
THE PROCEEDINGS OF THE
NEW ZEALAND SOCIETY
OF
ANIMAL PRODUCTION
VOLUME 62 2002

FACTORS LIMITING PASTURE PRODUCTION

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SUMMARY

The upper limit to the production of dry matter of crop and pasture species, as set by the amount of radiation energy that is converted to plant energy by the photosynthesis reaction, is discussed.

Data are presented which suggest that the maximum growth rate of pure stands of different species is determined by the amount of chlorophyll exposed to light of an intensity above 400 to 500 foot candles. From this a further limit to dry matter production is shown to be set by the growth form of species, and the shape and orientation of leaves in the light-absorbing canopy.

Comparisons made between the maximum annual yields of pasture and different crop rotations show little difference between pasture yields and the highest yielding crop rotations.

Results are presented showing the effect of various management practices on the yield, growth rate, and leaf growth of pastures. These results are discussed in terms of alterations of the light climate of pastures, the reduction in yields below potential yields being explained in part by incomplete utilization of light by the foliage of pastures.

Suggestions are made of ways of increasing both the potential production of dry matter per unit area of land, and the conversion of this energy into edible foods.

IT HAS OFTEN BEEN STATED (Watson, 1958a; Blackman and Black, 1959; Loomis, 1960; Kok, 1960; and others) that the primary limitation to biological production in any part of the world is set by photosynthesis. Furthermore, at present, throughout the world, a considerable amount of work is being carried out measuring or calculating the efficiency of photosynthesis in various organisms, plants, and plant communities, and attempting to find ways and means of increasing this efficiency. Basically this is the problem that we are all confronted with, and for this reason it is of more than passing interest for us to have some idea of maximum energy conversion figures that have been obtained for different plant associations, so that there is an incentive for increased efforts in research and improvement in farming practices.

The maximum energy conversion factor of absorbable radiation in plant growth, for short periods of time, approaches

20% for ammonium-fed algae (Van Oorschot, 1955; Myers, 1959), whereas for small lots of beet seedlings, grown in a measured field of white light, efficiency values of between 11 and 19% have been obtained (Wassink *et al.*, 1952). These values for cultured plant species compare with maximum recorded efficiency values of 9.5% for sugar-beet (Watson, 1958b; Blackman and Black, 1959), 8.0% for algae (Kok and Van Oorschot, 1954; Tamiya, 1957), and 4.9% for kale (Watson, 1958b), when each was grown as a pure stand under natural conditions.

Comparable data for crop or pasture species, growing under New Zealand conditions, are not available, as at no time have detailed growth rate measurements of both above and below ground dry matter accumulation been combined in the same study. For crop species, particularly root crops, such data are not difficult to obtain, but for species with fibrous root systems, such as pasture species under defoliation, measurements of root growth rate, and hence energy conversion values, are difficult to determine accurately. However, the results presented in Table 1, showing the maximum growth rate of pure stands of some pasture and crop species growing at Palmerston North in comparison with crops growing at other locations, give an indication of the production potential of these species.

The growth rate data shown have been presented in a previous publication (Brougham, 1960b) and are for dry matter increments above a cutting height of 1 in. from ground level for each stand. Those for crops growing at other locations have been presented by Blackman and Black (1959). These data suggest that the efficiency of conversion of absorbable radiation by crop and pasture species growing under New Zealand con-

TABLE 1: MAXIMUM GROWTH RATES OF SOME PASTURE AND CROP SPECIES GROWN AT PALMERSTON NORTH AND AT OTHER LOCATIONS

Species	*Rate of D.M. Production (lb/acre/day)*		*Per cent. Utilization of Absorbable Light Energy (4,000-7,000 A°)*
Maize	261	Above ground growth.	
Red clover	188		
Short-rotation ryegrass	169		
Perennial ryegrass	156		
Kale	127		
White clover	121		
Sugar-cane (Hawaii)	339	Total growth	
Maize (New Hampshire)	241		
Sugar-beet (England)	277		9.5
Kale (England)	187		4.9

TABLE 2: GROWTH RATES PER UNIT OF LEAF AREA AND CORRELATION COEFFICIENTS

Species	*Maximum Growth-Rate*	*Critical L.A.I.*	*Amount of Chlorophyll per sq.ft of Herbage*	*Growth Rate/ Critical L.A.I.*	*Growth Rate/ Total Chlorophyll*
White clover	121	3.00	129	40.3	0.936
Red clover	188	4.80	199	39.3	0.947
Kale	127	3.10	133	41.1	0.958
Short-rotation ryegrass	169	6.45	229	26.1	0.735
Perennial ryegrass	156	6.00	209	25.9	0.744
Maize	261	7.35	281	35.6	0.928
Correlation coefficient				+0.815*	+0.912**

*Significant at 5% level of probability. **Significant at 1% level of probability.

ditions is similar to that recorded at other locations. For example, using the same basis of calculation for the energy conversion values as used by Blackman and Black (1959), and assuming a radiation figure of 500 cal/cm^2/day as representing the average amount of incoming solar energy received at Palmerston North during the period of maximum growth, the energy converted in top growth of maize is 5.4%. If an allowance is made for root and stubble growth, the value for maize would approach that of sugar-beet (9.5%).

Both sets of data show that the upper limit to the production of dry matter from crop or pasture species is reached when approximately 10% of the light usable in photosynthesis is converted to plant energy (Kok, 1960). It is probable that this value represents the lower limit to maximum production, as the basis of measurement is harvested dry matter. Under field conditions, such measurement techniques may not account for energy that could be converted and respired between harvests of dry matter.

Marked differences between species in maximum rates of dry matter production per unit area of land of above ground growth are also shown in Table 1. An explanation of these differences is given by the results presented in Table 2, where correlation coefficients relating the growth rate values to both the total amounts of leaf and of chlorophyll per unit area of land, exposed to light above 400 to 500 foot candles (f.c.), are presented.* These latter are mid-summer values determined at local noon on sunny days.

* The first of these indices will be referred to hereafter as Critical L.A.I.

The significant correlation coefficients obtained suggest that, where other factors such as water, nutrients, and temperature are optimal for growth, the maximum growth rate of stands of species is determined by the total amount of chlorophyll exposed to light of an intensity above 400 to 500 f.c. (compensation point for dry matter increase in a number of species—Bohning and Burnside, 1956).

The Critical L.A.I. values presented in Table 2 show marked differences between species in their ability to expose leaf to light. From this, and the fact that such differences are significantly related to growth rate, a further limit to dry matter production is shown to be set by the growth form of species, and more particularly by the shape and orientation of leaves, their position in the light absorbing canopy, and the effect the uppermost leaves have on those lower down the canopy. From results such as these and from other work (Watson, 1956a, 1958a), conflicting suggestions have been made on the most desirable types of vegetation required for maximum utilization of incident radiation. For instance, Mitchell (1960) has suggested that maximum efficiency of utilization of both light and carbon dioxide would come from species with "a growth form similar to maize or any other tall-stemmed plant with either relatively small or linear leaves", whereas H. D. Pirie in a published discussion of a paper presented by Watson (1958b), suggests that what is needed is, "a tall, conical, heliotropic plant with leaves set parallel to the surface of the cone.". Watson, however, doubts the need for tall forms of vegetation in relation to photosynthetic efficiency. What can be said with some degree of certainty is that the most efficient species, as converters of usable light, are those that expose the greatest amounts of chlorophyll per unit area of stand to light above an intensity of 400 to 500 f.c. In addition, it would seem that chlorophyll concentration per unit area of plant tissue (that is, for all parts of the plant) is important (Gabrielsen, 1948).

The results presented in Table 2 also suggest that the activity of chlorophyll of the different species was similar and that the concentration of CO_2 available for growth and the utilization of it by the chloroplasts was the same for these species (Brougham, 1960b). As the height of the profile receiving light above an intensity of 400 to 500 f.c. ranged from 8 cm for white clover to 45 cm for maize, and the average density of chlorophyll per centimetre of profile ranged from approximately 16 mg per unit area for white clover to approximately 6 mg for maize (Brougham, 1960b), the suggestion that an extension of the light absorbing profile of vegetation would provide more efficient CO_2 circulation through the crop, resulting in a higher daily growth rate (Mitchell, 1960), needs more clarification. On the contrary, the above results suggest that chlorophyll in stands of different crop and pasture species, regardless of the structure of the light-absorbing canopy, are capable of maintaining favourable rates of photosynthesis under field conditions (Kok, 1960; Loomis, 1960). Within the stand, this air could be enriched by CO_2 released from decaying organic matter (Loomis, 1960; Brougham, 1960b).

The above discussion has been concerned with factors influencing the maximum growth rates of pastures and crop species under conditions where factors such as water, nutrients, and temperature are not limiting. Such conditions apply for only short periods of time during the year. During the rest of the year any number of the above factors can be limiting or can be induced as such by a multitude of cultural practices.

Crop species, because of their annual growth cycle, do not maintain throughout the year a complete land coverage with leaf canopies of sufficient density to intercept all light effective for growth. Pastures, however, under favourable management practices, can be grown to meet this objective. Such pastures then have the ability to convert all usable light into plant energy, if other factors are not limiting. Although the maximum growth rate of these pastures at their period of peak growth is not as high as those of other species (Table 1), the results presented in Table 3 show that the maximum annual production of pasture compares favourably with the maxima of other crop rotations. The yields shown were obtained under conditions of high soil fertility and adequate moisture.

TABLE 3: ANNUAL PRODUCTION OF PASTURE AND DIFFERENT CROP ROTATIONS FOR THE YEAR 1955-56 AT PALMERSTON NORTH.

Crop rotation	*Year*	*Yield (lb D.M./acre)*
Maize + Italian ryegrass	1955-56	21,900 (15,450 + 6,450)
Kale + Italian ryegrass	1955-56	19,600 (13,250 + 6,350)
Pasture (Short-rotation ryegrass + White clover)	1955-56	22-23,000
Maximum Recorded:		
Maize + Italian ryegrass	1958-59	27,650 (23,150 + 4,500)

22,000 lb D.M./acre/year is equivalent to an average daily yield of 60 lb D.M./acre.

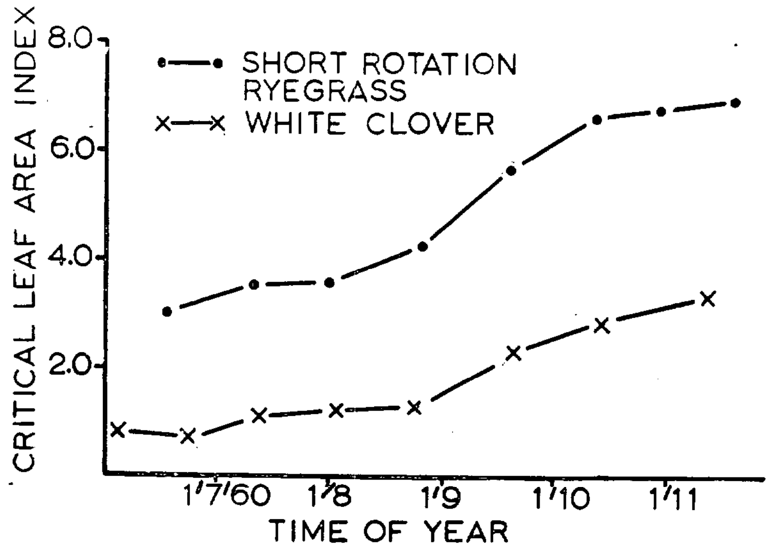

Fig. 1: Seasonal fluctuations in critical leaf area indices of pure stands of short-rotation ryegrass and of white clover.

In practice, limitations to these potential yields are determined by the reaction of the species used in pastures to the imposed environment.

Effect of Pasture Management

If pastures are left undisturbed for long periods of time, a balance between growth and decomposition of herbage occurs and a ceiling yield is reached which is dependent on the climate prevailing (Brougham, 1959). Under these conditions, gains in dry matter production from photosynthesis are at a maximum but are balanced by dry matter losses from respiration and decomposition of dead tissue. Because pastures show a tolerance to grazing, this natural balance between photosynthesis and respiration can be markedly altered by defoliation. This forms the basis of pasture management, with the aim being to harvest pastures so that the maximum amount of photosynthesis per unit area of land is allowed to proceed while losses of tissue through respiration and decomposition are reduced to a minimum. To achieve this, a leaf canopy of sufficient density to intercept all usable light throughout the year is required. The results presented in Fig. 1 show the seasonal fluctuations that occur at Palmerston North in Critical L.A.I. values of pure stands of short-rotation ryegrass and of white clover.

TABLE 4: DIMENSIONS OF CLOVER LEAVES IN PURE SWARDS OF WHITE CLOVER UNDER DIFFERENT MANAGEMENT SYSTEMS. (DECEMBER).

Management System	*Area of Laminae (sq.cm)*	*Length of Petiole (mm)*	*Leaf Age at Max. Dimensions (days)*
Undisturbed stand	32.0	375	20
Rotational grazing (six weeks spell)	12.0	250	25
Set-stocked swards	2.6	75	20

These results are similar to previous estimates (Brougham, 1958a), the values for the grass species being approximately two to three times those of the clover species throughout the year. They also show that midwinter values for both species are less than half the mid-summer values. These results are attributable to differences in the amount of light received, the elevation of the sun throughout the year, and to differences in leaf shape and orientation. They show one of the requirements necessary for maximum annual production from pasture.

In practice, because of unfavourable climatic conditions or faulty pasture management, this requirement is often not met. Some illustrations of this follow. In Table 4 is shown the marked reduction that can occur in the size of mature clover leaves under three different systems of pasture management.

In this case size was probably determined by the length of time the developing leaves were under light of an intensity low enough to allow cell division and elongation to occur. In the undisturbed stand, the leaves took longer to penetrate the

TABLE 5: EFFECT OF MANAGEMENT ON D.M. PRODUCTION FROM PASTURE DURING THE SUMMER.

Management System	*Yield (lb D.M./ Acre)*	*Species Yield* Ryegrass	Cocksfoot	Red Clover	White Clover	Other Species
Frequent and intensive (3-1)*	1,990	1,390	265	65	185	85
Frequent and lax (7-3)*	3,960	1,480	1,000	745	545	190

Both pastures were under the (7-3)* system of management until the start of the summer.

* (3-1)—Pastures defoliated to 1 inch when they attained a height of 3 inches.

*(7-3)—Pastures defoliated to 3 inches when they attained a height of 7 inches.

TABLE 6: EFFECT OF MANAGEMENT ON D.M. PRODUCTION FROM PASTURE DURING THE LATE AUTUMN, WINTER, AND EARLY SPRING (APRIL 1—AUGUST 5).

Management System	*Yield (lb D.M./acre)*	*Av. D.M. Production/acre/day*
18 weeks spelling	2,120	17
2 spells of 9 weeks	3,290	26
3 spells of 6 weeks	3,620	29

existing canopy and reach higher light intensities and therefore attained a larger size (Brougham, 1958b) Dry matter production would also be higher in these stands.

The results presented in Table 5 show the marked effect management has on production of grass during the summer period.

These results have been discussed previously (Brougham, 1960a) as have the results shown in Table 6 (Brougham, 1956b). Here long spelling over the winter was shown to have an adverse effect on herbage production.

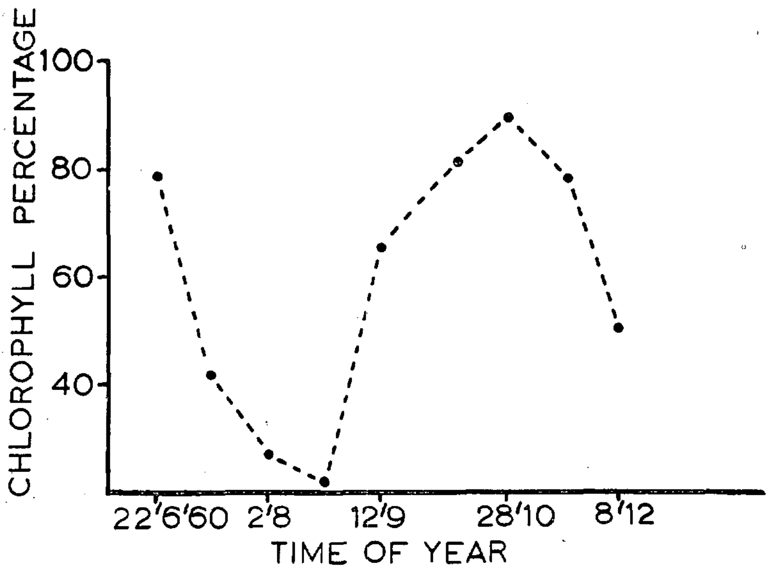

Fig. 2: Amount of chlorophyll in pure stands of short-rotation ryegrass under set-stocked management, as a percentage of that in the herbage of similar stands above the 95% light interception level.

Finally, Figure 2 shows the amount of chlorophyll present in pure stands of short-rotation ryegrass under set-stocked management at 7 breeding ewes per acre, as a percentage of that in the amount of herbage necessary to intercept 95% of available light in similar stands. Measurements were made from mid-winter to the beginning of summer. Both stands were under nitrogen fertilization and the light measurements were carried out at local noon on the days shown.

If it is assumed that the chlorophyll in both pastures showed the same activity in photosynthesis, then the set-stocked pastures produced much less dry matter per unit area than did the standard pastures. Productivity of the set-stocked pastures would have been very low between early July and late September, and from yield measurements which are not presented the amount of dry matter available for consumption was also low.

In most cases the above effects are due, at least in part, to an alteration of the light climate of the plant community, the reduction in yield below potential yields being due in part to incomplete utilization of light, or intense shading in the bottom layers of the pasture causing high decomposition losses.

Nitrogen Nutrition

The need for white clover in pastures as a nitrogen fixing agent has been shown by Sears *et al.* (1953), and its value as a high protein feed with desirable animal production qualities has been demonstrated by Sinclair *et al.* (1956) and Rae, A. L., *et al.* (pers. comm.). On the other hand, the potential maximum daily growth rate (Table 1) and annual yields of herbage obtainable from stands of this species (Sears *et al.*, 1953) are much lower than those obtained from other species. Also, because of its habit of growth, white clover does not tolerate competition from erect-leaved species. Two examples of this are shown by the results presented in Figs. 3 and 4.

Figure 3 shows the effect red clover has on leaf development of white clover over the first summer following an autumn sowing, while Fig. 4 shows the growth of white clover in competition with short-rotation ryegrass, under long spelling over the winter. Because of these and similar effects at other times of the year and the need to maintain the clover component of the sward in balance with the grasses, a further limit to dry matter production can occur and yield potentials be reduced.

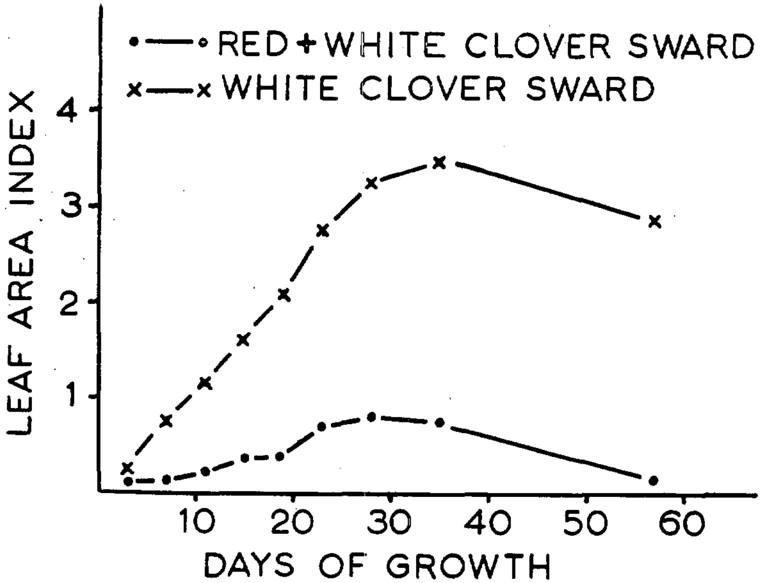

Fig. 3.
White clover leaf growth in stands with and without competition from red clover during the summer.

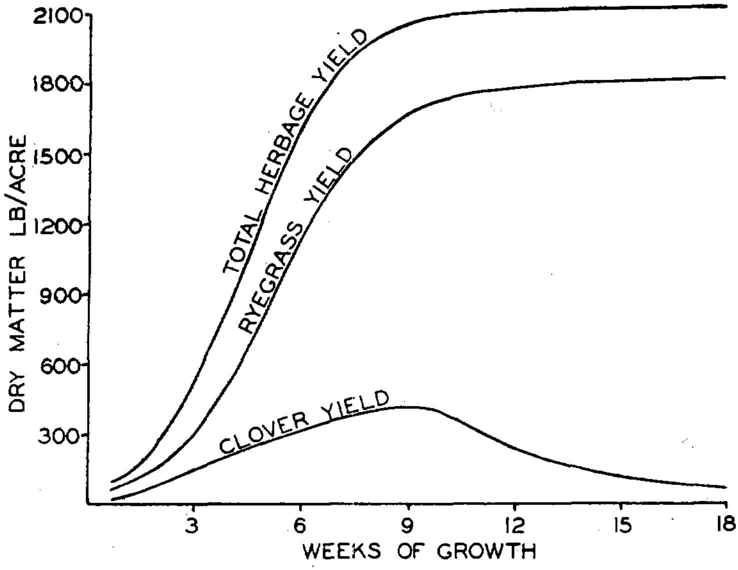

Fig. 4.
Growth of white clover in competition with short-rotation ryegrass under long spelling over the winter.

Other Effects

The size and the efficiency of the photosynthetic system of a plant community is also markedly influenced by factors such as soil fertility, the availability of plant nutrients and water, treading, pests and insects, the composition of the soil and its structure and characteristics, weather, and many other factors. The importance of some of these factors on the growth of crop species, as determined by changes in the size and efficiency of the photosynthetic system, has been well demonstrated by Watson (1947, 1956b) and others and will not be discussed in detail in this paper.

Finally, it is tempting to suggest various ways and means of increasing both the potential production of dry matter per unit area of land and the conversion of this energy into edible foods.

PLANT IMPROVEMENT

Dry Matter Production

The results presented above suggest that dry matter production, per unit area of land, is limited by the amount of chlorophyll exposed to light that is usable in the photosynthetic reaction. They suggest that potential productivity could be increased by breeding varieties of pasture plants with:

(a) A higher chlorophyll content per unit area of tissue (leaf, petiole, sheath and stem).

(b) A higher photosynthetic efficiency (Watson, 1956a; Cooper and Edwards, 1959).

(c) A leaf system which allows the maximum amount of leaf per unit area of land to receive light at intensities favourable for photosynthesis.

Such improvements could be made with the existing plant material growing within the limits set by the environment.

Animal Production

The above objectives must be allied with the fact that, within the existing framework of farming practice, dry matter is produced as a feed for farm animals. For this reason, consideration must also be given to efficiency of conversion values of different pasture and crop species. The results obtained by Flux *et al.* (1960), and Rae, A. L. *et al.* (pers. comm.) show that there are marked differences between strains of the same species of ryegrass, in their ability to grow animals, possibly because of differences in the carbohydrate to protein balance, or the type of these compounds present in the feed. Also the results obtained by Johns (1956), show that protein levels of pastures, growing under conditions of high soil fertility, are higher than those, throughout the year, required by the grazing animal for maximum milk or meat production. These results indicate that suggestions made for the introduction of new strains or species which suit a particular environment and have increased potential yield, can be misleading if the milk- and meat-producing qualities of such strains or species are low or unknown. This is shown by the results presented in Table 1, where the species with the lowest maximum daily growth rate, white clover, is known by farmer experience and by research result (Sinclair *et al.*, 1956; Flux *et al.*, 1960; Rae, A. L., *et al.*, pers. comm.) to have a high animal production potential.

It is also sobering to realize that the pasture plant material used as a basis for breeding and improvement in temperate zones today originates from plant material that was selected on the criterion of meat-producing ability at the start of grassland research as it is known today. From this it would seem that worthwhile improvements could be made to existing species in their milk- and meat-producing potentials by selecting varieties of plants of improved agronomic type under tests similar to those applied by Flux *et al.* (1960), Rae, A. L., *et al.* (pers. comm.) and Johns (1956).

ALTERATIONS TO CLIMATE

Another means of increasing the production potential of pasture is by altering on a large scale the climate under which pastures are growing. This is done in practice by providing water, through irrigation, during periods of drought, and by soil drainage schemes, to allow free drainage of soil during periods of excess rainfall. Well used, the latter could markedly reduce plant damage from treading at higher stocking rates.

Increases in production potentials would also come by raising temperatures and providing supplementary light during periods of low temperature and illumination. In this respect, the culture of algae, which are efficient converters of light energy, on wastelands in Israel, has indicated a plant upon which it might be practicable to use the techniques of temperature and light supplementation.

IMPROVEMENTS IN PASTURE MANAGEMENT

There is evidence to suggest that the relationship between utilization of dry matter produced and stocking rate is linear up to certain limits (Wallace, 1959; Suckling, 1959; McMeekan, 1960). Although these limits are not well defined at present, complete utilization of dry matter produced from pastures is not achieved with existing rates of stocking. Until this occurs on pastures where management procedures are such that maximum production is obtained, limits to production from this factor cannot be determined. However, it would seem that increased sub-division associated with more rapid stock movements and a greater use of supplementary feed could contribute to more efficient utilization. These, together with the incorporation of winter management procedures like those recomended by Wallace (1958), McKenzie (1960), and Tyrer (1960), would markedly reduce excessive plant damage and soil pugging damage caused by treading, two factors that have been shown by Edmond (1958, 1960) to become of greater importance in limiting growth as stocking rate increases.

Our existing farming lay-outs are designed for outdoor feeding throughout the year. For this reason, it would seem more logical to establish the limits of such systems first, rather than make major changes in farming procedures, such as those required for the "zero-grazing" system of management or some other system, before their value in increasing production potentials in New Zealand is known. Until this is done, the dry matter and animal producing ability of different pasture species and management procedures cannot be fully determined.

IMPROVEMENTS IN THE EFFICIENCY OF CONVERSION OF DRY MATTER PRODUCED

Under our existing farming practices, the cow, the sheep, and the pig, are used to convert the dry matter produced from pastures into edible foods. In discussing factors limiting pasture production and measuring their productivity through these animals, the final limit to production is the efficiency of conversion of different pastures by the animal. The marked increases in conversion values obtained in the broiler industry in the United States of America since the war, when compared with conversion values for cows, sheep, or pigs in this country, suggest that considerable improvements can be made in this respect by better feeding regimes, and through animal breeding (Brumby, 1959). The fact that animal variation is large for the characters needed in the conversion process (Rae, 1958) should facilitate these improvements.

* * *

Acknowledgment is made to Dr P. D. Sears, Director, Grasslands Division, D.S.I.R., for permission to use the crop yield data shown in Table 3.

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