treatment at harvest 5 (December 21st). Pasture characteristics of grazed and ungrazed (i.e. fenced off area adjacent to sheep) swards and sheep intake are given below:

	Grazed	Ungrazed	
Herbage availability	1187	8617	(kg DM ha^{-1})
Tiller length	6	47	(cm)
Plant number	6868	4789	(plants m^{-2})
Plant weight	0.022	0.180	(g)
Sheep intake	1232 (g OM day^{-1})		


6


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