Mean Leaf Area of the Canopy for Light Interception by Forages and Mean Retention Time of Feed in the Rumen for Feed Ingestion by Ruminants as Investigated using Simple Models

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Mean Leaf Area of the Canopy for Light Interception by Forages and Mean Retention Time of Feed in the Rumen for Feed Ingestion by Ruminants as Investigated using Simple Models

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This study was conducted to take up the following two subjects: (1) relationships between light interception by the forage canopy and its mean leaf area weighted by the light attenuation curve [MLA], and (2) relationships between feed ingestion by ruminants and mean retention time of feed in the rumen weighted by the feed disappearance curve [MRT], using simple models for forages and those for ruminants. The following results were suggested: (1) when the canopy leaf area index [L] was high the small coefficient of light extinction [K_f] enabled the canopy to have large MLA which could intercept more amount of light, whereas the saturation of light interception occurred in lower L when the canopy had large K_f, (2) daily feed intake [DFI] by ruminants increased with the increase in MRT^{-1} [=feed disappearance rate]. The present study using simple models suggested that MLA of the canopy of forages was like MRT^{-1} of feed in the rumen of ruminants as indices for the estimation of energy ingestion.

INTRODUCTION

Studies on the animal production from forages commonly extend from the forage production to the ruminant production researches.

It was suggested by Shimojo *et al.* (1995) that mean leaf area of the forage canopy weighted by the light attenuation curve [MLA] and its light interception characteristics gave a broad outline of the relationship between light extinction coefficient and the amount of light intercepted by canopy leaves at different levels of leaf area index. This suggestion was given a hint, in calculating MLA, from the calculation of mean retention time of feed in the rumen weighted by the feed disappearance curve [MRT] in ruminants (Faichney, 1993). This hint is, as it were, based on the analogy between MLA and MRT in the method of calculation, though it looks strange. It is known that MRT influences feed intake by ruminants (Minson, 1990; Faichney, 1993). MLA and MRT are subjects that have commonly been investigated in separate studies. However, taking up MLA and MRT in the same paper to estimate both light interception by forages and feed ingestion by ruminants is considered of interest from the viewpoint of looking at forage–ruminant relationships between these two subjects.

The present study was designed to clarify (1) relationships between MLA and light

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interception in forage canopies and (2) relationships between MRT and feed ingestion in ruminants, using simple equations for forages (Monsi and Saeki, 1953; Shimojo *et al.*, 1995) and those for ruminants (Blaxter *et al.*, 1956). These equations are considered too simple compared with modern equations (Sheehy and Johnson, 1993; Faichney, 1993), but they seem to be easy to treat and to be sufficient enough to deal with the present two subjects parallelly.

SIMPLE EQUATIONS FOR MLA AND MRT

Description of MLA and estimation of light interception by MLA

(1) MLA of the forage canopy

MLA of the forage canopy, that is equal to efficient leaf area [L_e] in our previous report (Shimojo *et al.*, 1995), is described as follows:

$$\mathrm{MLA}=\left\{\int_0^L F\cdot\exp(-K_f\cdot F)\,dF\right\}\Big/\left\{\int_0^L \exp(-K_f\cdot F)\,dF\right\}$$

$$=\frac{1}{K_f}\cdot\left\{1-\frac{K_f\cdot L}{\exp(K_f\cdot L)-1}\right\}, \qquad (1)$$

where F=cumulative leaf area index from the top to the jth layer of leaves, L=leaf area index of the canopy, K_f=light extinction coefficient of the canopy.

MLA is, as it were, an area of the two-dimensionally flattened leaf that is obtained by weighting the spatially distributed leaves by the light attenuation curve. MLA calculated at 3 levels of K_f and 9 levels of L is shown in Table 1. MLA with small K_f was higher than that with large K_f for all L, and the difference became larger with the increase in L.

(2) Light interception by unit MLA and by MLA

The amount of light intercepted by MLA might be the same as that intercepted by total leaves of the canopy. Using relative light intensity the amount of light intercepted per unit MLA [R_u] (designated previously as R in the report of Shimojo *et al.* (1995)) is estimated as follows:

Table 1. Mean leaf area [MLA] calculated at different levels of light extinction coefficient [K_f] and canopy leaf area index [L].

		K_f	
	0.30	0.60	0.90
0.50	0.244	0.238	0.231
1.00	0.475	0.450	0.426
2.00	0.901	0.805	0.715
3.00	1.278	1.073	0.895
L 4.00	1.609	1.268	0.999
5.00	1.897	1.405	1.055
6.00	2.145	1.498	1.084
7.00	2.357	1.560	1.098
8.00	2.535	1.600	1.105

$$R_u = 1 - \frac{1}{\exp(K_f \cdot L)} . \qquad (2)$$

R_u calculated at 3 levels of K_f and 9 levels of L is shown in Table 2. R_u with small K_f was lower than that with large K_f for all L, and the difference became smaller with the increase in L.

Thus, the amount of light intercepted by MLA [R_m] (designated previously as *Ie* (*R·Le*) in the report of Shimojo *et al.* (1995)) is expressed as,

$$R_m = R_u \cdot \text{MLA}$$

$$= \left\{1 - \frac{1}{\exp(K_f \cdot L)}\right\} \cdot \left[\frac{1}{K_f} \cdot \left\{1 - \frac{K_f \cdot L}{\exp(K_f \cdot L) - 1}\right\}\right]$$

$$= \frac{1}{K_f} \cdot \left\{1 - \frac{K_f \cdot L + 1}{\exp(K_f \cdot L)}\right\} . \qquad (3)$$

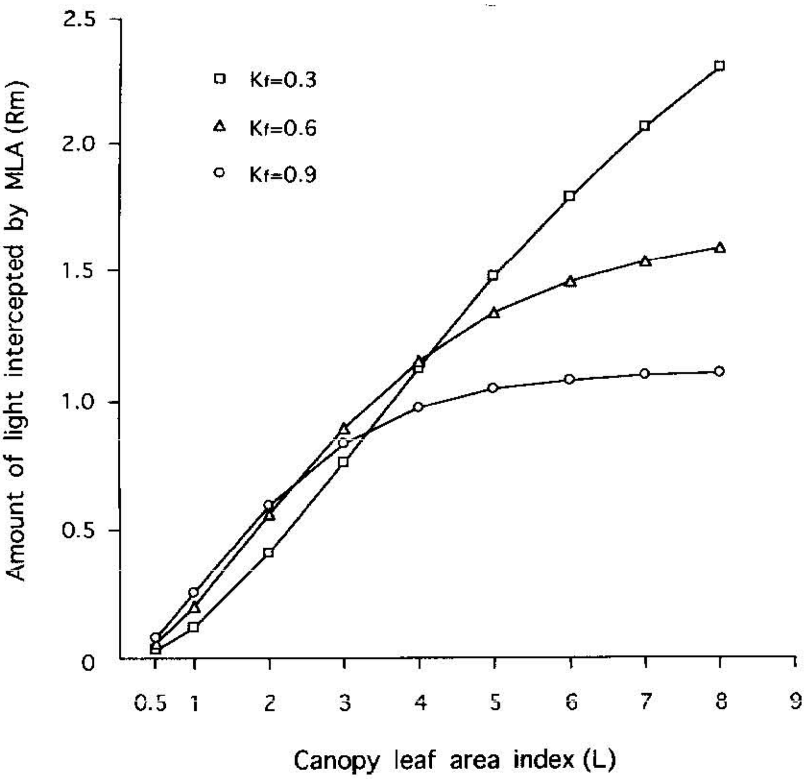

Fig. 1. Amount of light intercepted by MLA [Rm] at different levels of K_f and L in the simple model for canopy (MLA=mean leaf area weighted by light attenuation curve, K_f=light extinction coefficient, L=leaf area index).

Table 2. Amount of light intercepted per unit MLA [R_u] calculated at different levels of light extinction coefficient [K_f] and canopy leaf area index [L].

			K_f	
		0.30	0.60	0.90
L	0.50	0.139	0.259	0.362
	1.00	0.259	0.451	0.593
	2.00	0.451	0.699	0.835
	3.00	0.593	0.835	0.933
	4.00	0.699	0.909	0.973
	5.00	0.777	0.950	0.989
	6.00	0.835	0.973	0.995
	7.00	0.878	0.985	0.998
	8.00	0.909	0.992	0.999

Rm was calculated at 3 levels of K_f and 9 levels of L, giving 27 simple model canopies in the combination of L and K_f (Fig 1.). It is shown in Fig. 1 that (A) in very low L the large K_f allowed the canopy leaves to intercept more amount of light than the small K_f (Table 2), but (B) when L was high the small K_f enabled the canopy to have larger MLA (Table 1) which could intercept more amount of light than the large K_f, and (C) the level of L at which light interception was saturated seemed to be lower in large K_f than in small K_f (Fig. 1). These results seem to be in consistent with the work of Kubota *et al.* (1971) who showed similar tendency in the relationship between photosynthetic activity and K_f. Thus, from the estimation using the simple model for canopy, MLA of the canopy is considered one of the factors influencing the amount of light intercepted by forages.

Description of MRT of feed in the rumen and estimation of feed intake by ruminants

(1) MRT of feed in the rumen

MRT of feed in the rumen of ruminants given a ration every day might be estimated as follows (Faichney, 1993) when the simple equation for feed disappearance curve by Blaxter *et al.* (1956) is used:

$$\mathrm{MRT} = \left\{ \int_0^\infty t \cdot \exp\left(-K_r \cdot t\right) dt \right\} \Big/ \left\{ \int_0^\infty \exp\left(-K_r \cdot t\right) dt \right\}$$

$$= \frac{1}{K_r}, \qquad (4)$$

where K_r=feed disappearance rate (hr^{-1}) [FDR] ($\mathrm{FDR}=\mathrm{MRT}^{-1}$), t= hr.

(2) Amount of feed ingested by ruminants

One of the factors influencing the feed intake by ruminants is the amount of feed that is present in the rumen. The following calculation, $F_n(t)$, is done to estimate how many times as much amount as an animal eats daily are present in the simple model rumen. Thus,

$$F_n(t) = \sum_{j=0}^{n-1} \exp\{-K_r \cdot (t + 24 \cdot j)\}$$

$$= \frac{\exp(24 \cdot K_r) \cdot \{1 - \exp(-24 \cdot K_r \cdot n)\}}{\exp(24 \cdot K_r) - 1} \cdot \exp(-K_r \cdot t) \ , \qquad (5)$$

where $0 \leqq t(\mathrm{hr}) \leqq 24$, j (day) is numbered 0, 1, 2, ..., n–1.
Then, how many times as much as daily feed intake [DFI] are present in the simple model rumen after the steady–state is attained [$F_s(t)$] might be estimated as follows:

$$F_s(t) = \lim_{n \to \infty} F_n(t)$$

$$= \frac{\exp(24 \cdot K_r)}{\exp(24 \cdot K_r) - 1} \cdot \exp(-K_r \cdot t) \ . \qquad (6)$$

In equation (5) $F_n(t)$ estimates how many times as much as DFI are present in the simple model rumen during the adaptation period, n. When the adaptation period is 14 days the comparison of $F_{14}(0)$ with $F_s(0)$ at different levels of K_r is shown in Table 3. There were generally little differences between $F_{14}(0)$ and $F_s(0)$, suggesting that 14 days are considered long enough to adapt ruminants to new feeds, except for the feed with extremely low K_r. In the present study, $F_s(t)$ will be used to estimate how many times as much as DFI are present in the simple model rumen.

Table 3. Comparison between 14–day adaptation [$F_{14}(0)$] and steady–state [$F_s(0)$] in the estimation of how many times as much as daily feed intake are present in the simple model rumen at different levels of FDR [=MRT^{-1}] or corresponding MRT [=FDR^{-1}].

FDR	0.01	0.02	0.03	0.04	0.05	0.06	0.07	0.08	0.09	0.10
MRT	100.00	50.00	33.33	25.00	20.00	16.67	14.29	12.50	11.11	10.00
$F_{14}(0)$	4.52	2.62	1.95	1.62	1.43	1.31	1.23	1.17	1.13	1.10
$F_s(0)$	4.69	2.62	1.95	1.62	1.43	1.31	1.23	1.17	1.13	1.10

FDR: feed disappearance rate.
MRT: mean retention time of feed in the rumen.

The amount of feed that disappears from the simple model rumen per day might be estimated as follows:

$$F_s(0) - F_s(24) = \frac{\exp(24 \cdot K_r)}{\exp(24 \cdot K_r) - 1} - \frac{1}{\exp(24 \cdot K_r) - 1}$$

$$= 1 \ . \qquad (7)$$

Equation (7) suggests that this simple model rumen is based on the setting of daily feed disappearance being 1 for all K_r.

Equation (6), together with equation (7), suggests that $F_s(0)$ estimates how many times as much as DFI are present in the simple model rumen. Therefore, $F_s(0)^{-1}$ might give an index for DFI [DFI index], provided that the rumen size is the same between animals given feeds different in K_r. Thus,

$$
\begin{aligned}
\text{DFI index} &= \frac{1}{F_s(0)} \\
&= 1 - \frac{1}{\exp(24 \cdot K_r)} \\
&= 1 - \frac{1}{\exp\left\{24 \cdot \left(\frac{1}{K_r}\right)^{-1}\right\}} \cdot \qquad (8)
\end{aligned}
$$

Table 4. DFI index calculated at different levels of FDR [$=\text{MRT}^{-1}$] or corresponding MRT [$=\text{FDR}^{-1}$].

FDR	0.01	0.02	0.03	0.04	0.05	0.06	0.07	0.08	0.09	0.10
MRT	100.00	50.00	33.33	25.00	20.00	16.67	14.29	12.50	11.11	10.00
DFI index	0.21	0.38	0.51	0.62	0.70	0.76	0.81	0.85	0.88	0.91

DFI index: an index for daily feed intake.
FDR: feed disappearance rate.
MRT: mean retention time of feed in the rumen.

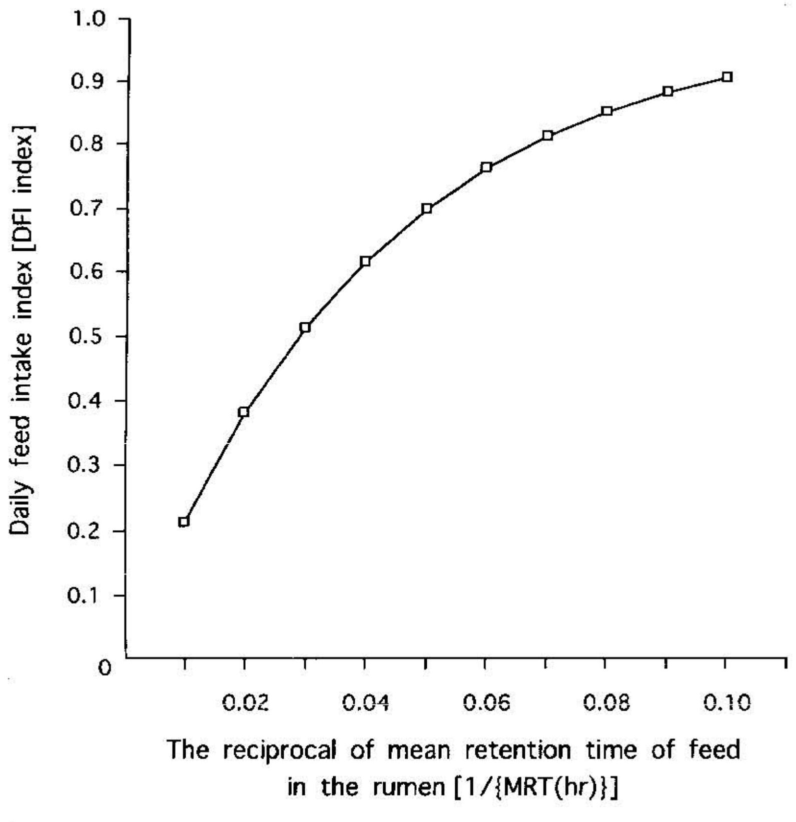

Fig. 2. Relationship between DFI index and MRT^{-1} in the simple model for rumen (DFI index=an index for daily feed intake, MRT^{-1}=the reciprocal of mean retention time of feed in the rumen (=feed disappearance rate [FDR])).

Equation (8) suggests that DFI index is influenced by K_r [FDR] or K_r^{-1} [MRT]. Table 4 shows DFI index at different levels of FDR or corresponding MRT. DFI index increased as MRT [FDR^{-1}] decreased. In other words, with the increase in MRT^{-1} [FDR] there was an increase in DFI index (Fig. 2). This suggests that there is high DFI when its MRT is short or MRT^{-1} is high in ruminants. These results appear to be in consistent with Australian works using tropical forages in which dry matter intake of feed is negatively correlated with its retention time in the rumen (Minson, 1990). Thus, from the estimation using the simple model for rumen, MRT is considered one of the factors influencing the feed intake by ruminants.

MLA of forage canopy and MRT of feed in the rumen

The present study is based on the pioneering equation (Monsi and Saeki, 1953) for calculating MLA of the forage canopy and on that (Blaxter *et al.*, 1956) for calculating MRT of feed in the rumen, respectively. Both equations are similar in the form despite the difference in what they describe. This is one of the reasons why we have decided to write this paper, though those equations have been much improved, from the original simple form, for forages (Sheehy and Johnson, 1988) and for ruminants (Faichney, 1993), respectively. It seems, however, that those pioneering equations are sufficient enough to give a broad outline of the present two subjects.

It is suggested that MLA influences the amount of light intercepted by forages and there is an influence of MRT on the feed intake by ruminants, even if these are based on the estimation using simple models. MLA and MRT are, therefore, related to photosynthesis by forages and energy ingestion by ruminants, respectively. Actually, MLA for the canopy might be like MRT^{-1} for the feed in the rumen as indices for estimating energy ingestion (Figs. 1 and 2). The large MLA and high MRT^{-1} (short MRT) might be expected to increase the ruminant production from forages in the country such as Japan, where there are many people and small land area is available for the production of forages and ruminants. There is, however, a problem of how the large MLA of canopy of the forage and its high MRT^{-1} in the rumen can be balanced, because large MLA tends to decrease forage digestibility due probably to the advanced maturity and this may decrease MRT^{-1}, resulting in the reduction in forage intake by ruminants. This problem will be overcome by breeding and processing of forages to increase both the yield and digestibility of dry matter (Jung and Allen, 1995).

It seems, anyway, to be of interest that MLA and MRT are obtained using the similar method of calculation. This might be due to a sort of conceptual analogy between forages and ruminants in the analytic method of estimating energy ingestion for their growth and production.

Conclusions

It is suggested from the present study using simple models that MLA of the canopy of forages is like MRT^{-1} of feed in the rumen of ruminants as indices for the estimation of energy ingestion.

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