Digestion of concentrate and of hay diets in the stomach and intestines of ruminants

2.* Young steers

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1. Two young steers, aged approximately 6 months and each fitted with a rumen and an abomasal cannula, were used to measure the flow of digesta to the abomasum over periods of 24 h. A diet of concentrates, at two levels, and a diet of hay cubes were given to the steers. Paper impregnated with chromium sesquioxide was inserted into the rumen twice daily.

2. The amount of digesta passing to the abomasum and the output of faeces were measured and the values were adjusted to give 100% recovery of chromium sesquioxide. Measurements were also made of concentrations of plasma glucose, of volatile fatty acids (VFA) in both the rumen and abomasal fluid, and of rumen fluid volume and outflow.

3. About 60–80% of the digestible dry matter and of the digestible energy of both diets disappeared from the forestomach (reticulo-rumen and omasum). The amounts of starch flowing through the abomasum differed little between diets and ranged from 29 to 77 g daily.

4. The volume of rumen fluid did not differ consistently between diets, but the outflow of fluid from the rumen was considerably higher when hay was given.

5. Diet had little influence on plasma glucose but affected the concentrations and molar proportions of VFA in the rumen fluid, and to a lesser extent in the abomasal fluid.

Sheep fitted with cannulas into various parts of the digestive tract have been used by Topps, Kay & Goodall (1968) to show that about 95% of the starch ingested as a concentrate diet was fermented in the rumen. Since some of the starch reaching the intestines may have been of microbial origin, degradative processes in the rumen are evidently very effective in breaking down dietary starch given at a high level. These observations in sheep led to speculation as to whether digestion in cattle receiving high-cereal diets followed the same pattern. Although it is well established that the digestive capabilities of cattle and sheep are very similar (Swift & Bratzler, 1959), anatomical differences, such as the size of the reticulo-omasal orifice, may cause different retention times in the rumen of certain parts of the diet and this might lead to differences in the extent to which they are degraded. Furthermore, a recent report by Karr, Little & Mitchell (1966) on work with yearling steers given high-maize diets indicated that large quantities of starch, as much as 38% of dietary intake, passed through the abomasum. Experiments were therefore carried out with two young steers fitted with rumen and abomasal cannulas in an attempt to obtain further evidence on this subject.

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EXPERIMENTAL

Animals and diets. Two young Friesian steers, approximately 6 months old and 120 kg in weight were used. After birth they were allowed to suckle their dams for 3 weeks and were then weaned on to an early weaning diet, which was changed to a mixture of bruised barley and a protein–mineral supplement when the calves were 8 weeks old. They were each fitted with a rumen cannula at the age of 4 months, and 2 weeks later a second cannula was placed in the fundus of the abomasum. Both operations were performed under paravertebral anaesthesia. The animals quickly recovered and when the experiment began their health and food intake appeared to be normal.

Table 1. *Composition of the diets (g/100 g food) and their digestibility*

	Water	Cellulose	Total nitrogen	Starch A*	Starch E†	Digestibility‡ of dry matter (%)
Period 1						
Concentrate	15·5	4·9	2·7	44·6	46·1	85·9
Hay	10·0	23·9	1·9	7·0	4·4	65·6
Period 2						
Concentrate	13·0	5·3	2·6	46·2	48·9	86·5
Hay	8·7	29·5	1·5	6·6	4·1	61·8

* Determined by the anthrone method (Clegg, 1956)
† Determined by an enzymic method (MacRae & Armstrong, 1966).
‡ Based on values given in Table 6.

Table 2. *Body-weights, food intakes and digestible energy (DE) intakes of two young steers receiving two diets in two periods*

Period	Diet	Steer	Body-weight (kg)	Food intake (kg/24 h)	DE intake per kg body-weight (kcal/24 h)
1	Concentrate	Charlie	110	2·0	53
	Hay	Buster	130	2·6	51
	Concentrate	Charlie	115	3·0	77
2	Concentrate	Buster	144	2·7	59
	Hay	Charlie	130	3·5	65
	Concentrate	Buster	153	3·5	74

The diets were the same as those used in the preceding study (Topps *et al.* 1968), but the foods were obtained from different batches of concentrate and hay cubes; hence their compositions differed a little from those of the diets given to the sheep. The compositions are given in Table 1.

Feeding and sampling. Whilst the steers were being trained and fitted with cannulas during the 2 months preceding the experiment, they were fed on chopped hay *ad lib.* and a restricted amount of concentrate containing rolled barley. Just before the experiment began this diet was gradually changed, over a period of 11 days, to 2 kg concentrate daily for one steer (Charlie) and 2·6 kg hay cubes for the other (Buster). These amounts provided similar quantities of digestible energy per kg body-weight

(see Table 2). The steers were maintained on these diets for 3 weeks during which collections of abomasal digesta and faeces were made. The amount of concentrate given to Charlie was then increased to 3 kg daily over a period of 4 days and this level of feeding was maintained for a further week during which a third collection of digesta and of faeces was made.

The diets given to each steer were then interchanged and the amounts given adjusted to provide levels of digestible energy per kg body-weight approximately 20% higher than those used initially so as to improve the rate of growth (see Table 2). This change of diet extended over 10 days with the gradual introduction of hay in place of concentrates and vice versa. The steers were kept on these diets for 3 weeks, when collections of digesta and faeces were made, followed by further collections from Buster during a week in which an increased quantity of concentrates was given. The quantity of concentrates was initially increased to 4 kg/day; this was not fully consumed and the amount was, accordingly, reduced to 3·5 kg.

During the experiment the steers were confined in pens with a metal grid floor raised a few inches above a concrete base. No bedding was provided so this system of housing allowed the daily collection of most but not all of the faeces; some urinary contamination was inevitable. The food was divided equally into two meals given at 09.00 and 16.00 h. At these times 9 g of paper impregnated with chromium sesquioxide were inserted via the cannula into the rumen; this supplied 5·55 g chromium sesquioxide daily. Water was available *ad lib.*

In the two periods when the steers received either the hay cubes or the lower level of concentrate, two collections of abomasal digesta, each over 24 h but separated by an interval of 6 days, were made. Samples of digesta, 40 ml in volume, were withdrawn at hourly intervals from the abomasum. The abomasal cannulas were closed by a combined cap and core to prevent solids settling in the barrel and to allow abomasal samples to be taken in controlled amounts. The samples from each steer were pooled over each daily collection period. They were cooled during collection to $-20°$ and subsequently stored at 0° until analysed. At 2 h intervals the pH of the digesta removed from the steers was measured with a Cambridge pH meter. Only one 24 h collection was made from each steer during the week in which it received the higher level of concentrate. This was made only 4 days after the high intake was attained since it was feared that the steers' appetite might become irregular if the high level of intake were prolonged.

A few days before each collection of digesta, samples of blood, rumen contents and abomasal contents were withdrawn from the steers immediately before the morning feed and 2 h later. Measurements made earlier had shown that for both diets the pH of rumen contents reached a minimum 2 h after feeding and this was assumed to correspond with the highest concentration of volatile fatty acids (VFA). The procedure for the sampling of blood and rumen contents has been described previously (Topps *et al.* 1968). About 50 ml of abomasal contents were withdrawn from each animal and prepared for the determination of VFA by the procedure used for rumen contents.

When the steers were receiving either hay cubes or the lower level of concentrate, 20 g of polyethylene glycol (PEG) in 250 ml of water were poured into the rumen

before the morning feed on 5 successive days. Samples of rumen fluid were taken after 1·5, 3, 6, 12 and 24 h to enable rumen fluid volume and outflow to be measured (Hydén, 1961).

On completion of the experiment, the steers were killed and examined.

Chemical analysis. PEG in rumen fluid was measured by the procedure of Hydén (1955). The other methods used have been described by Topps *et al.* (1968).

RESULTS

Growth and behaviour. The body-weight of the steers increased rather irregularly during the experiment. The most pronounced changes usually occurred after a change of diet and probably reflected, in part, a change in the weight of gut contents. During the 10 weeks of experimentation both steers gained approximately 27 kg in body-weight, an increase representing a normal but not a high rate of growth. Both animals had good appetites; the only time any food was left uneaten was when Buster was offered 4 kg of concentrates daily. The steers were frequently seen to be ruminating when given the hay cubes and this and other aspects of their behaviour indicated that they were fully functional ruminants. Rumination appeared to be very infrequent when the steers were given the concentrate diet.

Examination after slaughter confirmed the position of the abomasal cannulas in the lateral wall of the fundus. The rumen papillae of Charlie, 5 weeks after transfer from a concentrate to a hay diet, were flat and unpigmented. Those of Buster, 5 weeks after transfer from hay to concentrates, were very short, round and grey in colour but no clumping had occurred.

Rumen volume and outflow. The rumen fluid volumes of the two steers are shown in Table 3, together with the flow of fluid from the rumen. Results for the hay diet were rather variable and it was thought this was probably due to the difficulty of sampling the relatively dry rumen contents. The nature of the diet did not have any consistent effect on the volume of rumen contents. Buster had a much larger volume of rumen contents when receiving the concentrate ration than when receiving a nearly equal amount of hay, but this may perhaps be attributed to the growth of the animal. On the other hand, diet had a clear effect on the rate of flow of fluid from the rumen; outflow when hay was given was two or three times greater than that with the concentrate diet.

Chromium recovery. The amounts of chromium sesquioxide found in the 24 h samples of digesta and the average of that found in the incomplete daily collections of faeces are given in Table 4. These results have been used to calculate the flows of digesta and outputs of faeces containing the quantity of chromium given daily into the rumen. These values are also shown in Table 4. The two measurements of digesta flow made on each animal for each diet agreed well with each other, except that made when Buster was given 2·7 kg concentrate daily.

pH of the abomasal digesta. These values are shown in Table 5. Differences between diets appeared to be negligible, but the diurnal variation in pH was greater with the concentrate diet than with the hay cubes.

Amounts of various constituents passing through the abomasum and excreted in the

faeces. The amounts of dry matter, cellulose, starch, nitrogen and energy consumed, passing through the abomasum and excreted in the faeces are given in Table 6. The values are derived from flow rates and faecal outputs which were calculated to give 100% recovery of chromium. Values for dry matter, starch and cellulose are shown diagrammatically in Fig. 1.

Table 3. *Rumen fluid volume and outflow in two young steers receiving two diets in two periods*

(Each value is the mean with standard deviation of five determinations made on successive days)

Period	Diet	Steer	Body-weight (kg)	Food intake (kg/24 h)	Rumen fluid volume (l.)	Outflow (% of rumen volume/h)
1	Concentrate	Charlie	110	2·0	10·0 ± 0·39	5·1 ± 0·15
	Hay	Buster	130	2·6	10·1 ± 1·91	18·6 ± 3·27
2	Concentrate	Buster	144	2·7	17·7 ± 1·06	6·1 ± 0·67
	Hay	Charlie	130	3·5	13·0 ± 3·12	10·1 ± 1·04

Table 4. *Amounts of digesta and faeces collected, of chromium sesquioxide recovered, and of calculated flows of digesta and outputs of faeces equivalent to* 100% *recovery of chromium sesquioxide*

		Digesta			Faeces		
Steer	Diet (kg/24 h)	Sample weight (kg/24 h)	Cr_2O_3 recovered (g/24 h)	Calculated flow (kg/24 h)	Sample weight (kg/24 h)	Cr_2O_3 recovered (g/24 h)	Calculated output (kg/24 h)
	Concentrate:						
Charlie	2·0	1·028	0·325	17·6	0·888	3·63	1·36
		1·000	0·367	15·1	0·940	4·49	1·16
	3·0	1·000	0·240	23·1	1·708	4·88	1·94
Buster	2·7	1·074	0·210	28·4	1·485	3·48	2·37
		0·993	0·261	21·2	1·448	4·20	1·91
	3·5	1·004	0·180	30·9	2·424	6·44	2·09
	Hay:						
Charlie	3·5	0·947	0·240	21·9	5·364	4·79	6·22
		0·986	0·232	23·6	5·364	5·51	5·40
Buster	2·6	1·089	0·277	21·8	4·315	4·48	5·35
		1·000	0·242	22·9	4·235	5·83	4·03

Table 5. *Mean values and standard deviations for pH of abomasal digesta collected over 24 h periods from two young steers receiving three diets*

Diet	Charlie	Buster
Concentrate (lower intake)	1·96 ± 0·27	1·94 ± 0·25
Concentrate (higher intake)	2·19 ± 0·62	1·78 ± 0·36
Hay	1·74 ± 0·18	1·95 ± 0·21

About 60–80% of the digestible dry matter and digestible energy of both diets had disappeared from the alimentary tract before the digesta reached the fundus of the abomasum. Corresponding values for the digestion of cellulose could not be deduced owing to inconsistencies in the flow of cellulose through the abomasum. However, it

Table 6. *Amounts of dry matter, cellulose, starch, nitrogen (g/24 h) and energy (kcal/24 h) eaten, flowing through the abomasum and excreted in the faeces in two young steers receiving several diets*

(Values are based on flow rates adjusted to give 100% recovery of chromium sesquioxide. Abomasal contents were sampled for two 24 h periods except on the higher intake of concentrate)

Steer	Diet* (kg/24 h)	Food	Abomasum	Faeces	Food	Abomasum	Faeces
		Dry matter			Cellulose		
Charlie	2·0 C	1690	706 870	319	84	49 75	78
	3·0 C	2535	1168	432	125	120	92
Buster	2·7 C	2350	1272 1006	391	125	157 139	73
	3·5 C	3045	1712	428	162	330	81
Charlie	3·5 H	3194	1627 1720	1319	941	338 532	348
Buster	2·6 H	2340	1498 1138	882	560	272 215	229
		Starch A†			Starch E‡		
Charlie	2·0 C	892	48 77	9	921	38 62	5
	3·0 C	1338	76	16	1382	65	8
Buster	2·7 C	1247	66 57	18	1321	62 45	7
	3·5 C	1616	69	17	1713	77	9
Charlie	3·5 H	230	38 36	19	142	41 46	26
Buster	2·6 H	183	50 33	16	114	51 29	15
		Nitrogen			Energy		
Charlie	2·0 C	53	48 46	ND	7166	2817 3627	1332
	3·0 C	80	69	ND	10748	4958	1867
Buster	2·7 C	71	68 47	ND	10192	5367 4302	1697
	3·5 C	92	67	ND	13206	7584	1894
Charlie	3·5 H	53	55 61	ND	14421	7195 7494	5962
Buster	2·6 H	50	52 54	ND	10539	6537 4942	3967

* C, concentrate diet; H, hay diet.
† determined by the anthrone method (Clegg, 1956).
‡ Determined by an enzymic method (MacRae & Armstrong, 1966).
ND, not determined owing to contamination of faeces with urine.

was apparent that about 60% of the cellulose in the hay cubes was digested, very largely in the rumen. Cellulolysis appeared to be depressed when the steers were given the concentrate diet.

The amount of starch flowing through the abomasum was small and the quantity measured differed very little between diets. On the concentrate diet the amount of starch reaching the fundus of the abomasum was equivalent to only about 5% of that in the diet. Increasing the amount of concentrate given had little effect on the amount of starch flowing through the abomasum.

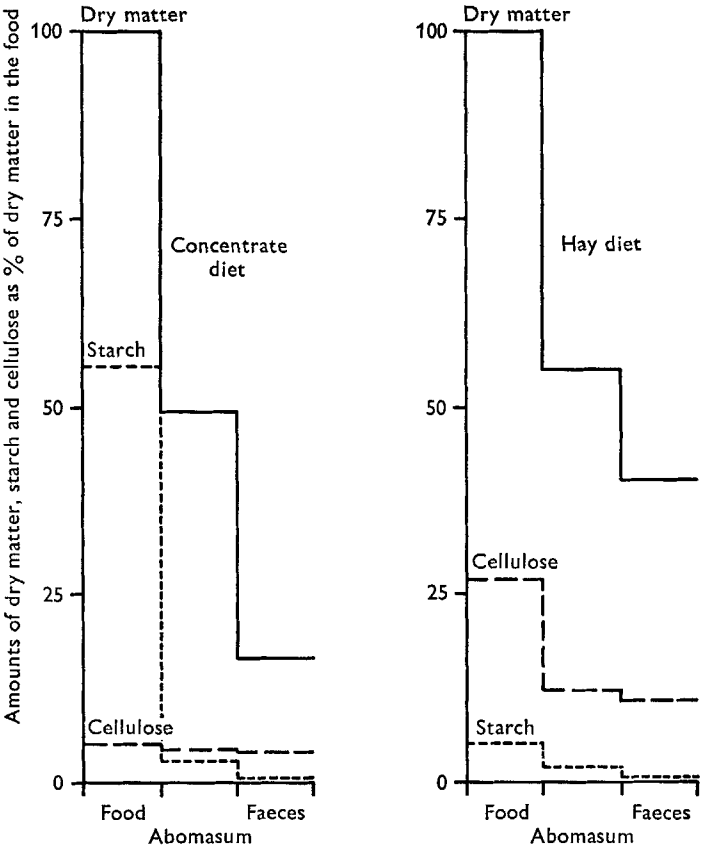

Fig. 1. Mean amounts of dry matter, starch and cellulose in the food, abomasal digesta and faeces of two young steers. In order to compare varying food intakes, the amounts are shown as percentages of the dry matter in the food eaten.

The amount of nitrogen flowing through the abomasum was about 18% less than the amount eaten when concentrates were given but about 8% greater when hay was given. No nitrogen determinations were made on the faeces because these were contaminated with urine.

Blood glucose concentrations and volatile fatty acid content of rumen and abomasal liquor. Table 7 gives the concentrations of glucose in the plasma and the concentrations and proportions of VFA in the rumen and abomasum before and 2 h after feeding. In

general, glucose levels in the plasma were a little higher on the concentrate diet than on the hay cubes, though this trend was not statistically significant, and did not vary with time of sampling.

With the concentrate diet, total concentrations of VFA in the rumen were lower than those obtained with the hay cubes before feeding, but appreciably higher 2 h later. The large increase in concentration of VFA found after giving the concentrates indicates a rapid fermentation of this diet. The proportion of acetate in rumen liquor was considerably less, whilst that of propionate was correspondingly more, when the steers were given concentrates than when they were given hay cubes. This difference became more pronounced when the intake of concentrate was increased. A similar

Table 7. *Mean values of plasma glucose concentrations and of concentrations and molar proportions of volatile fatty acids (VFA) in the rumen and abomasum of two young steers receiving three diets*

	Concentrate (lower intake)		Concentrate (higher intake)		Hay	
	Before feeding*	After feeding†	Before feeding*	After feeding†	Before feeding*	After feeding†
Plasma glucose (mg/100 ml)	96	90	106	86	83	82
Rumen total VFA (m-equiv./l.)	55·5	186·6	62·6	184·1	83·8	132·0
Acetic acid (%)	47·9	50·7	37·2	40·6	62·0	59·2
Propionic acid (%)	29·4	35·0	42·0	45·2	21·5	22·0
Butyric and higher acids (%)	22·7	14·3	20·8	14·2	16·5	18·8
Abomasum total VFA (m-equiv./l.)	7·5	10·8	8·6	10·6	10·3	11·1
Acetic acid (%)	54·4	54·8	41·1	44·8	64·7	64·8
Propionic acid (%)	28·6	29·8	36·7	44·8	23·0	23·8
Butyric and higher acids (%)	17·0	15·4	22·2	10·4	12·3	11·4

* Fed at 09.00 h. † 2 h after feeding.

difference between diets was observed in the molar proportions of acids present in the abomasum but to a lesser extent than that found in the rumen. Total concentrations of VFA in the abomasal digesta were only about 10% of those in the rumen contents and they showed only small variations between diets and between times of sampling.

DISCUSSION

The calculation of flow rates by the method adopted, i.e. to give 100% recovery of chromium, depends on the assumptions that the chromium can be recovered fully from the faeces, and that concentrations of chromium and other constituents of the digesta do not vary with the rate of flow. The validity of these assumptions could not be tested in this experiment, but previous work indicates their reliability. The assumption that the full dose of chromium administered can be recovered in the faeces probably introduces little error, for in previous experiments in this laboratory the fraction of the administered dose found in the faeces of sheep has varied from 102% (Bruce, Goodall, Kay, Phillipson & Vowles, 1966) to 93% (Topps *et al.* 1968). In addition, in the experiment of Bruce *et al.* (1966) it was found that the concentrations

of chromium and of other constituents in the digesta showed no tendency to vary with rate of flow except when the flow was exceptionally fast or slow. The technique used by Topps *et al.* (1968), whereby abomasal contents of sheep were sampled at hourly intervals, gave results which agreed well with those obtained using 24 h collections of digesta from sheep fitted with re-entrant duodenal cannulas. It is reasonable to assume therefore that the same technique used on young cattle is likely to give reliable results for the flow of digesta through the abomasum.

In general, the results shown in Table 6 are sufficiently consistent to support this last assumption. Calculation of the abomasal flow of cellulose gave impossible results for four of the six experiments in which concentrates were given, in that the abomasal flow appeared considerably greater than the amounts eaten or excreted. These anomalies may reflect difficulties in obtaining representative samples from the abomasum, for there was some indication of stratification of fibrous material, and also the difficulty of analysing samples containing very little cellulose.

Even if appreciable errors had occurred as a result of the method used to obtain flow rates, the general conclusion that only a small amount of dietary starch escaped rumen fermentation would still hold. The marked increase in concentration of VFA in the rumen after feeding, together with the lack of an appreciable rise in plasma glucose, may be regarded as evidence supporting this result. The difference between diets in the outflow of rumen fluid, which was much lower with the concentrate diet, suggests that starch is not flushed rapidly through the rumen. Increasing the amount of concentrate offered to the steers produced only a small increase in the amount of starch flowing through the abomasum. The results show, therefore, that young steers, like sheep, digest most of the starch contained in a diet rich in barley in their fore-stomachs (reticulo-rumen and omasum). The disagreement between these results and those of Karr *et al.* (1966) can only be due to differences in either the cereal component of the diet or experimental technique or to both of these factors.

Little information is available in the literature on levels and molar proportions of VFA found in abomasal liquor. Our results indicate that, as a result of absorption, concentrations of total VFA in the abomasum are only a small fraction of those in the rumen and that differences in concentration due either to diets or to times of sampling are small. If a comparison is made between molar proportions of acids in the rumen and abomasum, it appears that acetate tended to be a little higher whilst propionate and higher acids were a little lower in the abomasum, which may indicate a preferential absorption of acids other than acetic.

From the results of the work with sheep (Topps *et al.* 1968) and those presented above it is possible to make some assessment of the relative importance of rumen propionate and intestinal starch as sources of glucose for the ruminant. Various assumptions are made in drawing up this comparison so it must be emphasized that the values given are very approximate. For sheep given 650 g concentrate daily, supplying about 1950 kcal digestible energy, approximately 1400 kcal energy disappeared in the stomach (reticulo-rumen, omasum and abomasum). Assuming that 1200 kcal of this quantity were absorbed as VFA and that the proportion of propionate absorbed on a calorie basis was the same as that in the mixture of acids in the rumen (about 30%

of total), propionate contributed about 350 kcal energy per day. Up to 35 g starch were found to pass to the intestine of the sheep, which would have contributed 150 kcal energy at the most. When the sheep were given 850 g hay cubes daily a similar amount of energy disappeared in the rumen. If the same assumptions are made as those used for the concentrate diet, but in this instance with the molar proportion of propionate taken to be 22%, propionate contributed about 300 kcal daily. The amount of intestinal starch was approximately 13 g or less which would have provided about 50 kcal daily.

When the two young steers were given the lower level of concentrate an energy disappearance of 3900–5300 kcal/day was recorded between the mouth and abomasum. Assuming that 85% of this energy was absorbed and that rumen propionate was 32% of total VFA, the amount of energy obtained from propionate would have been about 1300–1800 kcal. On this diet up to 77 g starch flowed daily through the abomasum. This quantity would have contributed 323 kcal. With the higher intake of concentrate 5600–5800 kcal energy disappeared from the forestomach (reticulo-rumen and omasum) daily. Assuming that 4700 kcal of this energy was absorbed and that rumen propionate was 40% of total VFA, approximately 1900 kcal energy would have been contributed by propionate. Up to 77 g starch, equivalent to 323 kcal energy, was found to pass through the abomasum on this diet also. Similar calculations for the hay diet indicated that rumen propionate contributed 1000–1500 kcal energy daily, whilst the energy from intestinal starch would amount to only 214 kcal at the most.

Even when allowance is made for the rough and ready nature of these calculations it is apparent that with both diets propionate formed in the rumen is a much more important potential source of glucose than starch hydrolysed in the small intestine.

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