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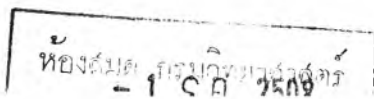
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The effect of silage made from grass at different stages of maturity on the yield and composition of milk

By J. C. MURDOCH

National Institute for Research in Dairying, Shinfield, Reading

(Received 12 March 1965)

SUMMARY. In cross-over experiments it has been established that milk yield increased and the fat and solids-not-fat (SNF) contents of the milk decreased when cows were given approximately 15 lb dry matter/day of early-cut silage compared with the values obtained by giving the same amount of silage made from herbage cut at a later stage of maturity.

Increasing the proportion of concentrates to silage in the cow's diet so that the milk yield remained unchanged increased the SNF content of the milk but had no effect on the fat content.

Supplementing early-cut silage with 5 lb hay/day increased the fat content of the milk, but had no effect on either milk yield or the SNF content of the milk.

Compared with a silage to which molasses had been added, untreated silage decreased milk yield, and increased the fat content without affecting the SNF content of the milk.

The importance of stage of maturity in determining the nutritive value of grass and grass products has been known for many years. Changes in the chemical composition of grass with advancing maturity were noted by Wilson in 1889, and later experiments confirmed that there is a decrease in the crude protein and an increase in the crude fibre and lignin content of grass as it becomes more mature (Fagan, 1928; Waite & Sastry, 1949; Homb, 1952; Kivimae, 1959). These changes in the chemical composition of grass appear to be due to changes in the leaf/stem ratio as the plant becomes more mature (Fagan, 1928; Waite & Sastry, 1949). Experimental results are also available which demonstrate that the digestibility of the dry matter and organic matter in grass declines with increasing maturity (Homb, 1952; Kivimae, 1959; Reid *et al.* 1959; Lloyd, Jeffers, Donefer & Crampton, 1961; Minson, Harris, Raymond & Milford, 1964). It has also been shown that the digestible, metabolizable and net energy of grass is negatively correlated with the maturity of grass (Armstrong, 1960; Lloyd *et al.* 1961). The digestible energy of grass and of the silage made from it have been shown to be of a similar order, but the digestible dry matter is lower in the silage than in the corresponding grass when the dry matter content of the silage is determined by oven-drying (Harris & Raymond, 1963). Nevertheless, the trend of decreasing digestibility of the dry matter of the silage with increasing maturity of the grass when harvested was evident, although less pronounced than that of the fresh grass. This effect of maturity of the herbage on the digestibility of the

silage and hay made from it has been demonstrated on many occasions (Kellner, 1915; Newlander, Ellenberger, Camburn & Jones, 1938; Watson, 1948; Harris & Raymond, 1963).

Milk production from cows given silage or hay made from grass cut at early and late stages of maturity has been determined in several experiments, and it has been shown that higher milk yields are obtained when the grass is conserved at an early stage of maturity (Trimberger *et al.* 1955; Slack, Kennedy, Turk, Reid & Trimberger, 1960; Castle, Drysdale & Watson, 1962; Murdoch & Rook, 1963). It has also been shown that the voluntary intake of a conserved food is positively correlated with its digestibility (Reid *et al.* 1959; Slack *et al.* 1960; Blaxter, Wainman & Wilson, 1961), and in some of the experiments noted above the higher milk production obtained from the early-cut forage was due to the combined effect of increased intake and the high nutritive value of the forage.

Changes in the composition of the milk obtained from cows given conserved food made from early- and late-cut herbage have also been observed, the fat and SNF content of the milk being lower when the cows were given early-cut silage (Murdoch & Rook, 1963). The experiments reported here were designed to confirm these findings and also to investigate possible methods of maintaining the fat and SNF contents of the milk when cows are given early-cut silage.

METHODS AND RESULTS

Friesian cows were used in all 4 experiments, and all the experiments began after the cows had reached peak yield. The silage for the experiments was made from unwilted herbage which was cut with a flail forage harvester and, unless otherwise stated, 2 gal molasses were applied to each ton of herbage before it was ensiled. In any one experiment, all conserved products were made from herbage from the same field which had received uniform treatment before the grass was harvested. The hay for expts. 1 and 4 was field-cured. All foods were given to the cows twice daily.

The digestibility values were calculated from the data obtained in experiments with wether sheep, each value being a mean of results obtained from 3 or 6 sheep.

The experimental period in all trials was 3 weeks. Milk yields were recorded daily, and data on milk composition were obtained from two 2-day composite milk samples taken during the final week of each experimental period.

Expt. 1. There were 2 objectives, the 1st being to confirm the results obtained in a previous experiment (Murdoch & Rook, 1963), in which the effect of silage and hay made from herbage at different stages of maturity on milk yield and composition was determined. The 2nd objective was to investigate the effect of changes in silage quality, due to differences in fermentation, on milk yield and composition.

Silages were made from herbage cut on 10 May, 25 May and 14 June, and hay was made from grass cut on 14 June. The standard amount of molasses was added to the 3 silages, but an additional silage was made on 10 May which received no molasses. All the products were made from a meadow fescue/timothy sward.

The 5 conserved products were tested in an experiment in the form of a 5 × 5 Latin square. It was intended that the cows should consume the same amount of dry matter of each of the silages and hay, but due to variations in the dry matter content

of the silages and refusals of food by the animals small differences in the intake of dry matter occurred (Table 2). The silage and hay were supplemented with the same amount of concentrates, the mean intake being 13.7 lb/day of a mixture containing 4 parts barley and 1 part decorticated groundnut cake. The concentrate ration was such that even with the best silage (cut 10 May) the nutrient intake was slightly lower than the animals' requirements for milk production, the amounts given daily being calculated according to milk yield at the beginning of the experiment and reduced by $\frac{1}{2}$ lb at weekly intervals throughout the experiment.

The data on the chemical composition of the foods show the normal decline in crude protein and increase in crude fibre content with increasing maturity of the herbage at cutting (Table 1). It was possible to determine the dry matter digestibility of only 3 of the conserved products but the decrease in digestibility with increasing maturity of the grass is evident from the data available.

Table 1. *Chemical composition and digestibility of foods (expt. 1)*

	pH value	Dry matter, %	Crude protein, Ether N-free Crude extract extract fibre g/100 g dry matter				Ash	Dry matter digestibility, %
Molassed silage, cut 10 May	4.18	19.7	20.6	4.7	36.4	27.0	11.3	79.1
Untreated silage, cut 10 May	4.77	17.7	22.0	4.9	31.9	28.0	13.3	—
Silage, cut 25 May	4.16	21.1	16.3	3.0	39.5	30.1	11.1	75.8
Silage, cut 14 June	5.10	32.9	12.4	2.0	40.4	35.8	9.4	—
Hay, cut 14 June	—	81.0	9.3	1.4	49.7	32.8	6.8	69.7
Concentrates	—	85.0	21.5	1.6	69.3	4.1	3.5	—

Table 2. *Effect of giving silage made from grass of different maturities on the yield and composition of cow's milk (expt. 1)*

	Molassed silage, cut 10 May	Untreated silage, cut 10 May	Silage, cut 25 May	Silage, cut 14 June	Hay, cut 14 June	S.E. of means
	Silage and hay intake, lb dry matter/day	15.1	14.1	14.6	13.5	
Milk yield, lb/day	32.3	30.1	31.1	27.2	27.7	± 0.65
F _{et} , %	3.39	3.63	3.76	4.12	3.94	± 0.08
SNF, %	8.49	8.49	8.60	8.71	8.78	± 0.08
F _{et} , lb/day	1.10	1.08	1.17	1.12	1.09	± 0.03
SNF, lb/day	2.75	2.55	2.68	2.37	2.43	± 0.06

No significant differences in the yield or composition of the milk were observed when the silage and hay made on 14 June were given to the cows (Table 2). Milk yield decreased as silage made from grass of increasing maturity was given to the cows, the differences being statistically significant ($P < 0.05$) except for that between the silages made on 10 and 25 May. The fat and SNF content of the milk increased with increasing maturity of the herbage at the time of cutting, the differences between all 3 treatments being statistically significant for the fat content of the milk ($P < 0.05$). A similar trend to that of milk yield was exhibited by the yield of SNF, but no significant treatment differences were observed in the yield of milk fat.

The untreated silage made on 10 May had a higher pH value than that of the molassed silage made on the same date (Table 1). When the molassed silage was given to the cows, a significantly higher milk yield and lower fat content of the milk was obtained than when the untreated silage was given, but the SNF content of the milk was unaffected. Again, there was no significant difference in the yield of milk fat but the yield of SNF was significantly lower ($P < 0.05$) when the untreated silage was given to the cows.

Expt. 2. With a single cross-over design using 10 cows, an untreated and a molassed silage were again compared. The 2 silages were made from a meadow fescue/timothy sward during the period 27 April–1 May, one silage being made with molasses the other ensiled untreated. The same quantity of dry matter of each silage was offered to the cows (Table 4), and the silages were supplemented with the same quantity of concentrates, this being a mixture of 3 parts barley, 1 part decorticated groundnut cake and 1 part bran. The mean intake of concentrates was 14.5 lb/day, the ration being calculated according to the milk yield of the cows at the beginning of the experiment and reduced by $\frac{1}{2}$ lb at weekly intervals throughout the experiment.

The untreated silage had a lower crude protein and a higher pH value and crude fibre content than the molassed silage, and the digestibility of the dry matter was higher for the molassed silage (Table 3). The results for milk production agree with those obtained in *expt. 1*, milk yield being significantly lower and the fat content of the milk higher ($P < 0.05$) when the cows received the untreated silage than when they were given the molassed silage (Table 4). There were no significant treatment differences in the SNF percentage of the milk or yield of milk fat, but again the yield of SNF was significantly lower when the untreated silage was given to the cows.

Table 3. *Chemical composition and digestibility of foods (expt. 2)*

	pH value	Dry matter, %	Crude protein	Ether extract	N-free extract	Crude fibre	Ash	Dry matter digestibility, %
			g/100 g dry matter					
Molassed silage	4.38	19.2	19.5	4.8	30.9	32.0	12.8	83.6
Untreated silage	5.17	18.1	18.4	4.5	28.1	34.3	14.7	77.7
Concentrates	—	87.1	22.5	2.2	65.1	5.9	4.3	—

Table 4. *Effect of giving molassed or untreated silage on the yield and composition of cow's milk (expt. 2)*

	Molassed silage	Untreated silage	S.E. of means
Silage intake, lb dry matter/day	13.3	13.9	—
Milk yield, lb/day	31.6	30.3	± 0.38
Fat, %	3.82	3.97	± 0.05
SNF, %	8.66	8.67	± 0.08
Fat, lb/day	1.19	1.20	± 0.03
SNF, lb/day	2.74	2.62	± 0.04

Expt. 3. Since the type of fermentation in silage had no effect on the SNF content of the milk, it was thought that the ratio of nutrients obtained from the silage and concentrates might be the explanation of the changes in milk composition due to the

stage of maturity of herbage at cutting. As the same quantities of dry matter of silage and concentrates were given to the cows, there was no difference in the ratio of silage to concentrates irrespective of the type of silage given to the cows. However, when digestible dry matter intake was considered it was clear that a greater proportion of nutrients was obtained from silage when it was made from early-cut herbage than when it was made from late-cut herbage. The object of this experiment was, therefore, to investigate the effect of varying the proportion of concentrates to silage on the yield and composition of milk.

The 2 silages used were made from S. 22 ryegrass cut on 9–11 May and 10–11 June. The experiment was in the form of three 4×4 Latin squares. The silages were supplemented with a concentrate mixture consisting of 3 parts barley, 1 part flaked maize and 1 part decorticated groundnut cake. The chemical composition of the foods is given in Table 5. Two of the treatments (A and B) compared were similar to those in expt. 1, the same quantity of dry matter of the early- and late-cut silage supplemented by the same quantity of concentrates being given to the cows. The remaining 2 treatments (C and D) consisted of decreasing the ratio of silage to concentrates with early-cut silage, and increasing that for the late-cut silage, the mean intakes of silage and concentrates being given in Table 6.

Table 5. *Chemical composition of foods (expt. 3)*

	pH value	Dry matter, %	Crude protein	Ether extract	N-free extract	Crude fibre	Ash
			g/100 g dry matter				
Silage, cut 9–11 May	4.42	18.6	20.2	3.6	36.3	28.6	11.3
Silage, cut 10–11 June	4.71	27.4	12.2	2.0	46.2	29.9	9.7
Concentrates	—	85.6	19.9	1.4	72.1	3.6	3.0

Table 6. *Effect of giving early- and late-cut silage with different quantities of concentrates on the yield and composition of cow's milk (expt. 3)*

	Early-cut silage, A	Late-cut silage, B	Early-cut silage, C	Late-cut silage, D	S.E. of means
Silage intake, lb dry matter/day	14.8	14.5	10.4	19.1	—
Concentrate intake, lb dry matter/day	11.0	11.0	14.4	8.4	—
Milk yield, lb/day	32.8	30.0	33.2	29.6	± 0.37
Fat, %	3.81	4.00	3.82	3.97	± 0.03
SNF, %	8.57	8.70	8.72	8.60	± 0.02
Fat, lb/day	1.25	1.20	1.27	1.17	± 0.02
SNF, lb/day	2.81	2.61	2.89	2.54	± 0.03

The results obtained when early- and late-cut silage were compared (Table 6, treatments A and B) were similar to those obtained in expt. 1. Compared with late-cut silage, the early-cut silage when given to the cows increased milk yield but decreased the fat and SNF contents of the milk significantly ($P < 0.05$). The yield of SNF was significantly greater with the early-cut silage than with the late-cut silage ($P < 0.05$), but no significant treatment difference was observed in the yield of milk fat. When the quantity of early-cut silage given to the cows was decreased

and concentrates increased (treatment C) the same milk yield was obtained as with treatment A but there was a significant increase in the SNF content of the milk, the reverse trend being observed when the amount of late-cut silage relative to concentrates was increased (treatments B and D). There was no significant difference in yield of milk fat or SNF between treatments A and C, and B and D.

Expt. 4. This experiment was designed to investigate whether by giving a small amount of supplementary hay with early-cut silage the fat content of the milk could be maintained. The experiment had a single cross-over design with 10 cows. The silage was made from a meadow fescue/timothy sward which was cut during the period 11–13 May.

The treatments compared were rations of 80 lb silage/day and 80 lb silage plus 5 lb hay/day. There were no refusals of hay, but some silage was refused by the cows and the mean intakes of silage on both treatments are given in Table 8. Both diets were supplemented by a mean of 8.8 lb concentrates/day, this ration being calculated according to milk yield at the beginning of the experiment and reduced by 1 lb at the beginning of the 2nd experimental period. The concentrates consisted of a mixture of 3 parts barley, 1 part decorticated groundnut cake and 1 part bran.

Table 7. *Chemical composition and digestibility of foods (expt. 4)*

	pH value	Dry matter, %	Crude protein	Ether extract	N-free extract	Crude fibre	Ash	Dry matter digesti- bility, %
Silage	4.32	20.6	16.8	3.4	35.8	26.9	17.1	78.1
Hay	—	87.4	7.5	1.5	48.6	35.1	7.3	—
Concentrates	—	87.6	21.4	2.2	64.9	6.7	4.8	—

Table 8. *Effect of giving hay with silage on the yield and composition of cow's milk (expt. 4)*

	Silage	Silage and hay	S.E. of means
Silage intake, lb dry matter/day	16.0	15.9	—
Hay intake, lb dry matter/day	—	4.4	—
Milk yield, lb/day	20.6	20.6	± 0.83
Fat, %	3.51	3.67	± 0.06
SNF, %	8.65	8.75	± 0.06
Fat, lb/day	0.70	0.74	± 0.02
SNF, lb/day	1.77	1.79	± 0.03

The chemical composition and dry matter digestibility of the silage are similar to those found in the early-cut silage in earlier trials (Table 7). No significant treatment differences were observed in milk yield, in the SNF content of the milk or in the yield of milk fat and SNF (Table 8). There was, however, a significant increase in the fat content of the milk ($P < 0.05$) when the cows were given hay in addition to silage and concentrates.

DISCUSSION

Silage and hay made from the same crop at the same mature stage of growth were compared in one trial (expt. 1) and no statistically significant differences in the yield or composition of the milk were observed when a similar amount of dry matter of

each of the 2 conserved foods, supplemented with the same quantity of concentrates, was given to the cows. It is clear that the nutrient intake from this hay or silage when supplemented with concentrates at the stipulated rate was inadequate for the cows' requirements (Table 2), and that any difference which might have existed between the silage and hay should have been apparent. The results from this experiment are in agreement with those obtained previously (Murdoch & Rook, 1963), and with the conclusions reached by Carter (1960) from a review of results from experiments conducted in America. If, however, one or other of the conserved products had not been conserved efficiently, this would be reflected by a decrease in milk yield, as is shown by the results from the 2 comparisons of untreated and molassed silages (expts. 1 and 2).

Milk yield decreased when silage made from increasingly mature herbage was given to the cows, while the fat and SNF content of the milk increased (expts. 1 and 3). Again these results agree with those reported previously (Murdoch & Rook, 1963). Trimberger *et al.* (1955) found a similar relationship between the maturity of the herbage and milk yield, but observed no changes in the fat content of the milk. In their experiments, however, the intake of silage dry matter was higher when the silage made from less mature herbage was given to the cows, and the intake of both early- and late-cut silage was considerably higher than in the experiments reported here. In agreement with our results Lambourne (1964) observed that the intake of digestible organic matter by goats was positively correlated with milk yield and, also, negatively correlated with the fat content of the milk, the highest intake of digestible organic matter being associated with the most digestible foods. Castle *et al.* (1962) reported an increased milk yield when cows were given early-cut hay than when they were given hay made from late-cut herbage; this was accompanied by a lower fat content in the milk though the decrease was not statistically significant, and no effect on the SNF content of the milk was observed.

As the early-cut silage given to the cows in an earlier trial had a high pH value compared with the later-cut silage (Murdoch & Rook, 1963), a comparison was made of 2 silages made from herbage cut at the same stage of maturity, one being untreated and the other molassed (expts. 1 and 2). This comparison was made, since it was possible that some of the treatment effects in the earlier experiment might be attributable to the difference in the content of fermentation products in the 2 silages. The results obtained in the 2 experiments in which silages with a low and high pH value were compared did not, however, yield any explanation of the earlier results. Similar changes in milk yield and composition were found in both experiments; the silage with a high pH value, when given to the cows, caused a decrease in milk yield and an increase in the fat content of the milk, but no treatment effect was observed on the SNF content of the milk. The dry matter digestibility of the untreated silage was considerably lower than that of the molassed silage (expt. 2), and the reduction in the milk yield when the untreated silage was given to cows was due to the lower nutritive value of this silage. On a theoretical basis, it appears unlikely that the energy supplied by the molasses added to the treated silage would result in a marked increase in its digestibility, and it is probable that the explanation of the lower nutritive value of the untreated silage lies in a greater loss of the more digestible nutrients during fermentation.

It has been demonstrated that when silage supplemented with concentrates is given there is an increase in the proportion of propionic acid found in the cow's rumen (Bath & Rook, 1965), and that intra-ruminal infusions of propionic acid have the specific effect of decreasing the SNF content of cow's milk (Rook & Balch, 1961). In expt. 3 the effect of varying the ratio of silage to concentrates given to the cows was determined, and, although the different ratios had no effect on milk yield or on the fat content of the milk, the SNF content increased when the proportion of concentrates in the ration relative to silage was greater. Logan & Miles (1963) in similar experiments found that increasing the proportion of concentrates to silage resulted in no significant changes in the protein and SNF contents of the milk. The results from the experiment reported here suggest that the low SNF content in the milk incurred by giving the cows early-cut silage can be remedied by increasing the concentrate supplement. This, however, is not a solution that would be favoured in practice since the object in making highly digestible silage is to reduce the amount of concentrate supplementation which will be required. Under farm conditions when silage is given in quantities similar to those given in these experiments, it is likely that the effect of maturity of the herbage at cutting on the SNF content of the milk would be even greater, since normally a greater amount of concentrates would be given with the late-cut silage to maintain milk yield at the same level than would be given with a diet of early-cut silage.

McClymont (1950) has shown that the fat content of the milk falls when cows are offered lush pasture, especially when this diet is supplemented with concentrates. He has also demonstrated that giving coarse roughage to the cows will maintain the fat content of the milk. The results from expt. 4 indicate that a supplement of hay made from mature herbage given with early-cut silage will increase the fat content of the milk by increasing the fibre content of the diet.

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Steam distillation of taints from cream

XI. The use of benzyl mercaptan (^{35}S) in a study of its vapour/liquid equilibrium relationships

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SUMMARY. Solutions of labelled benzyl mercaptan- (^{35}S) in water and cream were subjected to steam distillation in a continuous vaporization equilibrium still, and the concentrations of mercaptan in distillates and residues were obtained by measurement of the radioactivity in toluene extracts.

In the steam distillation from aqueous solution the vapour/liquid equilibrium relationship was not linear. The vapour/liquid equilibrium coefficient increased from 73 to 108 over the range of concentrations 0.01–0.05 ppm. in the liquid fraction at the time of partition.

In the steam distillation from cream containing 30% fat the relationship was linear, with an equilibrium coefficient of 1.35 over the range 0.1–0.6 ppm. in the cream at the time of partition.

The values of the vapour/liquid equilibrium coefficients are of the same order as those reported previously, 105 and 1.30, respectively, for which estimations were made by an absorption method.

The butterfat/water partition coefficient for benzyl mercaptan was found to be 160, which is consistent with the large difference found between the steam volatilities of the substance from water and from cream.

Benzyl mercaptan is the main constituent of the taint formed by heat treatment of cream from cows which have consumed the cruciferous weed, landcress (*Coronopus didymus*) (Forss, 1951).

The vapour/liquid equilibrium coefficient for benzyl mercaptan from water was found by McDowall (1965), using a continuous vaporization equilibrium still, to be 105 over the range of concentrations 1.0–2.0 ppm. in the liquid at the time of partition, and from cream to be 1.30 over the range of concentrations 3.0–30 ppm. in the cream at the time of partition. The concentrations of benzyl mercaptan in aqueous residues and steam distillates were estimated by McDowall by measurement of the absorption at 218 μm in a spectrophotometer. The concentrations in cream were calculated by difference.

The absorption method of estimation has the disadvantages: (a) that the lowest range of concentrations for which the coefficients can be measured is considerably higher than the concentrations of benzyl mercaptan in normal cress-tainted cream; and (b) that the concentration of benzyl mercaptan in cream cannot be measured directly.

It was considered that these disadvantages could be eliminated by the use of radioactively labelled benzyl mercaptan ($C_6H_5CH_2^{35}SH$). For measurement of the radioactivity in the distillate and residue it was necessary to extract the benzyl mercaptan with an organic solvent. In the following investigation toluene was used for the extraction.

EXPERIMENTAL

Efficiency of toluene in the extraction of benzyl mercaptan from water and cream

The following solutions were prepared using non-radioactive benzyl mercaptan:

1. 1% solution of benzyl mercaptan in toluene,
2. 10 ml toluene extract of 10 ml of 1% mercaptan in water,
3. 10 ml toluene extract of 10 ml of 1% mercaptan in cream.

One-ml samples of each toluene solution were analysed in an Aerograph Hy-Fi gas chromatograph fitted with a hydrogen flame ionization detector. The column was 6 ft \times $\frac{1}{8}$ in. stainless steel packed with 20% Apiezon M on 60/80 acid-washed firebrick: column temperature, 125 °C; carrier gas, nitrogen; flow rate, 30 ml/min.

Since the areas under the benzyl mercaptan peaks on all 3 chromatograms were equal, it appeared that the toluene would extract all of the benzyl mercaptan from solution in water and cream.

Measurement of vapour/liquid equilibrium relationships

A stock solution was prepared by dissolving 0.287 g of benzyl mercaptan containing 10 mc of the radioactive benzyl mercaptan (Radiochemical Centre, Amersham, England) in 1435 ml of water.

(i) *From water.* Aqueous solutions containing 0.2–1.0 ppm. of benzyl mercaptan were subjected to steam distillation in the continuous vaporization equilibrium still (McDowall, 1955). To reduce apparent losses of benzyl mercaptan from solution between the reservoir and the steam inlet the solutions were not preheated, but were allowed to come into contact with the steam while still cold. Even then some losses were observed, probably due to the tendency of benzyl mercaptan to adhere to the glass tubing. So that an overall balance of activity could be obtained, therefore, a sample of each solution was tapped off immediately before contact with the steam.

The liquid residue and steam distillate were collected, over a 4-min run, in flasks surrounded by ice. The volumes v_l and v_v , respectively, were measured. The volume of solution which had passed through the still in the 4 min (v_0) was measured by means of the graduated reservoir.

For each distillation 4 aqueous samples were analysed for radioactivity:

- s_0 , initial solution of known concentration;
- s'_0 , sample of s_0 tapped off before contact with steam;
- s_l , liquid residue after steam distillation;
- s_v , steam distillate.

Suitable volumes (10, 5, 2 or 1 ml) of these samples were extracted with 10 ml of scintillation grade toluene, so as to provide a count rate suitable for a liquid scintillation system. One ml samples of each toluene extract were dissolved in 2 ml of

scintillation liquid (NE 213, Nuclear Enterprises (GB) Ltd., Edinburgh) and counted at room temperature in a liquid scintillation system. By adjustment of the count rates, using a factor dependent on the amount of aqueous solution extracted, the concentrations of benzyl mercaptan (c_0, c'_0, c_l, c_v) were obtained in terms of the count rate/ml of each solution s_0, s'_0, s_l, s_v , respectively. An activity balance was calculated for each distillation.

(ii) *From cream.* Creams (30% fat) containing 0.2–0.8 ppm. of benzyl mercaptan were steam-distilled, and samples of distillate and residue were collected and analysed as in section (i).

Since there was no loss of mercaptan from the cream before contact with the steam it was not necessary to tap off the solution s'_0 . Counts were, therefore, made only on samples s_0, s_l, s_v .

Butterfat/water distribution coefficient

Butterfat (50 g) and 50 g aqueous solution of 0.4 ppm. active benzyl mercaptan were held in each of 3 conical separating funnels in water baths at 43, 58 and 74 °C for 30 min. During this time the funnels were shaken frequently. The 2 phases were then separated (McDowall, 1959*a*). The concentration of benzyl mercaptan in the aqueous layer (c_w) was obtained from the count rate of a toluene extract and the concentration in the butterfat (c_f) was calculated by difference. The butterfat/water distribution coefficient (m_k) was derived from the concentrations in the 2 phases at equilibrium.

RESULTS

Vapour/liquid equilibrium relationships

(i) *From water.* Typical results and calculations for a run are shown below:

Concentration of benzyl mercaptan in solution (s_0) to be distilled = 0.6 ppm.

Volume of s_0 steam distilled, $v_0 = 95$ ml.

Volume of residue (s_l) collected, $v_l = 106$ ml.

Volume of distillate (s_v) collected, $v_v = 17$ ml.

Concentrations of benzyl mercaptan in the 4 solutions collected (s_0, s'_0, s_l, s_v):

$$\left. \begin{array}{l} c_0 = 26795 \\ c'_0 = 21252 \\ c_l = 1273 \\ c_v = 112270 \end{array} \right\} \text{counts min}^{-1} \text{ ml}^{-1}.$$

Hence $(c_v/c_l) = 88.2$.

Activity balance:

$$\begin{aligned} \text{total no. of counts into still} &= c'_0 \times v_0 \\ &= 2018940 \end{aligned}$$

$$\begin{aligned} \text{total no. of counts out of still} &= \text{no. in } s_v + \text{no. in } s_l \\ &= (c_v \times v_v) + (c_l \times v_l) \\ &= 2043528 \end{aligned}$$

$$\text{difference} = 24588 \text{ counts}$$

$$\% \text{ difference} = 1.2.$$

The difference in the activity balance did not exceed 5% in any run. This limit was considered to be satisfactory.

The relationship between c_v and c_l for all runs is shown in Fig. 1. The results indicate a rise in the vapour/liquid equilibrium coefficient from 73 to 108, as the concentration in the liquid increased.

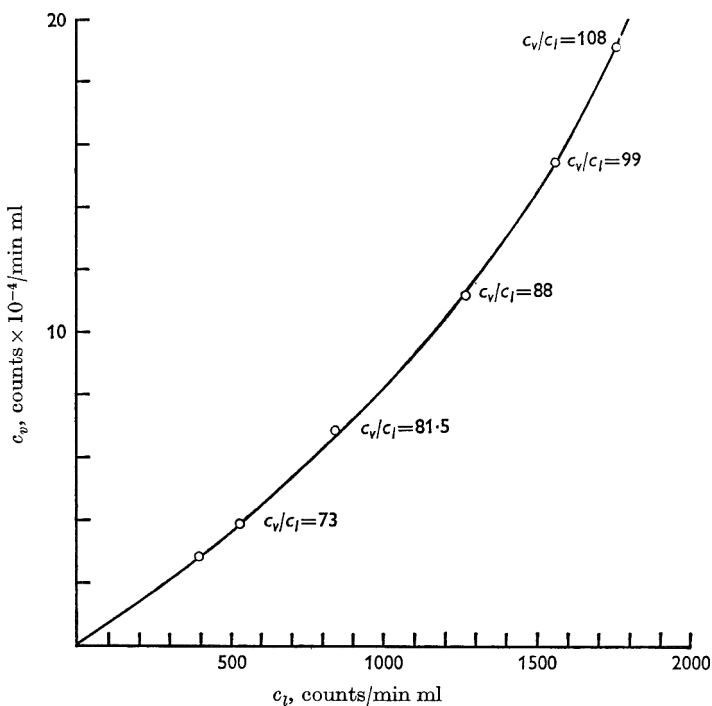


Fig. 1. Vapour/liquid equilibrium relationship for benzyl mercaptan in water.

(ii) *From cream.* The yellow coloration caused by dissolved carotene in the toluene extracts of cream was expected to effect some quenching of the count rate of these solutions. It was necessary to obtain a measure of the magnitude of this quenching.

Fig. 2 relates the concentrations (c_0) in counts $\text{min}^{-1} \text{ml}^{-1}$ of each prepared solution of benzyl mercaptan in water (curve *A*) and in cream (curve *B*) to its known concentration in ppm.

Count rates of the toluene extracts of the cream solutions were, however, obtained 16 days after those of the water solutions. Hence in curve *A'* the count rates of curve *A* have been adjusted to allow for radioactive decay corresponding to this 16-day interval. If there were no quenching caused by the carotene in the toluene extract, curve *B* should coincide with curve *A'*. It is evident, however, from Fig. 2 that some quenching did occur to the extent of a 16% decrease in count rate.

The count rates obtained for c_l have therefore been corrected to compensate for the above loss due to quenching. Values obtained for c_0 were also corrected before activity balances were calculated.

From Fig. 3 over the range of concentrations 0.1–0.6 ppm. in the cream at the time

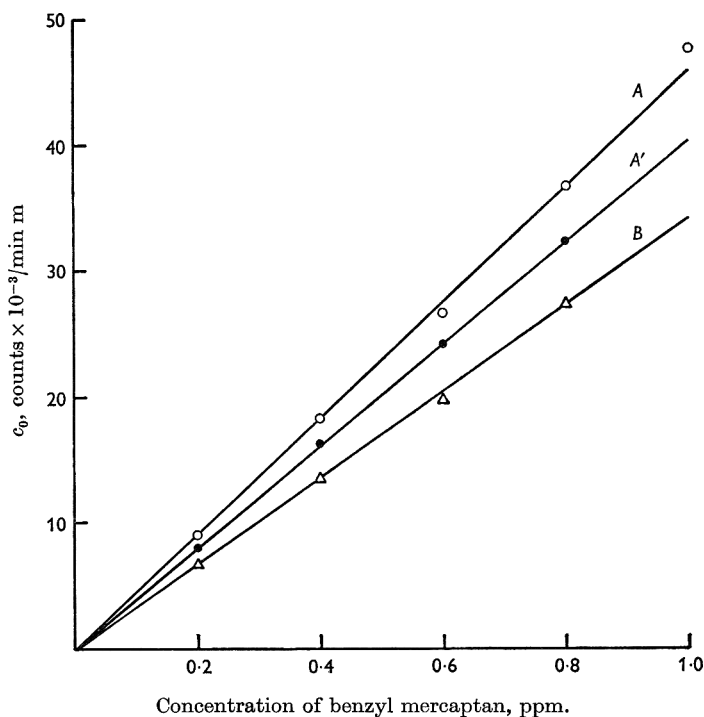


Fig. 2. Relationship between activity and known concentrations of aqueous and cream solutions containing benzyl mercaptan.

of partition the relationship was linear, $c_0/c_1 = 1.35$. Each activity balance agreement was again within the 5% limit.

Butterfat/water distribution coefficient

The results are shown in Table 1.

Table 1. *Effect of temperature on the coefficient of distribution of benzyl mercaptan between butterfat and water*

Temperature, °C	* Count rates/ml			c_f/c_w
	c_0	c_w	c_f	
43	14 626	176	14 450	82
58	14 626	144	14 482	101
74	14 626	115	14 511	126
100	—	—	—	160†

* Count rates/ml of fat/water suspension (c_0), aqueous phase (c_w) and fat phase (c_f).

† By extrapolation.

The relation of partition coefficient to temperature between 43 and 74 °C was linear. The value 160 was obtained by extrapolation on the assumption that the linearity would continue up to 100 °C.

DISCUSSION

The magnitude of the values for vapour/liquid equilibrium coefficients for benzyl mercaptan in water and cream obtained in this investigation are in reasonably good agreement with the values, 105 and 1.30, respectively, found by McDowall (1965) using the absorption method. The decrease in c_v/c_l noted by McDowall at concentrations below 1 ppm. of benzyl mercaptan in water was confirmed. The reason for the curvilinear nature of the equilibrium plot at these low concentrations is not known. The results, however, do extend the findings of McDowall (1965) that benzyl mercaptan can be readily steam-distilled from aqueous solution to very low concentrations of mercaptan.

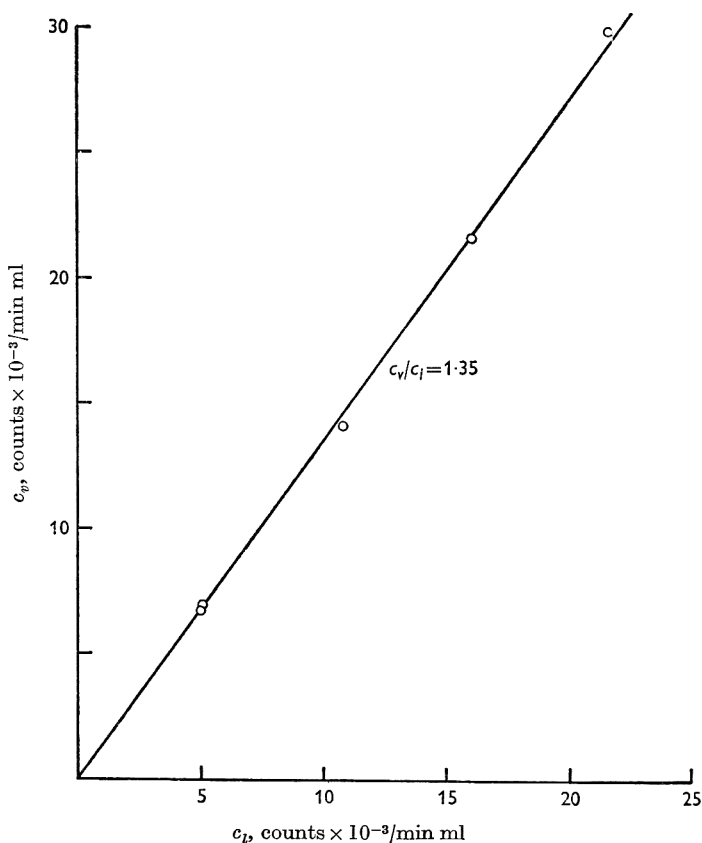


Fig. 3. Vapour/liquid equilibrium relationship for benzyl mercaptan in cream containing 30% fat.

The values of the vapour/liquid equilibrium coefficients for mercaptan over water and cream were related as expected from the formula derived by McDowall (1959*b*), namely

$$m_e = m_s \frac{100}{100 - F(1 - k)},$$

where m_c is the vapour/liquid equilibrium coefficient for a tainting substance in cream,
 m_s is the vapour/liquid equilibrium coefficient for the substance in skim-milk,
 F is the percentage fat content of the cream,
 k is the butterfat/water partition coefficient at 100 °C for the tainting substance.

Thus for an m_c of 1.35 for benzyl mercaptan (Fig. 3) with F at 30 % and k at 160 (Table 1) the calculated value of m_s was 66 compared with the experimental value of 73. In this comparison the assumption has been made that the partition coefficient between butterfat and skim-milk is the same as that found for butterfat and water.

As found by McDowall (1965), using the absorption method, the steam volatility of benzyl mercaptan from cream is so low, because of the relatively high solubility of the substance in fat, that complete removal of it by steam distillation in cream treatment equipment is not feasible in normal butter factory practice.

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The effect of incomplete milking or of an extended milking interval on the yield and composition of cow's milk

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SUMMARY. The effect of incomplete milking or of an extended milking interval on the yield and composition of cow's milk has been investigated. At the 1st milking after either treatment, the yield of milk was augmented by a carry-over of milk but at the 2nd milking the yield was invariably depressed and then increased until the original yield, or slightly less, was recovered within 5 days. The concentration of lactose and potassium decreased and of sodium, chloride, whey proteins and casein increased during the period of the treatment, and on the resumption of normal milking the original composition was rapidly recovered. The changes in the composition of fat were less clearly defined because of residual milk effects but over the period of the treatment and the succeeding 6 milkings the effect was invariably to increase fat percentage. The differing effects on composition resulted in a more marked effect on the yields of lactose, potassium and casein than on those of sodium, chloride or the whey proteins throughout the treatment and recovery periods. When milk was removed in portions after an extended milking interval there were decreases in the concentrations of lactose and potassium and increases in those of sodium and chloride throughout normal milking. When the residual milk was obtained after an injection of oxytocin the composition of the portions of milk resembled that of the first portions of milk removed from the udder. The possible effects of the treatments on the secretory cells and the permeability of the udder tissue are discussed.

If over a period of days the removal of milk from the udder is incomplete, there is a reduction in the rate at which milk accumulates within the udder. The effect varies from cow to cow and increases with the degree and duration of incomplete milking (Dodd & Clough, 1962; Schmidt, Guthrie & Guest, 1964). On the resumption of normal milking, the original yield is progressively recovered but the recovery time is greatest following a complete suspension of milking for several normal milking intervals (Elliott, Dodd & Brumby, 1960).

At the first of a series of incomplete milkings (Dodd & Clough, 1962) or after a single extended milking interval of up to 24 h (Bailey, Clough & Dodd, 1955), the milk obtained has a low fat content because of the retention within the udder of an unusually high proportion of the milk fat. If, however, the effect of either treatment is measured over several milkings it is usually found that the fat content of the milk obtained over the whole period is unaffected (Johansson, 1949; Dodd & Clough, 1962)

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or only slightly changed. Where changes in the fat content are detected there is usually an increase (Bailey *et al.* 1955; Elliott *et al.* 1960) but Bailey, Clough, Dodd, Foot & Rowland (1953) observed a decrease in fat content when the incomplete milking continued for 6 weeks. There are, however, characteristic changes with length of milking interval in the concentrations of other milk constituents, more particularly a decrease in lactose content and an increase in chloride and, to a lesser extent, in protein contents, and these effects persist for some time after the resumption of normal milking (Hansson, Dassat & Claesson, 1954).

Garrison & Turner (1936) have suggested that an increase in pressure within the udder as milk accumulates impairs the activity of the secretory cells: the rate of excretion of milk from the alveolar cells is reduced, the permeability of the cells to certain constituents of the blood, including chloride, is increased and, to maintain osmotic equilibrium of milk with blood, lactose synthesis is depressed. Johansson & Claesson (1957), however, consider that the changes in milk composition with increasing length of milking interval are due to an increased resorption of milk as the pressure within the udder rises. Lactose, it is suggested, is easily resorbed and its concentration in milk therefore decreases and the concentrations of proteins which are less readily resorbed and of chloride consequently increase.

The present experiments were designed to give further information on the effects of the suspension of milking or of the incomplete removal of milk from the udder on milk composition and on the secretion of various milk constituents, and to provide a basis for a more detailed consideration of the origin of the effects.

EXPERIMENTAL

Experimental procedure

Two series of experiments were done. In the 1st (expts. 1–4), with cows milked at 12-h intervals after an initial control period of 4 days, comparisons were made between quarters of the udder of a single cow of the effects on milk yield and composition of: (a) normal milking, (b) removal of only 50% of the expected yield at 4 successive milkings, (c) removal of only 50% of the expected yield at 8 successive milkings and (d) the suspension of milking for 4 successive milkings (60 h). Treatments were allocated to quarters at random. In expts. 1 (cow 49) and 2 (cow 66) all treatments were introduced at the same milking, but in expts. 3 (cow 091) and 4 (cow N20) the introduction of treatments was phased so that all finished at the same milking. There was a post-treatment period of 7 days in which the cows were milked normally at 12-h intervals.

The 2nd series of experiments (expts. 5–11) was designed to give information on changes in the composition of milk throughout milking after suspension of milking for 24 h, 36 h or 60 h. One cow was used for each experiment. Milk was not removed from either one or two quarters of the udder for a period of 24, 36 or 60 h, as appropriate, whereas milk from the other quarters was removed at 12-h intervals (Table 6). At the end of each extended milking interval, the milk from one unmilked quarter and from one other quarter was removed in portions of about 200 ml. An intravenous injection of oxytocin (20 i.u., Syntocinon; Sandoz Products Ltd., London, W.1) was then given and the residual milk from the same 2 quarters removed also in portions

of about 200 ml. In expts. 5, 6, 9, 10 and 11 the milk was then removed in portions of 200 ml from the 2 remaining quarters.

Animals and management

Cows 49 (Friesian) and 66 (Friesian) were in the 2nd month of their 2nd lactation and frequent bacteriological examinations of their milk throughout the previous and current lactations had not detected any infection of the udder. Cow 091 (Ayrshire) was in the 2nd month of her 5th lactation and had been infected in the right hind quarter of her udder in her 1st lactation. Cow N 20 (Friesian × Shorthorn) was in the 7th month of her 6th lactation and had been infected in all four quarters of the udder. All cows were, however, free of infections of the udder throughout the period of the experiments. Seven Friesian cows were used for the second series of experiments. All cows had been free of bacterial infection and their milk was negative to the Whiteside test throughout the current lactation.

The animals were housed individually in loose boxes and given a diet of hay (12 lb/day) and a concentrate mixture balanced for milk production (4 lb/gal of milk produced). In expts. 1–4, they were milked at 12-h intervals with an individual quarter milking machine which had graduated transparent cylinders that enabled the amount of milk removed from 2 of the quarters to be observed. The machine was operated at a vacuum of 15 inHg, a pulsation rate of 60 c/min and a pulsation ratio of 3:1. Unless a quarter was deliberately left incompletely milked it was machine stripped at the end of milking. In expts. 5–11 the cows were milked normally except when the milk of the separate quarters was removed in 200-ml portions by milking alternately into 2 glass containers inserted into the milking line.

Sampling and methods of analysis

At each milking in expts. 1–4, the yield of milk removed from any quarter was measured and a sample taken. In the second series of experiments (expts. 5–11), a sample was taken of each portion of milk. The samples were analysed for total solids, fat, lactose N, total, non-casein N and non-protein N, sodium, potassium and chloride by the methods described previously (Wheelock, Rook & Dodd, 1965). In certain samples the whey proteins were fractionated by the methods of Aschaffenburg & Drewry (1959).

RESULTS

Effects of incomplete milking on milk yield and composition (Expts. 1–4)

A similar pattern of change in milk yield and composition was obtained for each of the 3 experimental treatments (b), (c), (d) illustrated in Fig. 1.

Milk yield. At the 1st milking of the post-treatment period, the yield of milk was augmented by a carry-over of milk left in the quarter during the experimental period and was much above that obtained at milkings in the pre-treatment period. At the 2nd milking, however, the yield was invariably depressed but the yield then increased progressively at successive milkings until the original yield, or only slightly less, was recovered. Both the extent of the depression in milk yield and the delay in recovery varied with the severity of the imposed treatment: the effects were least in quarters

from which only 50% of the expected yield was removed at 4 successive milkings and most marked in quarters in which milking was suspended for 60 h. The most dramatic change in milk yield was observed with cow N20, in the quarter in which milking was suspended for 60 h. At the 2nd and 3rd milkings of the post-treatment period the yield was only 160 and 151 g, respectively, as compared with a pre-treatment yield for the quarter of 1900 g, but the original yield was recovered by the 9th milking, i.e. in as short a time as for the other animals on the same treatment, whose reduction in yield was much smaller.

During the period when experimental treatments were applied to other quarters, the yield of milk from control quarters invariably increased. The mean percentage increases for each of the 4 cows during the 4 milkings when there was incomplete removal of milk from each of the other quarters, over the mean yields for the 4 milkings before the introduction of treatments, were 15.5 ± 8.1 , 7.9 ± 4.6 , 11.2 ± 6.2 and 6.5 ± 3.9 . Individually, none of these effects was statistically significant ($P > 0.05$) but an analysis of variance indicated a significant overall effect ($P < 0.05$). With the reintroduction of normal milking in other quarters, the yields of milk in control quarters returned to the original level.

Table 1. *Effect of incomplete removal of milk from the udder on milk fat content*

(Values are the mean, with s.e., for the effect of each treatment in a single quarter of the udder of each of 4 cows.)

Treatment	Milk fat content, %	
	For 4 milkings before treatment started	For period of treatment and the 6 succeeding milkings
Removal of only 50% of expected yield at 4 successive milkings	3.17 ± 0.18	3.33 ± 0.16
Removal of only 50% of expected yield at 8 successive milkings	3.12 ± 0.17	3.40 ± 0.15
Suspension of milking for 4 successive milkings (60 h)	3.18 ± 0.15	5.30 ± 0.42

Fat percentage and yield. During periods of partial removal of milk from the udder, fat content was initially depressed but then tended to recover. However, with all the treatments, fat content was high at the 1st few milkings of the post-treatment period, but returned to normal by the 4th or 5th milkings. Over the period of the treatments and the succeeding 6 milkings the average effect (Table 1) was invariably to increase fat percentage, but a statistically significant ($P < 0.05$) increase was observed only with the suspension of milking for 60 h.

Concentration and yield of constituents other than fat (Tables 2-5). Characteristic changes in the concentrations of non-fatty constituents were observed with all the treatments (Fig. 1). The concentrations of lactose and potassium decreased and of sodium, chloride, the whey proteins and, to a lesser extent, of casein increased. These effects were apparent in the milk obtained during the period when the treatments were being applied but invariably were more pronounced in the milk removed at the 2nd milking of the post-treatment period, and then persisted for some time. With the most severe treatment, the suspension of milking, the original milk composition was

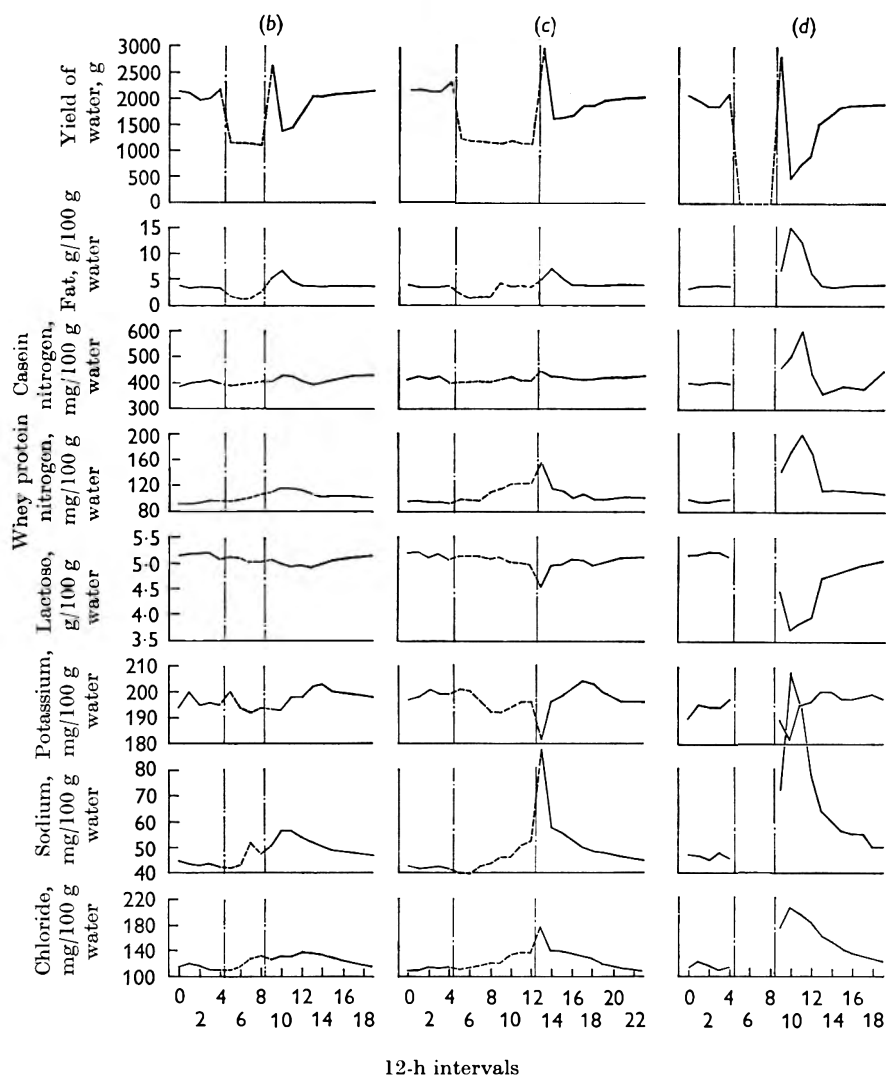


Fig. 1. (expts. 1-4). The changes in the yield of water in milk and in the concentrations in milk of fat, casein N, whey protein N, lactose, potassium, sodium and chloride. (b) When at 4 successive milkings only 50% of the expected yield was removed; (c) when at 8 successive milkings only 50% of the expected yield was removed; and (d) when milking was suspended for 4 successive milkings. Values are the average for single quarters in each of 4 cows. —, Complete milking; - - -, treatment period.

not regained until about the 9th or 10th milking after the resumption of milking. With all treatments the concentrations of sodium and of whey proteins were still above the pre-treatment values at the 12th milking of the post-treatment period. The recovery in potassium content was more rapid than in lactose content and at about the 5th and 6th milkings of the post-treatment period potassium content was temporarily above the pre-treatment value.

During the period of experimental treatment, the yields of all the constituents were depressed (Table 2), the differing effects on composition resulting in a more marked reduction in the yields of lactose, potassium and casein than in those of sodium, chloride or the whey proteins. The yield of sodium was, on average, less affected than that of chloride, and overall this difference was statistically significant ($P < 0.05$) (see Table 5). With the more severe treatments there was also a tendency for the effect on the yield of casein to be less marked than that on lactose or potassium.

Table 2. *Effect of incomplete removal of milk from the udder on the yields of the milk constituents during the period of treatment*

(The average yield of a constituent for the period of treatment and the 1st milking on the resumption of normal milking is expressed as a percentage of the average yield at 4 milkings before the introduction of the treatment. Mean values, with s.e., are given for the effect of each treatment in a single quarter of the udder in each of 4 cows.)

Constituent	Treatment		
	Removal of only 50% of expected yield at 4 successive milkings	Removal of only 50% of expected yield at 8 successive milkings	Suspension of milking for 4 successive milkings (60 h)
Fat	62.3 ± 12.4	59.8 ± 6.3	53.1 ± 5.6
Casein	66.3 ± 2.6	62.3 ± 1.6	31.3 ± 4.0
Lactose	67.7 ± 2.1	60.0 ± 2.7	22.7 ± 1.3
Potassium	66.7 ± 3.9	60.2 ± 2.3	26.7 ± 1.1
Whey proteins	76.0 ± 5.0	81.6 ± 7.6	41.8 ± 9.2
Sodium	75.1 ± 3.1	81.6 ± 5.2	43.7 ± 5.4
Chloride	71.7 ± 4.9	72.8 ± 4.8	41.0 ± 5.2

Table 3. *Effect of incomplete removal of milk from the udder on the yields of the milk constituents after the resumption of normal milking*

(The average yield of a constituent at the 3rd to the 6th milkings of the post-treatment period is expressed as a percentage of the average yield at 4 milkings before the introduction of the treatment. Mean values, with s.e., are given for the effect of each treatment in a single quarter of the udder in each of 4 cows.)

Constituent	Treatment		
	Removal of only 50% of expected yield at 4 successive milkings	Removal of only 50% of expected yield at 8 successive milkings	Suspension of milking for 4 successive milkings (60 h)
Fat	95.3 ± 8.7	93.4 ± 2.2	74.7 ± 1.5
Casein	88.1 ± 8.6	82.5 ± 2.2	59.6 ± 6.3
Lactose	85.5 ± 7.9	80.3 ± 3.1	55.4 ± 4.6
Potassium	91.0 ± 9.0	84.3 ± 3.4	57.8 ± 5.8
Whey proteins	100.4 ± 8.7	91.0 ± 4.9	75.9 ± 7.5
Sodium	106.4 ± 5.4	99.6 ± 4.7	78.7 ± 6.9
Chloride	102.4 ± 6.1	96.1 ± 5.9	78.1 ± 5.1

In the period immediately following the resumption of normal milking (Table 3), there was a rapid recovery in the yields of all the constituents which followed roughly the recovery in milk yield. The more marked effects of treatments, on the yields of lactose, potassium and casein, persisted into the recovery period but potassium yield recovered more rapidly ($P < 0.05$) than that of lactose (Table 5). After the yield

of milk from a quarter had recovered to about its pre-treatment value (Table 4), on average the yields of sodium, chloride and soluble protein were slightly above their pre-treatment yield, with the single exception of the yield of chloride for quarters from which only 50% of the expected yield had been removed at 8 successive milkings. For sodium, the overall effect was statistically significant ($P < 0.05$). The original yields of casein, lactose and potassium were not fully recovered by the 7th day after the resumption of normal milking with the 2 most severe treatments, but the recoveries were of the same order as for that of water in milk.

Table 4. *Effect of incomplete removal of milk from the udder on the yields of the milk constituents after the original yield of milk from the quarter had recovered to about the pre-treatment level*

(The average yield of a constituent at the 7th and 8th milkings of the post-treatment period is expressed as a percentage of the average yield at 4 milkings before the introduction of the treatment. Mean values, with s.e., are given for the effect of each treatment in a single quarter of the udder in each of 4 cows.)

Constituent	Treatment		
	Removal of only 50% of expected yield at 4 successive milkings	Removal of only 50% of expected yield at 8 successive milkings	Suspension of milking for 4 successive milkings (60 h)
Fat	108.4 ± 6.0	104.8 ± 4.3	99.7 ± 1.5
Casein	103.8 ± 6.4	93.5 ± 2.0	93.0 ± 2.4
Lactose	99.7 ± 4.9	92.3 ± 3.0	91.1 ± 4.2
Potassium	95.8 ± 6.0	96.1 ± 5.3	94.0 ± 4.3
Whey proteins	109.9 ± 5.5	101.5 ± 4.1	104.4 ± 16.1
Sodium	110.0 ± 3.9	102.0 ± 3.3	107.1 ± 1.9
Chloride	106.4 ± 7.9	91.0 ± 3.5	102.2 ± 5.9
Water	101.0 ± 5.1	92.2 ± 2.2	94.4 ± 2.9

Effects of an extended milking interval on the variations in the composition of milk throughout a milking

For quarters milked at regular 12-h intervals there was no change throughout milking in the concentrations of the constituents of the milk removed when expressed on a water basis, apart from the rise in the fat content as milking progressed. This result was obtained both when the quarter was first milked normally and the residual milk removed after the injection of oxytocin and when the complete milking was preceded by the injection of oxytocin.

In contrast, with the extended milking intervals, there were changes in the concentrations of both fatty and non-fatty constituents of the milk removed throughout the course of milking and the pattern of changes differed according to the time of injection of oxytocin. Without an initial injection of oxytocin there were decreases in the concentrations of lactose and potassium and increases in the concentrations of sodium and chloride throughout the milking (Fig. 2). After the injection of the oxytocin, however, there was an abrupt change. The successive portions of residual milk removed were of more constant composition and, apart from fat content, approached in composition that of the 1st portions of milk removed from the udder. The lactose content of the 1st portions of milk and of residual milk was, however, less than that of the milk from control quarters, and the difference increased with length

Table 5. *Effect of incomplete removal of milk from the udder on the ratios in milk of casein to lactose, potassium to lactose, sodium to lactose and chloride to sodium*

(The average ratio for (i) the period of treatment and the 1st milking of the post-treatment period, and (ii) the 2nd to the 6th milkings of the post-treatment period is expressed as a percentage of the average ratio for 4 milkings before the introduction of the treatment. Mean values, with s.e., are given for the effect of each treatment in a single quarter of the udder in each of 4 cows.)

Treatment	Casein/lactose		Potassium/lactose		Sodium/lactose		Chloride/sodium	
	(i)	(ii)	(i)	(ii)	(i)	(ii)	(i)	(ii)
Removal of only 50% of expected yield at 4 successive milkings	97.9 ± 3.7	103.0 ± 2.4	98.6 ± 2.9	106.3 ± 2.8	110.0 ± 3.2	126.1 ± 12.6	95.4 ± 4.2	96.4 ± 4.2
Removal of only 50% of expected yield at 8 successive milkings	105.2 ± 1.5	103.1 ± 2.9	100.7 ± 2.0	105.1 ± 2.8	136.2 ± 6.5	124.1 ± 7.0	89.8 ± 5.5	96.5 ± 5.0
Suspension of milking for 4 successive milkings (60 h)	128.2 ± 19.8	99.7 ± 4.5	108.8 ± 3.2	104.0 ± 3.2	178.4 ± 23.9	143.8 ± 13.0	93.8 ± 3.0	100.1 ± 5.0

Table 6. *The effect of an extended milking interval on the variations throughout milking in the lactose content of the milk*

(The changes were characteristic for all cows and the details are shown for 1 cow in Fig. 2. Lactose content, g/100 g water.)

Expt. no.	Length of milking interval, h	Oxytocin injected after normal milking				Oxytocin injected before normal milking			
		Average value for 1st 200-ml portions of milk*	Minimum value throughout milking	Average value for residual milk	Average value for control quarter	Average value for 1st 200-ml portions of milk*	Minimum value throughout milking	Average value for control quarter	
5	24	5.13	4.76	5.17	5.21	5.07	4.54	5.16	
6	24	5.05	4.52	5.04	5.17	4.97	4.51	5.17	
7	36	5.05	3.97	4.99	5.63	—	—	—	
8	36	5.04	4.54	5.06	5.53	—	—	—	
9	36	5.03	3.73	4.55	5.23	5.18	4.09	5.25	
10	60	4.49	4.11	4.36	5.28	4.49	4.01	5.24	

of milking interval (Table 6). Changes in whey protein and casein contents were less regular. Whey protein content tended to show the same pattern as did the contents of sodium and chloride and this was the result mainly of changes in the proteose-peptone and globulin fractions and in the residual albumin fraction, which includes serum albumin. In 5 of the 7 experiments, casein content tended to increase throughout a milking, and the concentration in residual milk was similar to that of the

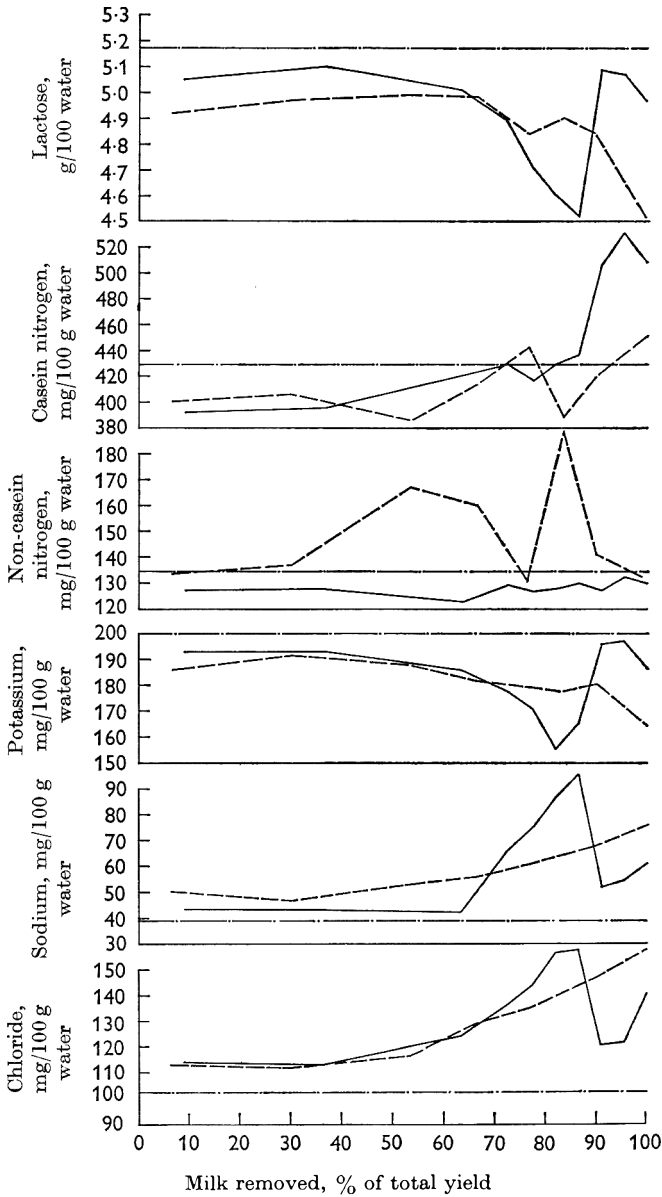


Fig. 2 (expt. 6). Changes in composition of milk throughout milking after an extended milking interval of 24 h. —, Milk first removed without an injection of oxytocin and then the residual milk removed after an injection of oxytocin; - - -, injection of oxytocin given before milking began; — · —, average value for the 2 quarters milked out after a 12-h interval.

last portion of milk removed before the injection of oxytocin. In the other 2 experiments, there was no obvious change. The lactose to casein ratio of the 1st portions of milk from experimental quarters decreased with increasing length of milking interval by comparison with the corresponding portions for the milk from control quarters (Table 7).

Table 7. *The effect of an extended milking interval on the lactose to casein ratio of the 1st portions of milk*

Expt.	Cow	Length of milking interval, h	Experimental quarter, lactose/casein	Control* quarter, lactose/casein
5	40	24	1.47	1.48
6	230	24	1.29	1.21
7	116	36	1.17	1.38
8	187	36	1.06	1.17
9	Y 64	36	1.16	1.16
10	127	60	0.78	1.09
11	161	60	1.05	1.35

* 12-h milking interval.

Changes in composition similar to the above were observed when an injection of oxytocin was given before milking was begun except that there was no abrupt recovery in composition towards the end of milking. To determine whether this effect of time of injection of oxytocin was due to a less complete removal of milk when oxytocin was injected before milking started, in expts. 9 and 11 a 2nd injection was given after milking had been completed. The quantity of milk removed after the 2nd injection was in all instances about 5% of that already obtained and was not influenced by the time of the 1st injection of oxytocin.

DISCUSSION

Our results confirm earlier evidence (Hansson *et al.* 1954) that a period of incomplete removal of milk from the udder or an extended milking interval results not only in a temporary loss of secretory ability but also in characteristic changes in the composition of the secreted milk. The concentrations of lactose and potassium are depressed whereas the concentrations of sodium, chloride, casein and whey proteins are increased. The responses in fat content are variable, owing to residual milk effects, but on average the content is increased.

The experiments described provide no direct evidence of the causes of the changes in milk secretion, but the accumulation of the products of secretion within the udder could inhibit synthetic processes and cause a temporary loss of secretory ability. In addition, however, engorgement of an udder quarter with milk could have important physical effects: it may restrict blood flow and also alter temporarily, and possibly permanently, the permeability of udder tissue. Direct experimental evidence of a restriction in blood flow is not available, but the most likely explanation of the temporary increase in the yield of milk from control quarters during the period when other quarters were incompletely milked is that there was an increased, compensatory flow of blood through the control quarter over the experimental period. A change in the permeability of udder tissue would be important in 2 respects. It could increase

the relative rate of entry of any transudate of blood plasma (see Barry & Rowland, 1953) into milk. Also, in combination with an increase in pressure within the udder, it could facilitate the resorption of water-soluble synthesized constituents, for example lactose (see Johansson & Claesson, 1957), which would be accompanied by water because of the need to maintain milk in osmotic equilibrium with blood (Wheelock *et al.* 1965).

The less marked effects of incomplete milking or of an extended milking interval on the secretion of constituents thought to be of extracellular origin, namely sodium, chloride and the serum proteins, are most simply explained in terms of a temporary alteration in the permeability of udder tissue as pressure within the udder increases, but the tendency for the yields of these constituents to increase beyond their original level on the resumption of normal milking indicates a more permanent effect. The changes after an extended milking interval in the concentrations of water-soluble constituents throughout a milking, and the abrupt recovery in composition observed in the residual milk, are also consistent with a more marked effect of an increase in udder pressure on the excretion of fluid from the alveolar cells than on the rate of entry of transudate from blood, as is the lack of any abrupt change in composition towards the end of milking when oxytocin was given before milking began. Milk excreted in response to oxytocin injection would then, however, be diluted with the much larger bulk of milk already present in the udder and the abrupt change of composition might be obscured. On the other hand, the decrease in lactose to casein ratio observed in milk removed from the udder after an extended interval, and the tendency for the ratio to decrease with the successive portions of milk removed, are more consistent with a preferential resorption of lactose. Where changes in lactose to casein ratio were observed, the changes in the lactose to potassium ratio were much less marked. This must indicate that either potassium and lactose are resorbed at a similar rate or, alternatively, that the main loss of lactose is from the secretory cell rather than from the milk in the ducts and cisterns of the udder: potassium is mainly cellular in origin and its secretion in milk is dependent on the rate of expulsion of cellular contents into the alveolar lumen, which in turn appears to be closely related to the rate of synthesis and secretion of lactose.

The less marked effects of incomplete milkings on the yield of fat than on the yields of lactose and casein are probably the results partly of fat being present in the secretory cell as a discontinuous phase and partly of the ability of fat droplets to pass through the apex of the alveolar cell without rupture, which will prevent its accumulation within the cell.

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The effect of milking throughout the whole of pregnancy on the composition of cow's milk

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SUMMARY. The changes in yield and composition of milk when 4 cows were milked throughout the whole of pregnancy have been studied. The yield decreased to a minimum 1–20 days before parturition and then gradually increased. The changes in composition before parturition were similar to those observed in late lactation but more pronounced. The content of proteose-peptone plus globulin increased in late pregnancy with a sharp peak, of about 5 times the value observed in mid-lactation, within the last 10 days before parturition, and then decreased rapidly. After parturition milk yield increased rapidly and the changes in composition were less marked than in animals with the usual 'dry period'. The results are discussed in relation to current knowledge of colostrum formation.

The effect of stage of lactation on milk composition has been extensively studied in cows under commercial conditions of milk production, when it is usual to have a non-lactating or 'dry' period of 30–80 days between consecutive lactations. Towards the end of lactation, concurrent with the decline in the yield of milk, the concentrations of all the protein fractions and of sodium and chloride increase, and those of lactose and potassium decrease (Rook & Campling, 1965). The colostrum and milk obtained at the 1st milkings of the succeeding lactation have, however, in addition to a characteristically high content of globulins and proteose-peptones, markedly higher concentrations of all the major milk proteins and a lower concentration of lactose than that of milk secreted towards the end of lactation. However, there is a rapid recovery in the 1st days of lactation of a composition more typical of milk secreted in the main lactation period. It is known that when milk is allowed to accumulate in the udder for 60 h marked changes in composition occur (Wheelock, Rook & Dodd, 1965*b*), and this effect may contribute to the characteristic composition of colostrum.

In our experiments the effects of the accumulation of milk within the udder have been eliminated by milking throughout the whole of the normal 'dry period' and so it has been possible to study the effect of pregnancy on milk composition.

EXPERIMENTAL

Four pregnant Friesian cows in their 1st lactation were used. They were housed and managed with other cows in the Institute herd except that twice-daily milking was continued throughout the whole of pregnancy. The cows were milked in a cow-

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shed with bucket-type milking machines using a hygiene routine designed to prevent the transfer of udder pathogens from cow to cow. At monthly intervals, and more frequently at the time of calving, the cows were milked with a milking machine designed for the separate collection of the milk from individual quarters.

All the cows grazed with the herd and were given 10 lb/day of a mixture of concentrates until 6 weeks before calving. From then until calving they were given 12 lb hay and 16 lb of the concentrate mixture/day. Regular bacteriological and Whiteside tests were made for the presence of udder infections (Crossman, Dodd, Lee & Neave, 1950) and none was detected in any of the cows' udders throughout the experiment. Individual samples, or on certain occasions weighted, composite samples representing 1- or 2-day periods, were analysed for total solids, fat, lactose, total N, non-casein N and non-protein N, sodium, potassium and chloride by the methods previously described (Wheelock, Rook & Dodd, 1965*a*). The whey proteins were fractionated by the methods of Aschaffenburg & Drewry (1959).

RESULTS

Similar results were obtained for all the cows and for the separate quarters of each cow. Those for a typical quarter are given in Fig. 1. The normal lactational trends in milk yield and composition were observed until shortly before parturition. In the 4 cows yield was at a minimum 20, 10 and 9 days and 1 day, respectively, before parturition. With the fall in yield there were the expected progressive increases in fat, solids-not-fat (SNF), protein, sodium and chloride contents and decreases in lactose and potassium contents and in the potassium to lactose ratio (cf. Rook & Campling, 1965; Walsh & Rook, 1964). From then until parturition, yield increased slowly and there was an associated increase in fat content but, with the exception of the proteose-peptone plus globulin fraction, the concentrations of proteins remained steady. The content of proteose-peptone plus globulins increased slowly to a maximum 1-10 days before parturition and then decreased rapidly. After parturition milk yield increased rapidly and the characteristic falls in protein and fat contents of early lactation were observed, but, since the protein contents of the milk at parturition were considerably less than those characteristic of colostrum, the changes in protein content were less marked than in animals with the usual 'dry period' before parturition.

For all 4 cows the concentrations of lactose, potassium, sodium and chloride, when expressed on a water basis, showed a characteristic sequence of changes in the immediate pre- and post-partum periods (Fig. 2). Some days before the minimum in yield, there was a sharp decrease in potassium content and corresponding increases in sodium and chloride contents, without any distinctive change in lactose content. As the minimum in yield was reached, however, lactose content also began to fall, but the contents of sodium and chloride then steadied and the trend in potassium content was immediately reversed. The potassium content subsequently reached a maximum equivalent to that of the previous lactation at or about parturition when the original potassium content was regained. A day or so after parturition the contents of sodium and chloride began to decrease and the lactose content to increase until, shortly after parturition, values typical for the previous lactation were obtained.

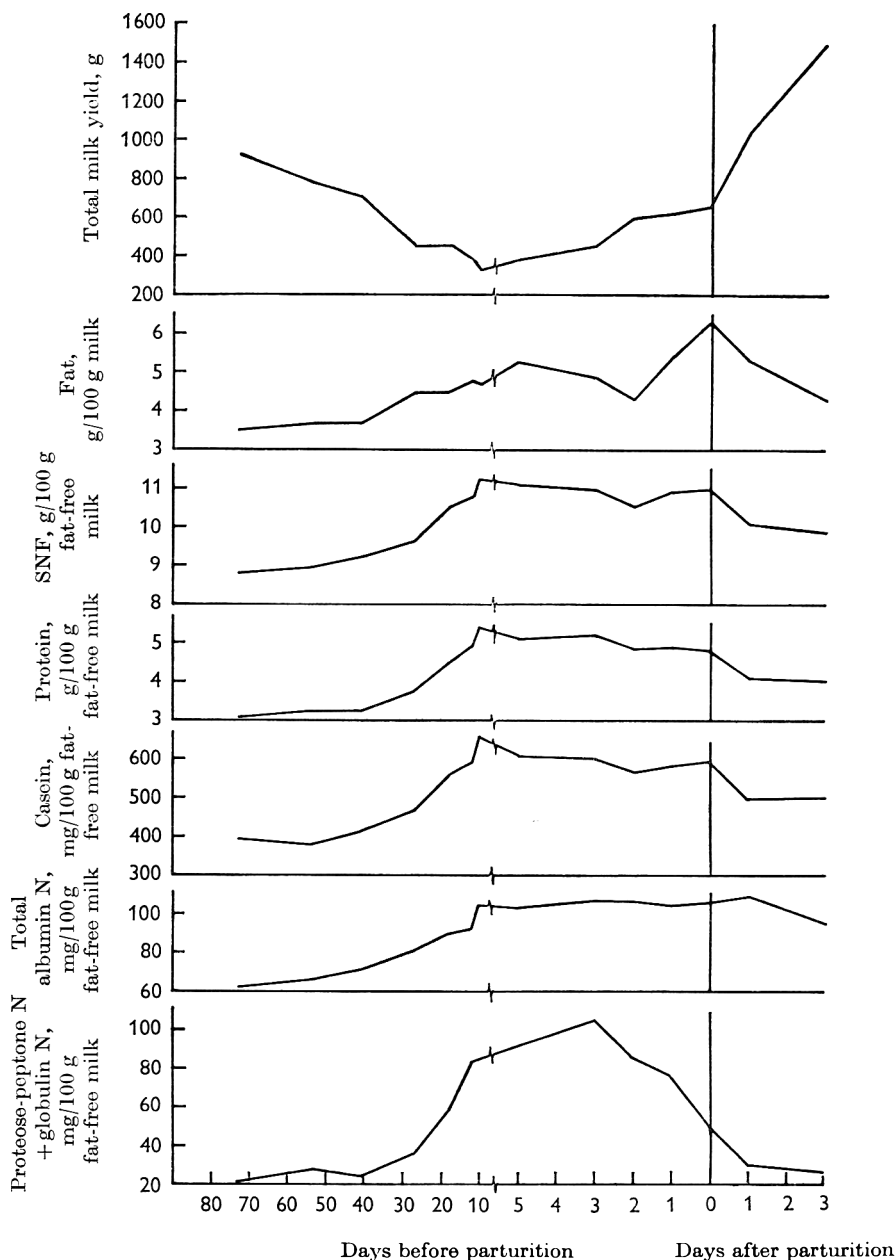


Fig. 1. The changes in the yield of milk and concentrations of fat, SNF, protein, casein N, total albumin N, and proteose-peptone + globulin before and after parturition. The results illustrated are typical but obtained for one quarter of one cow.

The rectilinear relationship between potassium content and milk yield over the period of change in potassium content is shown for 1 cow in Fig. 3. In the main, movements in sodium and chloride concentrations were linearly related but in 1 cow over the 12th–2nd day before parturition sodium content increased without a corresponding change in chloride content (Fig. 4).

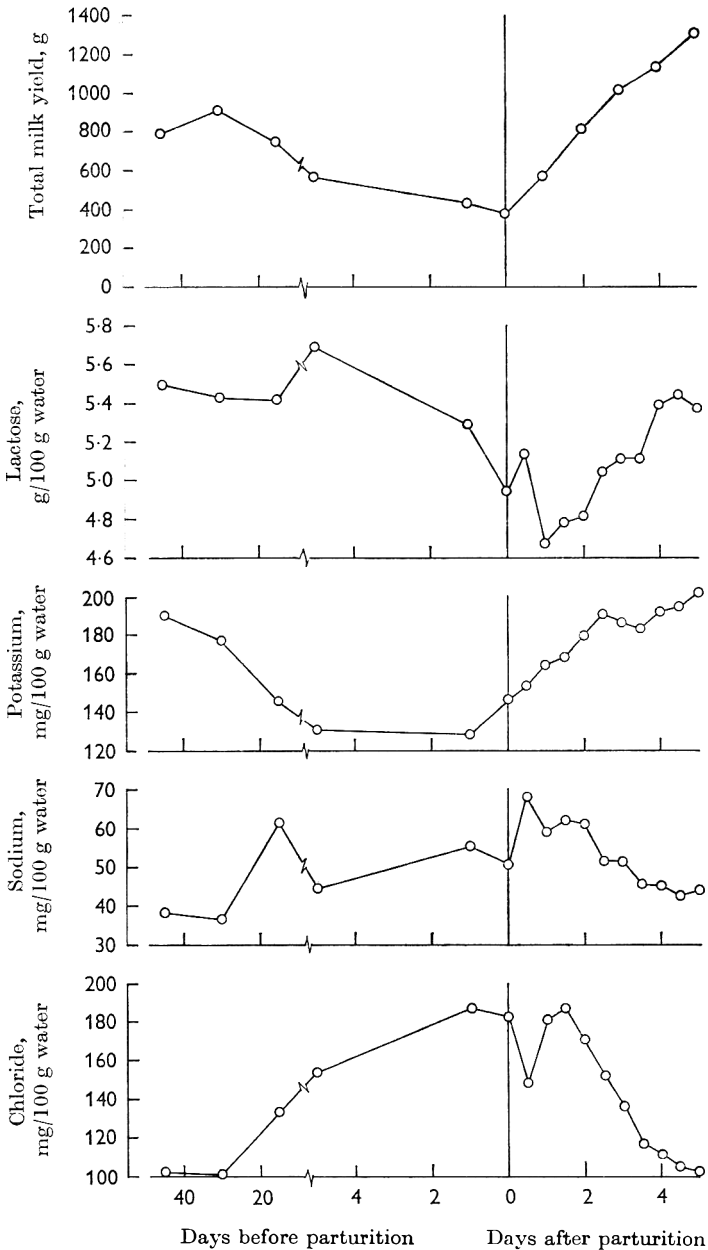


Fig. 2. The changes in milk yield and concentrations of lactose, potassium, sodium and chloride before and after parturition. The results illustrated are typical but obtained for one quarter of one cow.

DISCUSSION

The normal lactational trends in milk composition are well established, and studies of the effects of milking until parturition (Eckles & Palmer, 1916) and of pre-partum milking (Rowland, Roy, Sears & Thompson, 1953) have already indicated that the abnormally high concentrations in colostrum of casein and other proteins synthesized

within the udder are probably mainly the result of an accumulation of milk within the udder before parturition, and that the highest rate of secretion of colostrous globulins into the udder can occur several days before the act of parturition. Our results are in line with these observations.

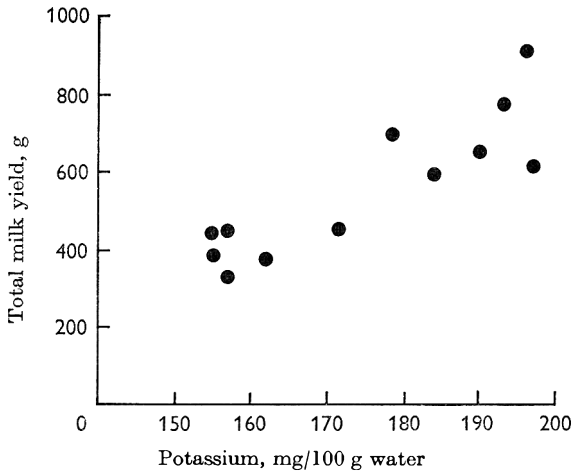


Fig. 3. Variations in the yield of milk with the changes in potassium concentration before parturition. The results illustrated are typical but obtained for one quarter of one cow.

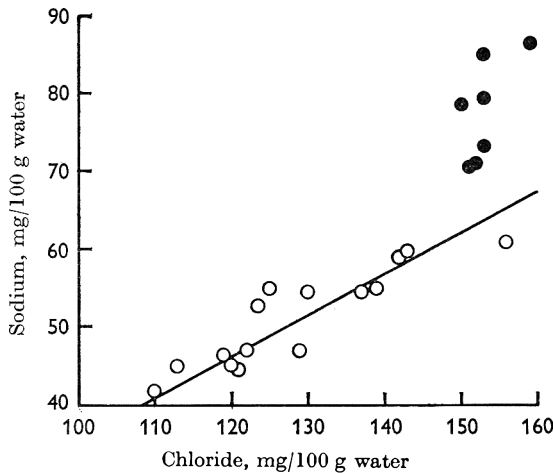


Fig. 4. Variations in the sodium content with changes in the chloride content in the milk of one quarter of one cow. ●, Samples taken between the 12th and the 2nd day before parturition; ○, samples taken throughout the remainder of the experiment. The line represents the regression of these points.

The slightly lower lactose content and the decrease in potassium to lactose ratio characteristic of late lactation (Rook & Campling, 1965; Walsh & Rook, 1964) were observed also in the present experiments. These changes and the concomitant increases in sodium and chloride contents have been explained as the result of an alteration in the primary secretion (Turner, 1946) or, as seems more probable, of a change in the relative volumes of primary secretion and transudate of plasma from which the main part of the sodium and chloride of milk is considered to be derived

(Barry & Rowland, 1953). The detailed examination of the changes in mineral contents possible in the present work suggests that the decrease in the potassium to lactose ratio arises from a replacement of potassium by sodium, unrelated to a change in lactose content. This replacement of potassium by sodium may be the result of a decreased metabolic activity of the secretory cells, since the high potassium concentration in the cells relative to the extracellular fluid is maintained by a process requiring metabolic energy (Ussing, 1960). The observed relationship between the yield of milk and the concentration of potassium in the period before parturition supports this view.

It is generally believed that the maintenance of the mammary gland in a state of functional integrity is dependent upon continued application of suckling or milking stimuli (Selye, 1934; Benson & Folley, 1957) and it has been assumed that, when cows are dried-off at the end of lactation, involution takes place. Secretion will continue for some time after the cessation of milking but milk accumulating in the udder must eventually be largely resorbed. The usually extremely low yield of milk obtained at the beginning of pre-partum milking (cf. Rowland *et al.* 1953) indicates that there is little carry-over of fluid within the udder from the end of milking in one lactation to the beginning of milking in the next. Where pre-partum milking is practised, however, measurable yields of milk can be obtained several days before parturition, and it is evident also with animals under normal management conditions that a considerable volume of milk accumulates in the udder several days before parturition. Under such conditions a partial resorption of milk constituents may occur. Lactose, and with it water, because of the need to maintain isotonicity of milk with blood, is resorbed most readily and this process must contribute to the low lactose and the high casein content of colostrum. The accumulation within the udder of immune globulins contributing to osmotic pressure will result also in some decrease in lactose content. Where, as in the present experiments, cows are milked throughout the whole of pregnancy and milk is not allowed to accumulate within the udder, the very low lactose content characteristic of colostrum is not observed.

We are grateful to Mr T. K. Griffin, Miss M. Weston, Miss S. Fletcher and Miss E. Jenkins for skilled technical assistance.

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The effect of intravenous injections of oxytocin during milking and the removal of residual milk on the composition of cow's milk

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SUMMARY. After an injection of oxytocin and the removal of residual milk, the milk obtained at the next milking had an increased content of sodium, chloride and whey proteins and a decreased content of lactose. The effect persisted for several milkings. It is suggested that this was due to a direct effect of oxytocin on the permeability of the mammary epithelium and that oxytocin should be used with caution in certain types of milk secretion experiment.

After the physiological process of milk ejection has occurred most of the milk present in the udder of a dairy cow can be removed by milking. The remainder, known as residual or complementary milk, is retained in the udder but can largely be removed by milking again after an injection of oxytocin which causes a further ejection of milk (Johansson, 1940). Not all the residual milk is removed by the method (Johansson, 1952) but the quantities remaining in the udder and carried over to the next milking are very small. Consequently, fluctuations in milk yield due to variations in the quantity of residual milk can be minimized by this technique. It is especially useful where milking intervals are short and difficulties in stimulating a normal milk ejection can be expected (Smith, 1947) or where the rate of secretion of milk during various milking intervals is being determined (Elliott, 1959). In these experiments it has usually been assumed that the technique does not affect the rates of secretion of the constituents of milk as distinct from their relative rates of removal from the udder.

Sprain, Smith, Tyler & Fosgate (1954), however, have observed an increase in milk yield when the residual milk was removed at successive milkings. Also, in preliminary experiments in which oxytocin was used to remove the residual milk we noticed that the milk obtained had unexpected values for the sodium and lactose contents. To investigate the possibility that this technique directly affects milk secretion a series of short experiments was carried out.

EXPERIMENTAL

Four Friesian cows in their 2nd lactation were housed in loose boxes and given a daily diet of 12 lb hay and 5-6 lb/gal of a concentrate mixture balanced for milk production. They were accustomed to a routine of being milked and offered food at 6-h intervals.

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Experimental details are given in Table 1. One cow was used for each experiment. During the preliminary control and post-treatment periods milking was carried out in a normal manner, the stimulation for milk ejection being limited to udder washing a short interval before the start of milking. In the experimental period the normal milking procedure was followed by the injection of oxytocin (20 i.u. Syntocinon, Sandoz Products Ltd., London, W. 1) and the removal of residual milk. A bucket milking machine designed for the separate collection of the milk of individual quarters was used for all milkings. At the first 2 milkings of the treatment period in expts. 1 and 2 the milk from 1 quarter of each cow was collected in serial portions of about 200 ml, to determine the effect of the treatment on variations in composition throughout the course of a milking. In expt. 5, after the oxytocin injection, the residual milk was not removed from 1 quarter to determine whether the observed changes in milk composition were dependent on the removal of the residual milk or not.

Table 1. *Experimental details*

Expt.	Duration, no. of 6-h milking intervals		
	Control period	Treatment period	Post-treatment period
1	7	8*	8
2	7	8*	8
3	3	4	4
4	3	4	4
5	2	1†	4

* At the 1st and 2nd milkings of the treatment period the milk from 1 quarter of each cow was removed in portions of about 200 ml.

† Milk was not removed from the right hind quarter.

Milk samples were taken from all the milk obtained from individual quarters at each milking and were analysed for total solids, fat, lactose, total N, non-casein N and non-protein N, sodium, potassium and chloride by methods previously described (Wheelock, Rook & Dodd, 1965). The whey proteins were fractionated by the method of Aschaffenburg & Drewry (1959). During the course of the experiments aseptically taken foremilk samples were tested by bacteriological plating and Whiteside tests (Crossman, Dodd, Lee & Neave, 1950). These indicated that the cows were free from udder infection.

RESULTS

Milk composition

Because of variations in the fat content of the milk when the residual milk is removed and throughout the course of a milking (Johansson, Korkman & Nelson, 1952; Johansson, 1952) all the results have been expressed on a water basis. In all the experiments the composition of the non-fatty fraction of the milk obtained at the first milking of the treatment periods was similar to that of the milk obtained during the preliminary control periods. Thereafter, during the treatment period the milk had a considerably changed composition. Sodium, chloride, casein and non-casein N contents were increased and there was a corresponding decrease in lactose content (expts. 1, 2, Fig. 1; expt. 5, Table 2). The increase in non-casein N content was the

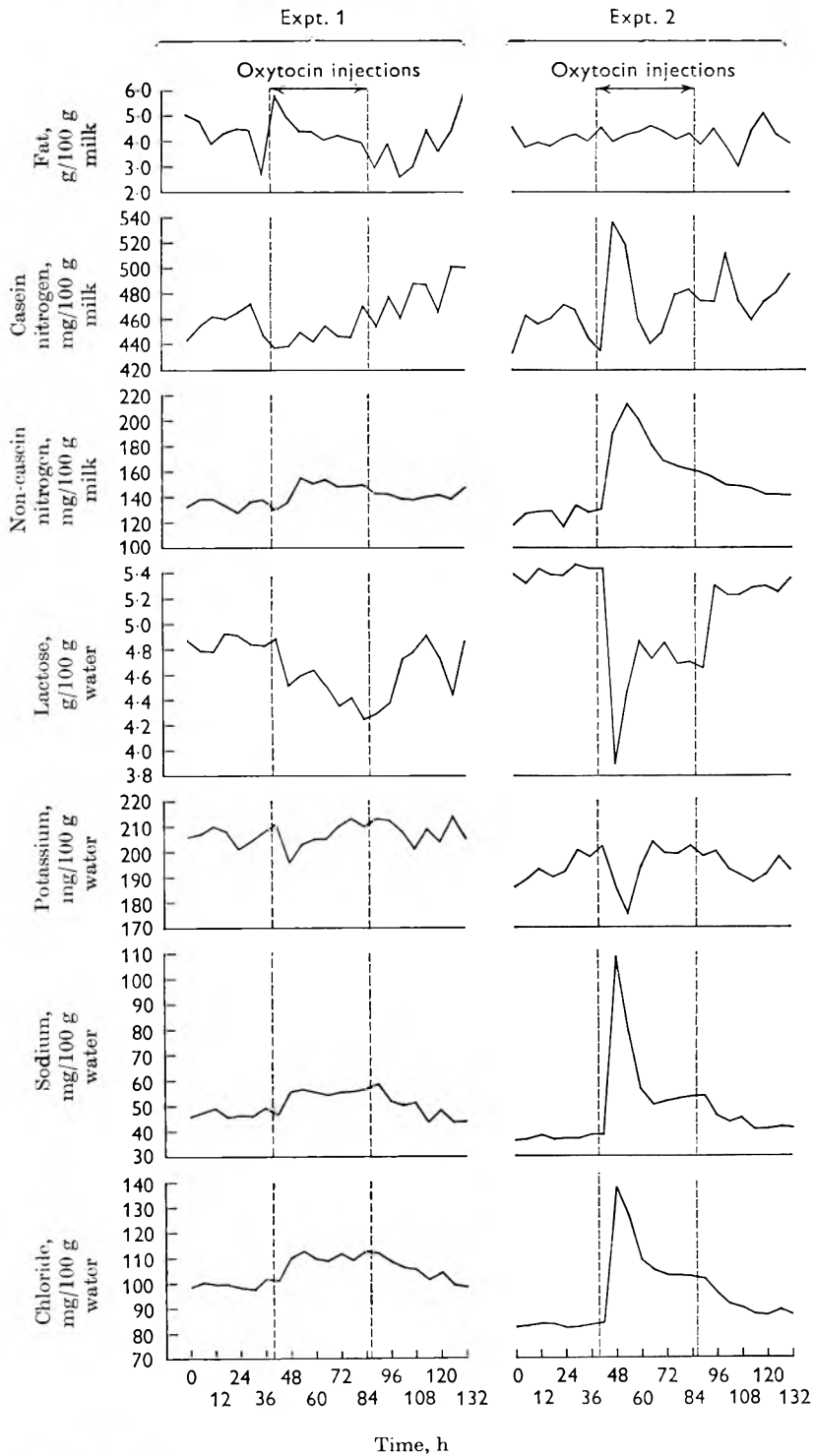


Fig. 1. The changes in the contents of fat, casein N, non-casein N, lactose, potassium, sodium and chloride when the residual milk was removed after oxytocin injection.

result mainly of increases in the contents of the proteose-peptone plus globulin fraction and in the residual albumin fraction. The extent and timing of the changes varied, however, from cow to cow; in expt. 1 the effects increased throughout the period of use of oxytocin, whereas in expt. 2 the effects were more marked at the first 2 than at subsequent milkings; in expts. 3 and 4 there was no marked change in the magnitude of the effect throughout the treatment period.

Table 2. *The changes in contents of lactose, potassium, sodium and chloride in milk when an oxytocin injection was given at one milking only*

(The residual milk was removed from the right fore quarter but not the right hind quarter after oxytocin injection (expt. 5).)

Milking	Time, h	Lactose, g/100 g H ₂ O		Potassium, mg/100 g H ₂ O	
		Right fore	Right hind	Right fore	Right hind
1	0	4.96	4.82	211	220
2	6	4.86	4.88	208	213
3	12	4.83	—	210	—
3*	12	4.91	—	213	—
4	18	4.57	4.61	195	208
5	24	4.82	4.70	204	207
6	30	4.74	4.84	202	209
7	36	4.85	4.92	211	216

Milking	Time, h	Sodium, mg/100 g H ₂ O		Chloride, mg/100 g H ₂ O	
		Right fore	Right hind	Right fore	Right hind
1	0	53.5	46.9	118	107
2	6	57.4	47.4	124	120
3	12	61.2	—	128	—
3*	12	59.0	—	125	—
4	18	74.8	54.9	160	136
5	24	53.8	52.0	125	117
6	30	59.6	51.2	125	117
7	36	60.7	51.1	123	117

* Residual milk.

Table 3. *Changes in the ratio of lactose to casein following intravenous injections of oxytocin and removal of residual milk*

(Values are the average for the control, treatment and post-treatment periods. The residual milk was removed only during the treatment period.)

Expt. no.	Ratio of lactose to casein		
	Control period	Treatment period	Post-treatment period
1	1.06	1.00	0.97
1	1.05	0.94	0.94
2	1.20	1.03	1.12
2	1.07	0.93	1.04
3	1.08	0.99	1.02
3	1.07	0.93	1.04
4	1.29	1.15	1.12
4	1.20	1.13	1.23

The potassium content was decreased at the 1st milking following the use of oxytocin but, unlike the other constituents, the original concentration was recovered by the 4th milking of the treatment period in expts 1-4.

A decrease in the lactose to casein ratio was observed in the milk of all the cows after an injection of oxytocin at the previous milking (Table 3).

At the 1st milking of the treatment period there was no change in the contents of lactose, potassium, sodium and chloride in the 200-ml samples removed serially throughout milking after the injection of oxytocin. At the 2nd milking, when differences in total composition were first observed, the serial 200-ml samples were

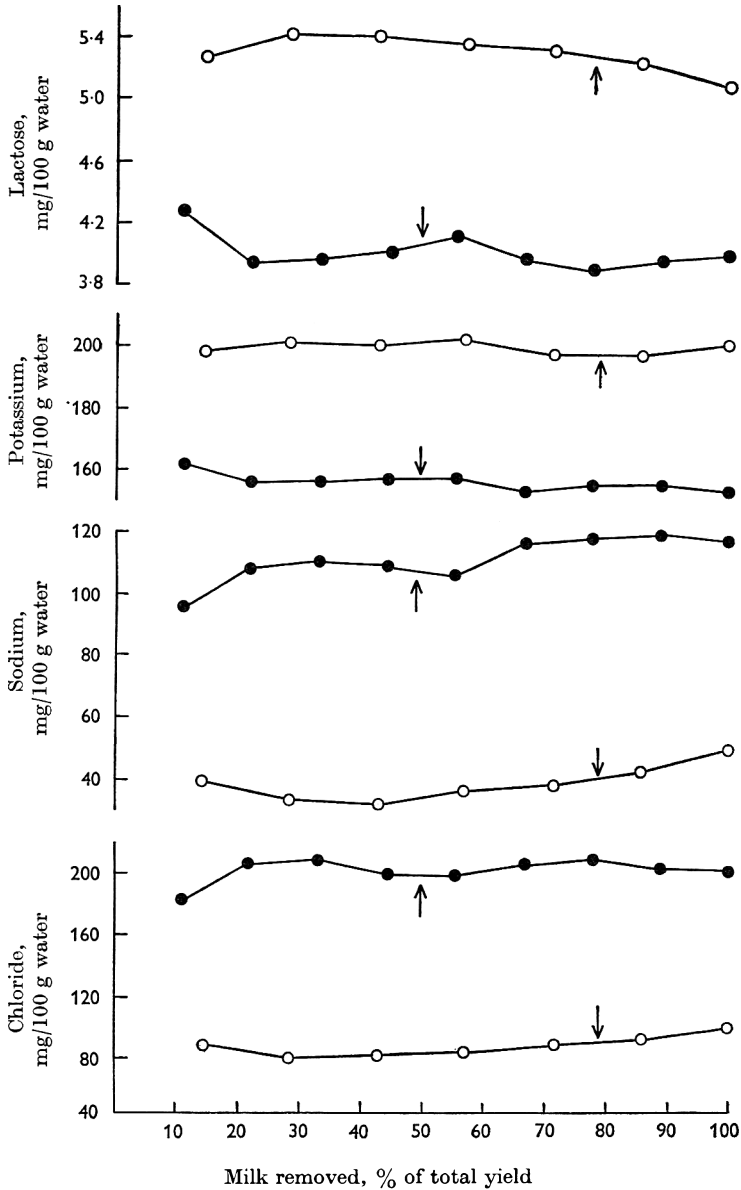


Fig. 2 (expt. 1). The changes in the contents of lactose, potassium, sodium and chloride throughout milking in 1 quarter when the residual milk was removed after oxytocin injection. ○, 1st milking of the treatment period; ●, 2nd milking of the treatment period; ↓, injection of oxytocin given.

Table 4. *The effect of intravenous injections of oxytocin given during milking on the yields of milk and of milk constituents in 1 quarter*

(Milking was normal during the control and post-treatment periods, but during the treatment period the residual milk was removed after an injection of oxytocin during the treatment period. The values are means, with s.e. To eliminate carry-over effects the yields for the 1st milking of the treatment period and of the post-treatment period have not been included in those calculations.)

Expt. no.	Period	Yield, g/day							
		Milk	Fat	Casein (N × 6.38)	Non-casein-N	Lactose	Potassium	Sodium	Chloride
1	Control	2684 ± 71	114 ± 27	68.4 ± 1.3	3.16 ± 0.10	113 ± 2.8	4.84 ± 0.26	1.10 ± 0.03	2.77 ± 0.08
	Treatment	2724 ± 64	117 ± 26	68.4 ± 2.0	3.55 ± 0.11***	106 ± 2.3	4.92 ± 0.15	1.32 ± 0.04***	3.36 ± 0.09**
	Post-treatment	2476 ± 166	98 ± 26	66.9 ± 12.2	3.05 ± 0.24	101 ± 7.9	4.52 ± 0.40	1.02 ± 0.08	2.71 ± 0.23
2	Control	4544 ± 82	185 ± 8	115.1 ± 1.4	4.96 ± 0.05	214 ± 3.3	7.60 ± 0.11	1.47 ± 0.02	3.36 ± 0.05
	Treatment	3748 ± 137	161 ± 8	99.6 ± 2.0***	5.96 ± 0.26**	150 ± 8.7***	6.36 ± 0.32**	2.05 ± 0.18**	4.68 ± 0.25*
	Post-treatment	3784 ± 153	158 ± 8	100.6 ± 5.4	4.80 ± 0.06	173 ± 7.8	6.34 ± 0.30	1.34 ± 0.07	3.25 ± 0.19
3	Control	2500 ± 327	109 ± 20	64.6 ± 8.9	2.94 ± 0.36	108 ± 13.4	4.28 ± 0.53	1.32 ± 0.18	2.78 ± 0.36
	Treatment	2680 ± 40	99 ± 3	69.7 ± 1.1	3.30 ± 0.20	108 ± 3.7	4.68 ± 0.18	1.64 ± 0.07	3.52 ± 0.13
	Post-treatment	2920 ± 328	83 ± 23	76.0 ± 8.4	3.55 ± 0.43	122 ± 14.2	5.52 ± 0.66	1.53 ± 0.18	3.36 ± 0.40
4	Control	2820 ± 118	96 ± 1	61.5 ± 2.8	2.51 ± 0.13	124 ± 5.8	5.30 ± 0.27	1.09 ± 0.07	3.57 ± 0.11
	Treatment	2892 ± 85	104 ± 2	67.9 ± 0.7	2.99 ± 0.14	121 ± 2.7	5.48 ± 0.28	1.22 ± 0.04	3.96 ± 0.11
	Post-treatment	3380 ± 74	113 ± 7	83.2 ± 6.1	4.00 ± 0.31	139 ± 2.1	6.72 ± 0.13	1.34 ± 0.02	—

Significance of difference between values for treatment and control; ***, $P < 0.001$; **, $P < 0.01$.

again all of the same composition (Fig. 2). Thus, the changes in composition at the 2nd milking were independent of the oxytocin injection at that milking and must have resulted from the injection of oxytocin at the previous milking.

The characteristic changes in composition were also observed when an injection of oxytocin at the previous milking was not followed by the removal of residual milk, but the effects were less marked because of dilution with the milk left from the previous milking interval (expt. 5, Table 2).

The changes in composition persisted for several milkings of the post-treatment period but the original composition was recovered by the end of the period.

Yields of milk constituents (Table 4)

The yields of sodium, chloride and non-casein N were invariably increased during the period of treatment. There was no consistent effect on the yields of fat, casein, lactose and potassium but in one cow the yield of milk and of all the milk constituents was markedly depressed. The experiments were, however, of short duration and fluctuations in yield from milking to milking may have masked certain changes.

DISCUSSION

The observed changes in milk composition following the injection of oxytocin and the removal of residual milk persisted for several milking intervals after the technique was discontinued. These changes in the continuous process of milk secretion are similar to those normally observed in milk during late lactation. The main effect was an increase in the secretion of sodium, chloride and whey proteins, which suggests that there is an increase in the entry of a transudate from blood plasma (Barry & Rowland, 1953). That the changes were due to an increased permeability of the mammary epithelium is supported by the observations that oxytocin increases the output of sodium and chloride in the urine of rats (Fraser, 1942) and increases the rate at which sodium is transferred across isolated frog skin (Fuhrman & Ussing, 1951).

An alternative explanation that the changes in the composition of the milk were due to the removal of the residual milk from the udder was not supported by the results of expt. 5, which demonstrated that secretion was affected when the residual milk was not removed after an injection of oxytocin. Since both at the 1st and 2nd milkings of the treatment period there was no change in the composition of the residual milk compared with that removed before the injection of oxytocin, the change cannot have been the result of an immediate effect related to the action of oxytocin in ejecting the milk.

In view of the observed effects of oxytocin on milk composition, its use must be considered suspect for certain types of milk secretion experiment. The profound changes in the output in milk of sodium, chloride and whey proteins in response to oxytocin injections may, however, provide a useful experimental basis for the study of the secretion of these constituents in milk.

We are grateful to Mr T. K. Griffin, Miss M. Weston, Miss S. Futcher and Miss E. Jenkins for skilled technical assistance.

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Changes in moisture distribution caused by partial reworking of butter shortly after churning

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SUMMARY. Samples of butter were reworked at various times after removal from the churn, either in a laboratory mixer or by pressing between a microscope slide and cover glass. Moisture distribution was studied by microscopic examination and by indicator papers.

Reworking within 30 min of completion of the original working caused no change in moisture distribution but delayed reworking caused aggregation of water droplets. The further the setting of the butter had proceeded before reworking, the greater was the extent of aggregation.

Cream-cooling treatments which resulted in a softer butter delayed or decreased the aggregation of droplets caused by reworking.

A theory is suggested relating changes on reworking with the formation of a crystal structure on setting.

The operations of patting or bulk packing of butter involve a certain amount of working. Such working may disturb the moisture distribution, producing colour irregularities or even making the butter leaky. An increase in the interval between churning and patting or packing makes the occurrence of such defects more likely. Von Mohr & von Mohr (1954), for example, have shown that, with summer butter, printing immediately after working did not affect droplet size or distribution. Printing 24 h later, however, increased the maximum droplet size from 10–20 μm to 30 μm . With winter butter of low iodine value von Mohr, Wortmann & Peters (1954) recommended an '8–19–16 °C' temperature treatment of the cream to avoid brittleness, and printing the butter as soon as possible after working to minimize formation of large moisture droplets.

Colour irregularities known in New Zealand as 'packer streak' can be produced when butter is bulk-packed within 1 or 2 h after churning. Typical and extreme instances of this defect are shown in Plate 1. According to Dolby (1956) the lighter-coloured parts are composed of butter which has passed through the packer without being worked and contain water droplets of similar size distribution to those in the original butter. The darker and more streaky parts of the butter have undergone some working in the packer and contain larger water droplets.

From trials with a small-scale packer, Dolby (1956) concluded that streaky colour was intensified by:

- (1) Increase in time between working and packing.

(2) Holding the butter at a lower temperature (40 °F as compared with 55 or 80 °F) before packing.

(3) Underworking the butter.

(4) Cooling the cream rapidly after pasteurization to a temperature below that at which it was to be churned instead of cooling it slowly over the last 5–10 deg F.

The present investigation was planned to study the effect on moisture distribution of subjecting the butter to a small amount of working at various times after churning.

METHODS

Butter manufacture. Experimental butters were made as described by Dolby (1954, 1959).

Reworking of butter

Butter samples taken from the churn were held at 55 °F. They were reworked either on a microscope slide (micro method) or in a laboratory mixer (macro method). Microscope slides and mixer were brought to 55 °F before reworking was started.

Micro method. The principle of the method was based on the observation by von Mohr & von Drachenfels (1956) that in making a 'squash' preparation of butter for microscopic examination large irregular droplets were formed if the temperature of the butter was low (50 or 68 °F), but that aggregation of droplets did not take place at a higher temperature (77 °F) at which the butter was more fluid. The pressing out of the butter can be considered a partial working.

A piece of butter 0.5–1.0 mm in diam. was detached with a needle from a freshly exposed surface of the sample and was placed in a counting chamber 0.01 mm deep. A coverslip was placed over the butter and was pressed down gently with a microscope slide laid on top of the coverslip. The preparation was then ready for microscopic examination. When the water droplets in a sample were to be examined without disturbing their size distribution, squash preparations were made in the same way but with counting chamber and butter at 73 °F.

Macro method. About 500 g of the butter was placed in a hand-operated sigma-blade mixer in which one blade made 2 revolutions to 1 revolution of the other blade. The working given was the minimum which would ensure that all the butter received some working. It was standardized at 50 revolutions of the faster-moving (1 rev/sec) blade.

Samples of butter reworked in the laboratory mixer were examined both microscopically and by means of bromophenol blue indicator paper (Knudsen & Sørensen, 1938) applied to a freshly cut surface of the butter.

Photographic technique

Colour variations in butter were recorded by photographing a freshly cut surface through a deep blue filter (Wratten No. 47; C5) on microfilm and printing on high-contrast paper.

An orange filter was used in photographing indicator papers.

RESULTS

Micro method. Preparations made at 55 °F within a few minutes of removal of the butter from the churn showed size distributions of water droplets similar to those in preparations made at 73 °F; i.e. the working of the butter in preparing the slide caused no aggregation of water droplets. When the butter had been allowed to set for some hours the making of the preparation caused aggregation of droplets. Repetition of the experiments on 12 churnings gave similar results.

Typical photomicrographs reproduced in Plate 2 indicate the changes. Plate 2*a* shows that some enlarged droplets were visible in the preparation made at 3 h, and in that made at 24 h very large irregular droplets were present. In another experiment (Plate 2*b*) there was some aggregation of droplets even in preparations made 1¼ h after churning and pronounced aggregation at 4 h and 24 h.

Macro method. In 3 trials, each involving 3 churnings, samples reworked 5 min and 30 min after removal from the churn gave no evidence of change in droplet size when compared with samples from the same churn which had not been reworked.

Reworking at 1½ h caused some aggregation of water droplets and at 4 h or 24 h it caused obvious aggregation (see Plate 3). Although all 3 churnings showed similar effects, the aggregated droplets formed in churning 1 were not so large as those in churnings 2 and 3.

The differences between churnings with different temperature treatments of the cream were shown in a much more striking manner by indicator paper tests on the reworked samples from the same experiment (Plate 4*a*).

Aggregation of droplets to a size which could just be detected by indicator paper occurred with churning 3 in the sample reworked at 1½ h and was more pronounced in samples reworked at 4 and 24 h. With churnings 1 and 2 leakiness was found only in the samples reworked 24 h after churning. The results of a repetition of this experiment are shown in Plate 4*b*. Here slight leakiness was found in samples from both churnings 2 and 3 reworked at 4 h. In the samples reworked at 24 h there was an increase in leakiness from churning 1 to churning 3.

DISCUSSION

The partial reworking of the butter, either in a mixer or between a microscope slide and coverslip, caused no appreciable change in the size of the droplets if the reworking was done within 30 min after the butter was removed from the churn. Delayed reworking caused an aggregation of droplets the extent of which increased as the period between working and reworking increased. It can be seen from Figs. 3 and 4 that if, in making the butter, the cream was rapidly cooled to below churning temperature (churnings 2 and 3) or if the butter was washed with warmer water (churning 3) the butter became leaky on reworking at an earlier stage than did butter made from slowly cooled cream (churning 1) or washed with colder water (churning 2).

It seems likely that methods of cream cooling or churning which result in a hard and brittle-bodied butter (Dolby 1954, 1959) accelerate and intensify the changes which cause aggregation of water droplets on reworking. Such methods also produce butter which sets more quickly (Wood & Dolby, 1965). Conversely, methods which

produce a softer-bodied butter reduce the setting rate and also minimize the aggregation of water droplets in patting or bulk packing of butter.

It is interesting to speculate on the change which occurs in the setting of butter so that a working operation which at one time causes subdivision of water droplets at another time causes an aggregation.

Thomé & Samuelsson (1956) suggested that it is the butterfat crystals which keep the water phase dispersed, that the smaller the crystals the easier the dispersion, and that the coarsening of moisture droplets is probably caused by the growth of the crystals.

The findings of de Man & Wood (1959), however, indicate that the setting of butter is dependent not on the growth of crystals but on the orientation of the finer crystals (*c.* 1 μm in size) and the building up of a structure. Is it this formation of a structure in the butter which determines its behaviour on partial working?

Mulder, Den Braver & Welle (1956), in an entirely different hypothesis, proposed that the alteration in dispersion of water caused by printing machines was due to the low speed of the working involved. In their view the working of butter could cause both aggregation and subdivision of droplets; high shearing forces favoured subdivision while low shearing forces favoured coalescence. In support of this hypothesis they quoted experiments in which butter which had been worked dry in a churn was rendered leaky by reworking in such a way that the shearing forces acting on the butter were low. Mulder *et al.* (1956) did not state the interval of time between working and reworking in their experiments. Since some of the butters were factory butters reworked in the laboratory and as some were held in rooms at a variety of temperatures before reworking, it seems likely that there was an interval of at least a few hours during which setting could take place.

In the present work it was not found possible to cause any aggregation of droplets by slow working except where time was allowed for some setting to take place. While the magnitude of the shearing forces involved in reworking butter may well have some effect on the subdivision or aggregation of water droplets, it is clear that the degree of setting is of much more importance.

When butter is taken from the churn it is a soft plastic mass in which a small shearing force readily produces a flow. After setting it has a more rigid structure and the first operations of reworking may cause crushing or fracturing rather than flow. This fracturing may allow water droplets to flow together. The effect will obviously be intensified in a hard, brittle butter or in one reworked at a lower temperature. It is only when the butter has been reworked to such a state that the structure of fat crystals has been broken down and the material has become more fluid that water can be re-emulsified. This process is most obvious in the reworking of butter taken from cold storage. Even when the butter has been brought to a suitable temperature before reworking, the first reworking operations bring about a copious evolution of water.

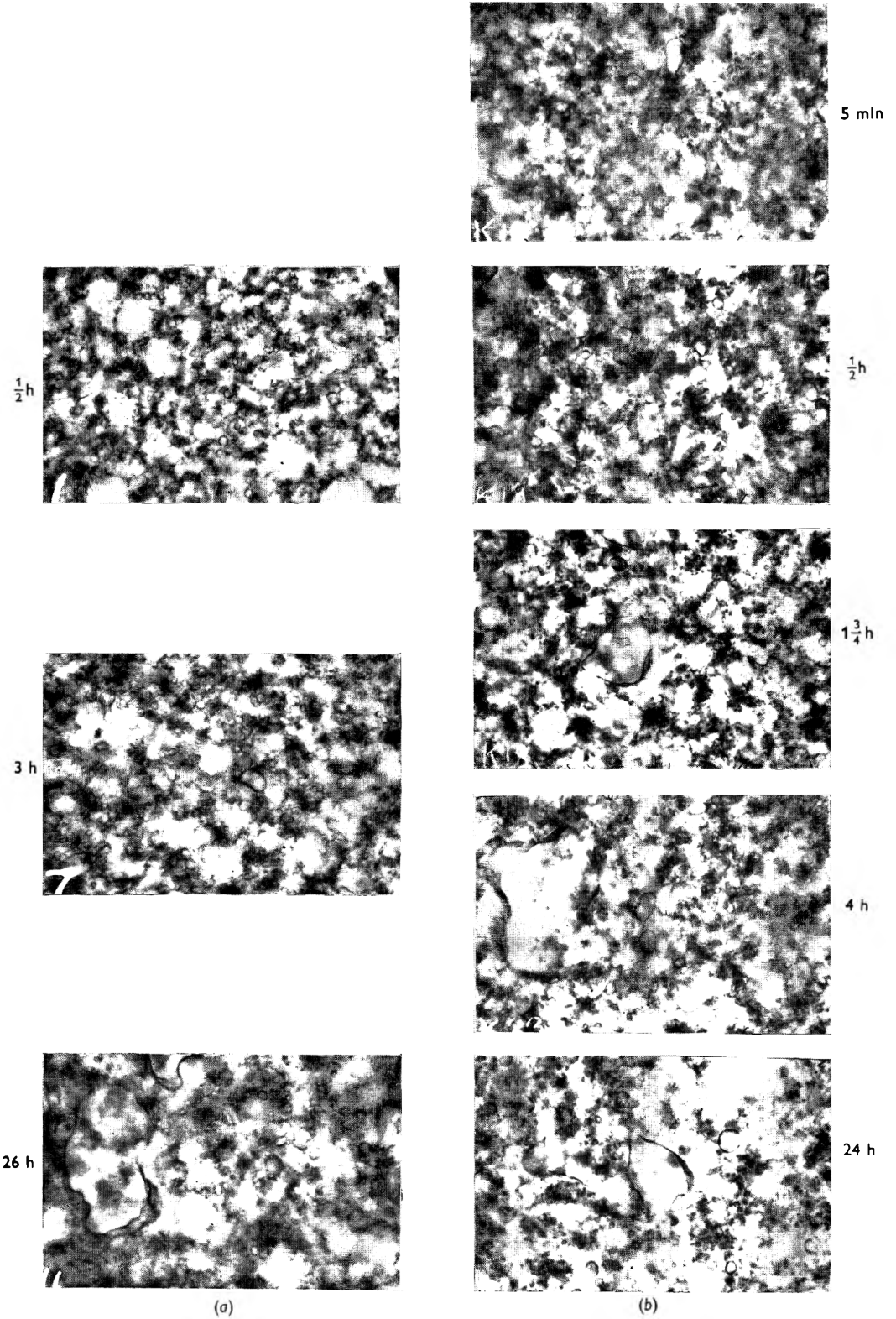
The point at which working of butter begins to cause a coalescence instead of a subdivision of water droplets must therefore be the point at which setting has proceeded far enough for a structure of a certain rigidity to be formed. Any measures which reduce the setting rate will increase the period during which the butter can be patted or bulk packed without detriment to quality.

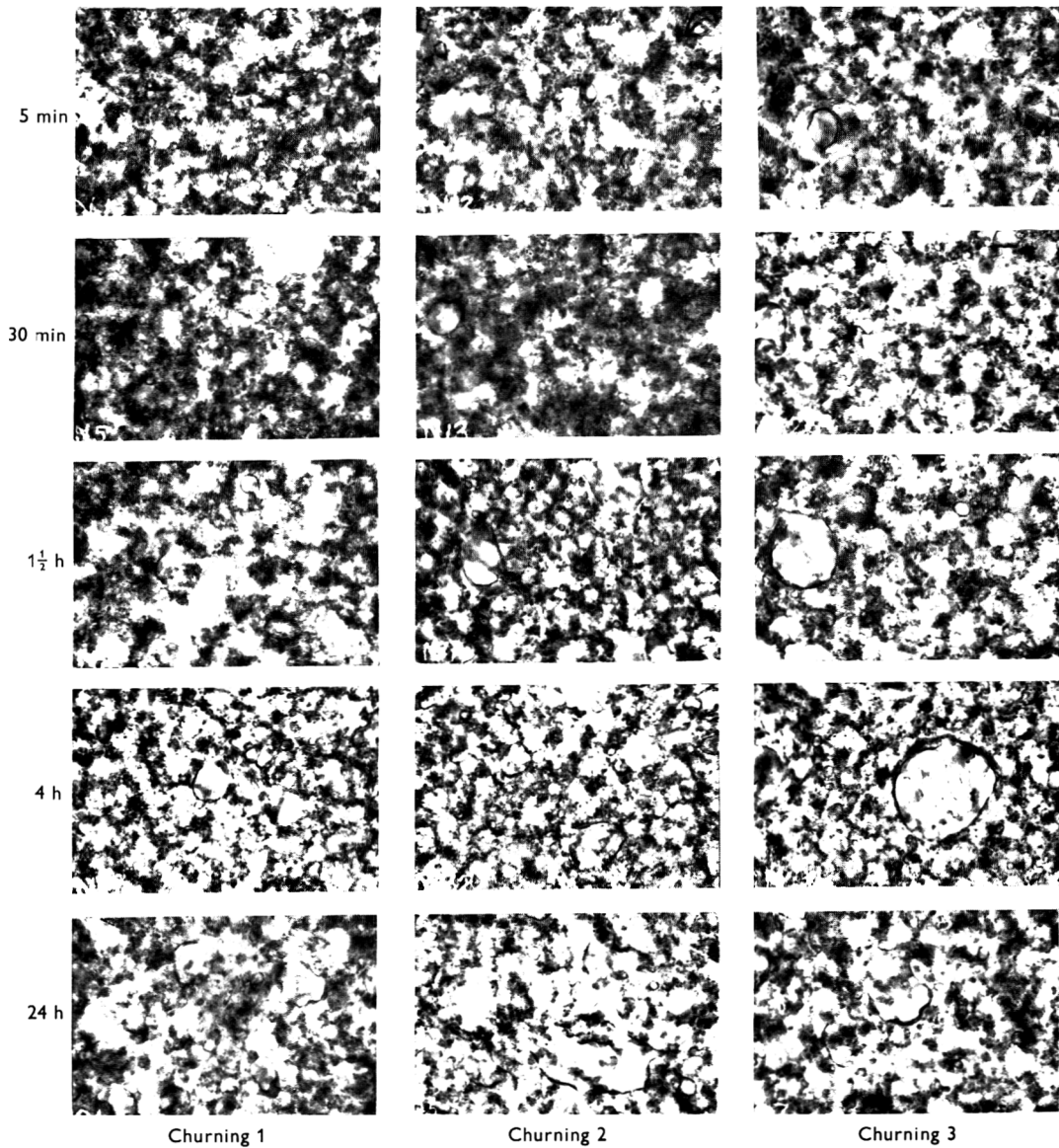


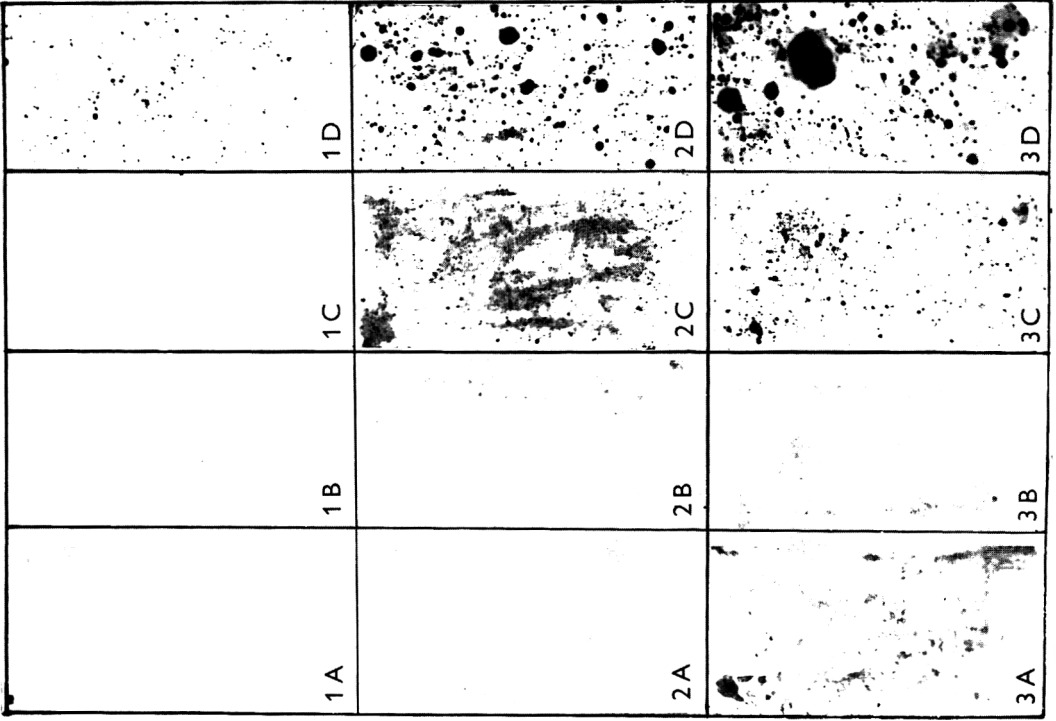
(a)



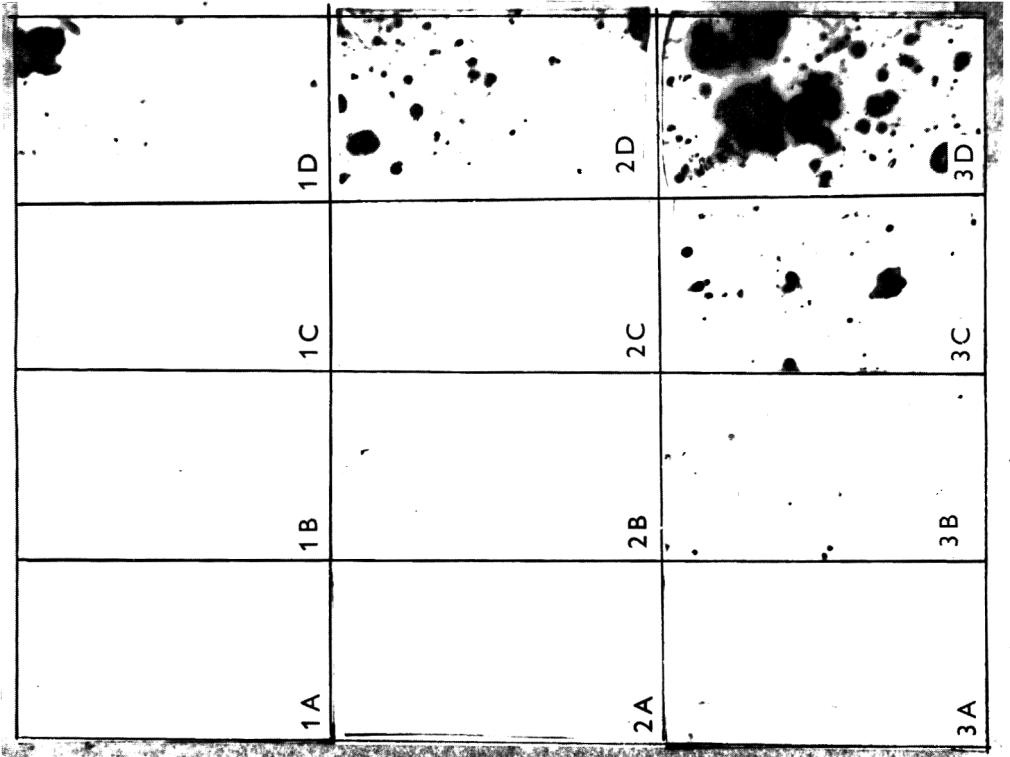
(b)







1/2 h 1 1/2 h 4 h 24 h (b)



1/2 h 1 1/2 h 4 h 24 h (a)

The author is indebted to Mr B. S. LeHeron for the experimental buttermaking and to Miss M. E. Burton for assistance with laboratory work.

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EXPLANATION OF PLATES

PLATE 1

'Packer streak' in butter. (a) Typical example; (b) extreme example of defect.

PLATE 2

Photomicrographs of squash preparations made at 55 °F on butter from 2 churnings at various times after the end of working.

PLATE 3

Photomicrographs of samples of butter from 3 churnings reworked at various times after end of original working. Churning 1. Cream cooled rapidly to 54 °F, churned at 50 °F, washed at 40 °F. Churning 2. Cream cooled rapidly to 40 °F, churned at 50 °F, washed at 36 °F. Churning 3. Cream cooled rapidly to 40 °F, churned at 50 °F, washed at 47 °F.

PLATE 4

Indicator paper tests showing leakiness in butter from 3 churnings reworked at various times after original working; (a) and (b) show results for duplicate experiments. Churning conditions as for Plate 3.

The influence of cream-processing methods on the rate of setting and final hardness of sweet cream butter

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SUMMARY. Cream-cooling rates, cream-pre-cooling treatments (Alnarp) and seasonal changes in the chemical composition of butterfat were found to influence the setting rate of butter. Vacreator pasteurization, however, especially at high steam intensity, had the greatest effect. Comparative hardness values of butter made from plate-pasteurized and Vacreator-pasteurized cream were 1.5 and 2.9 kg and 4.4 and 8.3 kg at the end of $\frac{1}{2}$ and 5 h, respectively, after the completion of working. The highest setting rate, which resulted in a hardness of 6 kg at the end of 30 min, was recorded for butter made from Vacreator-pasteurized cream which was rapidly cooled to 5 deg F below normal churning temperature and churned after holding for 30 min. Abrupt breaks noted in the setting curves of this rapidly setting butter lead to speculation that changes in the butterfat crystal form may be involved.

In general, the final hardness values of butter stored at 45 °F for 30–50 days were not greatly influenced by the setting rates observed at 55 °F during the 5-h period immediately after the completion of working. Exceptions to this observation were obtained when the cream was rapidly cooled to or slightly below churning temperature and also when the cooling of plate-pasteurized cream was delayed at 65 °F for 3–4 h before final cooling to the churning temperature.

The causes of the differences observed in the setting and final hardness values of butters made from plate- and Vacreator-pasteurized cream were not determined and warrant further investigation.

In discussing the phenomenon of setting hardness of butter, Mulder (1949) expressed surprise that so little research had been reported on this important property of butter. Since then Prentice (1953), Huebner & Thomsen (1957) and de Man & Wood (1958, 1959*a, b*) have contributed to the information available on the setting of sweet cream butter made by conventional and continuous buttermaking methods. These investigations have focused attention on the effect of working, storage temperatures and method of manufacture.

Paucity of information on the influence of thermal treatments of cream, including methods of pasteurization, on the setting and final hardness of sweet cream butter prompted the present investigation. Such data should be valuable in determining the possible effect of setting immediately after working on the development of colour

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and texture defects of butter during moulding and packing operations and, also, in establishing the effect of setting on the power requirements of working and moulding operations.

METHODS

Buttermaking. Cream for the churnings to be compared was bulked in a receiving vat. Except in certain experiments in which a plate-pasteurizer was used, all cream was heat-treated in a Vacreator. The pasteurizing temperature was normally 205–207 °F, with 15 inHg and 28 inHg vacuum on first and second units, respectively, and a treatment intensity of 3.5–4 lb steam/gal cream (350–400 Btu/lb cream). The cream was cooled in a plate heat exchanger and run into holding vats. These vats were fitted with propeller stirrers and were cooled with water circulated through the vat jackets, the circulation being controlled by a thermostat in the cream. Cream was normally held in the vat overnight at the temperature chosen for churning (45–50 °F, depending on seasonal variations) and was then churned in a Silkeborg cubical stainless steel churn. The granules were washed with water at 40–43 °F. The churn barrel was cooled with a spray of chilled water when necessary to prevent the temperature of the butter during working from exceeding 55 °F.

Hardness determinations. The penetrometer method of Kruisheer & Den Herder, as modified by Wood & de Man (1956) and by de Man & Wood (1958), was used. A FIRA NIRD extruder (Prentice, 1954), was modified to drive the disk plunger into the butter at the rate of 4 cm/min. The forms for sampling and holding the butter during incubation and testing were cylinders 1.15 in. long cut from 2 in. o.d. stainless steel tubing and sharpened at one end.

Samples taken immediately after the completion of working were cut out of a layer of the butter. Butter held in storage at 45 °F was sampled by forcing the sharpened end of the sampling cylinders into slices cut from the bulk samples, taking care to avoid fracturing or mechanically working the butter.

Up to 5 h after manufacture of the butter, setting hardness was measured at 55 °F on samples maintained at this temperature in a water bath. The hardness of butter stored at 45 °F was measured after tempering the samples at 62.6 ± 0.6 °F for 24 h. A lower testing temperature, e.g. 55 °F, was unsatisfactory for the Kruisheer and Den Herder penetrometer method of hardness determination as a cleavage in the structure of butter occurred in many samples when the force applied exceeded some 5 kg. All hardness determinations were made in duplicate and are expressed in kg/4 cm².

RESULTS

The results are presented in the form of setting curves representative of the data obtained for each cream treatment.

Comparison of 3 cream-cooling methods

A modified Alnarp pre-cooling procedure (Dolby, 1953) and 2 methods representing extremes of commercial practice in New Zealand were compared. The cream was treated in a Vacreator and cooled as follows:

Churning 1. Pre-cooled to 39–40 °F, held for 8 sec in a holding tube and reheated to 65 °F in a plate heat exchanger with heating water not exceeding 78 °F; held at

65 °F in a vat for 3–4 h then cooled slowly to churning temperature and held overnight.

Churning 2. Cooled in a plate cooler to 6–7 deg F above churning temperature, further cooled slowly in a vat over 3 h to churning temperature and held overnight.

Churning 3. Cooled in a plate cooler to 2–3 deg F below churning temperature, allowed to rise to churning temperature in a vat and held overnight.

Results obtained are shown in Fig. 1. The setting rates for churnings 2 and 3 were the same over the first hour of setting. Thereafter the setting rate for churning 2 decreased more rapidly than for churning 3. The time required to attain a hardness of 4 kg (churnings 2 and 3, 1½ h; churning 1, 4 h) is indicative of the difference in the setting rate of these butters. In cold storage at 45 °F the setting rates for all churnings were similar, but the hardness values in kg at the end of 30 days storage were as follows: churning 1, 5.4; churning 2, 7.5; churning 3, 9.5.

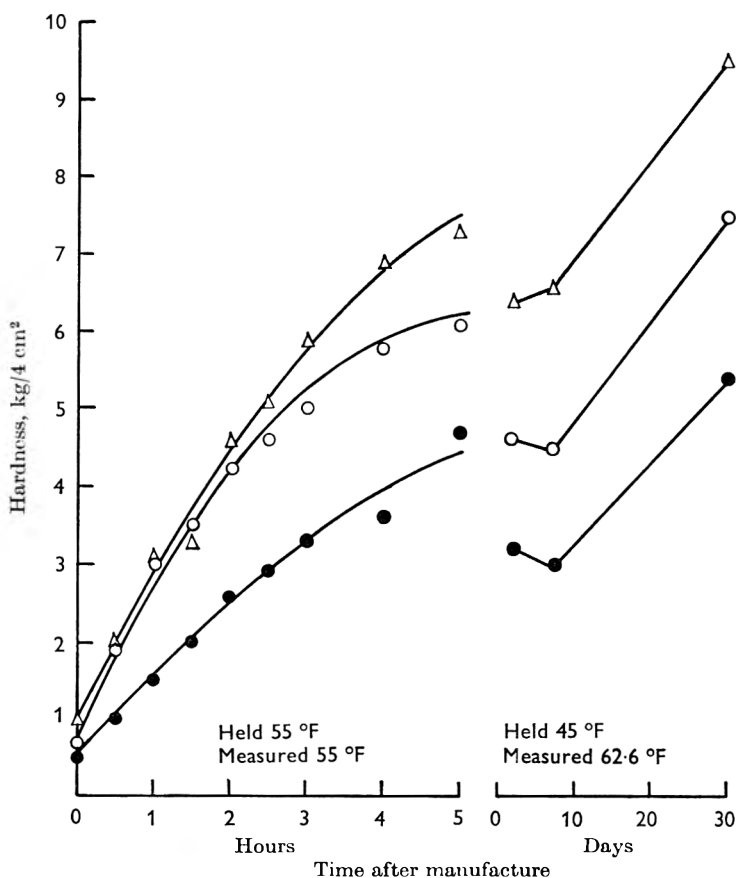


Fig. 1. Setting curves for butter made from cream given different cooling treatments.
●, Churning 1; ○, churning 2; △, churning 3.

The effects of seasonal variations in butterfat composition on setting rates of butter are illustrated in Fig. 2, which shows setting curves for butter manufactured under the conditions of churning 2 during the months October–March. The butterfat constants and churning temperatures are given in Table 1. The marked increase in setting rate with decrease in iodine value of fat is very striking.

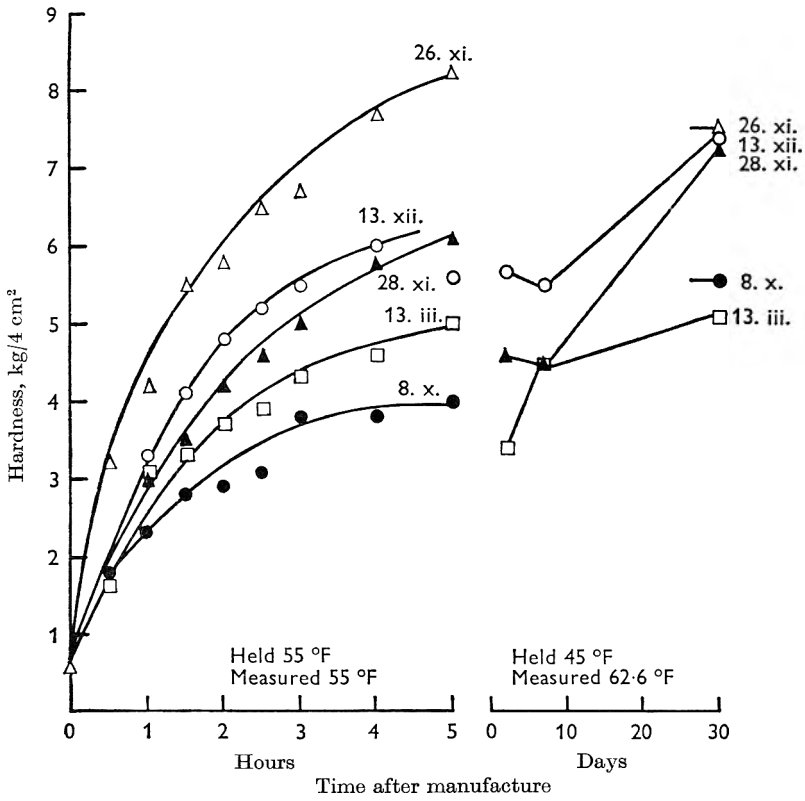


Fig. 2. Seasonal variations in setting rate of butter churned under similar conditions. Day and month of churning is shown on each graph.

Table 1. Seasonal variations of butterfat constants and churning temperatures*

Date	Iodine value	Refr. index	Soft pt., °C	Churn Temp., °F	Hardness, kg/4 cm ²	
					At 55 °F 5 h	At 62.6 °F 21 days
8. x.	34.0	1.4539	33.1	46	4.0	5.6
22. x.	32.4	1.4536	33.0	48	5.3	6.1
26. xi.	31.0	1.4533	34.1	49.5	8.3	7.5
13. xii.	31.4	1.4535	33.8	49	5.6	7.6
17. i.	32.8	1.4538	34.3	48.5	6.4	6.8
28. 1.	33.4	1.4539	33.8	48	6.1	7.5
13. iii.	35.2	1.4541	34.4	47	5.0	5.1

* No. 2 churnings only (see text).

The effect of the time interval between pasteurization and churning

The cream, after pasteurization in a Vacreator, was treated as follows:

Churning 1. Rapidly cooled in a plate cooler to 5 deg F below normal churning temperature, held at this temperature for 30 min and then churned.

Churning 2. Rapidly cooled in a plate cooler to 2 deg F below normal churning temperature, held for 1 h at this temperature and then churned.

Churning 3. Cooled in a plate cooler to normal churning temperature and churned at this temperature after holding overnight.

The setting rates recorded for the butter from churnings 1 and 2 (Fig. 3) were quite spectacular. The setting hardness of churning 1 was 6 kg at the end of 30 min. The times required by the other churnings to reach this hardness level were: churning 2, 1½ h; churning 3, 3 h. This difference in the setting rate and final hardness was not continued when the butter was stored at 45 °F for 30 days. Over this period the hardness of butter from churnings 1 and 2 increased less than that of butter from churning 3, which received a normal cooling temperature treatment, so that the final hardness of all the butters at the end of 30 days' storage was within the range of 7.2–7.7 kgs.

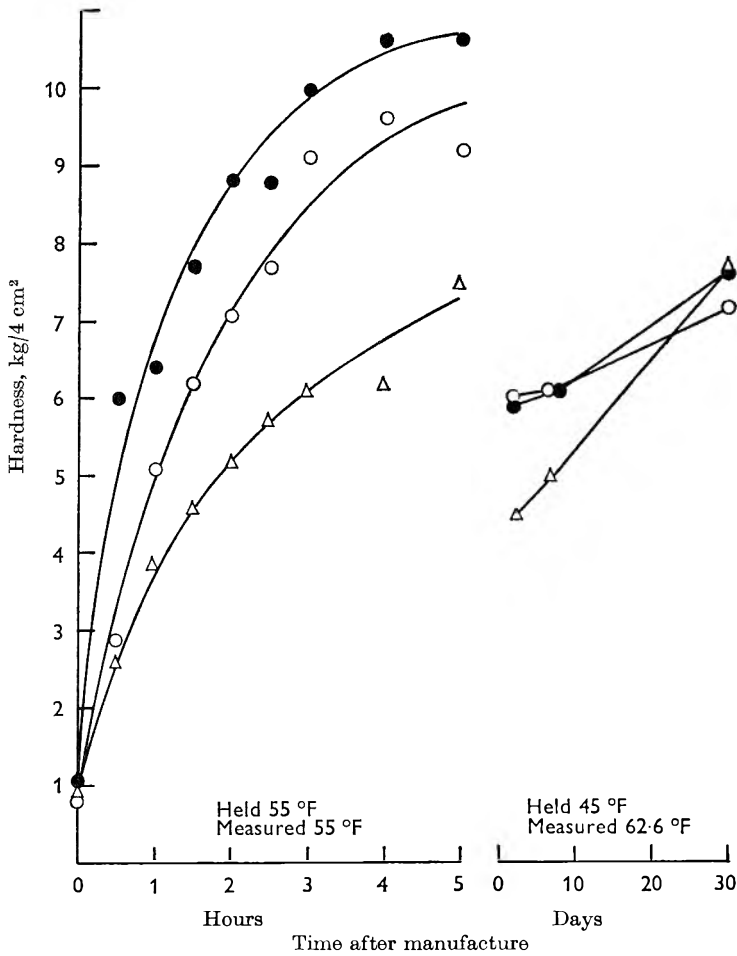


Fig. 3. Setting curves for butter churned at different times after pasteurization.
 ●, Churning 1; ○, churning 2; △, churning 3.

In some of these comparisons, pronounced changes occurred in the setting rates of churnings 1 and 2 within the first 2 h of setting. This was most apparent for churning 1, which received the most drastic cooling treatment followed by churning after holding for only 30 min. The setting curves of Fig. 4 represent the data for the butter churned on 31 October. All replicates of these churnings lacked plasticity and had a short-grained or carrotty texture.

The effect of the method of pasteurization

The heat treatments of the cream were as follows:

Churning 1. Pasteurized at 185–190 °F, with holding for 10 sec in a plate heat exchanger.

Churning 2. Vacreator-pasteurized at low steam treatment intensity—122 Btu/lb of cream.

Churning 3. Vacreator-pasteurized at high steam treatment intensity—614 Btu/lb of cream.

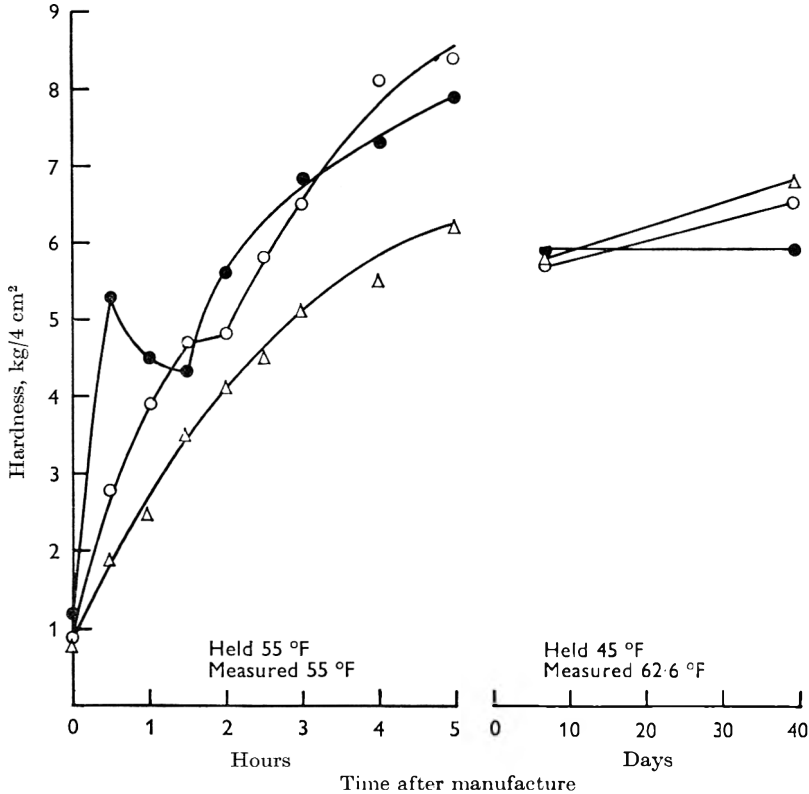


Fig. 4. Setting curves for butter churned at different times after pasteurization.
●, Churning 1; ○, churning 2; △, churning 3.

After pasteurization, cream for all churnings was cooled to 53 °F in a plate cooler and held at this temperature for 30 min in holding vats before being brought to the churning temperature at which it was held until the next day.

The data obtained (Fig. 5) show that the butter made from the Vacreator-pasteurized cream, especially churning 3, which received the highest intensity steam treatment, had much higher setting rates at 55 °F than the butter made from the plate-pasteurized cream. The times for the butter to attain a hardness value of 4 kg—1, 2 and 3 h for churnings 3, 2 and 1, respectively—indicate the differences in the setting rates. The setting hardness values of the 3 churnings were in the same order at the end of 2 days of storage at 45° F. Thereafter the hardness differences narrowed until all churnings had essentially the same hardness at the end of 30 days of storage.

The effect of modifications of the Alnarp (Swedish) cream-pre-cooling method

(a) Vacreator-pasteurized cream

After Vacreator treatment the cream was cooled as follows:

Churning 1. Pre-cooled in a plate heat exchanger to 45 °F, held at this temperature for 2 h, then raised in temperature to 65 °F in a water-jacketed vat with water at a temperature not exceeding 78 °F. After holding at 65 °F for 4 h the cream was finally cooled to and held at the churning temperature overnight.

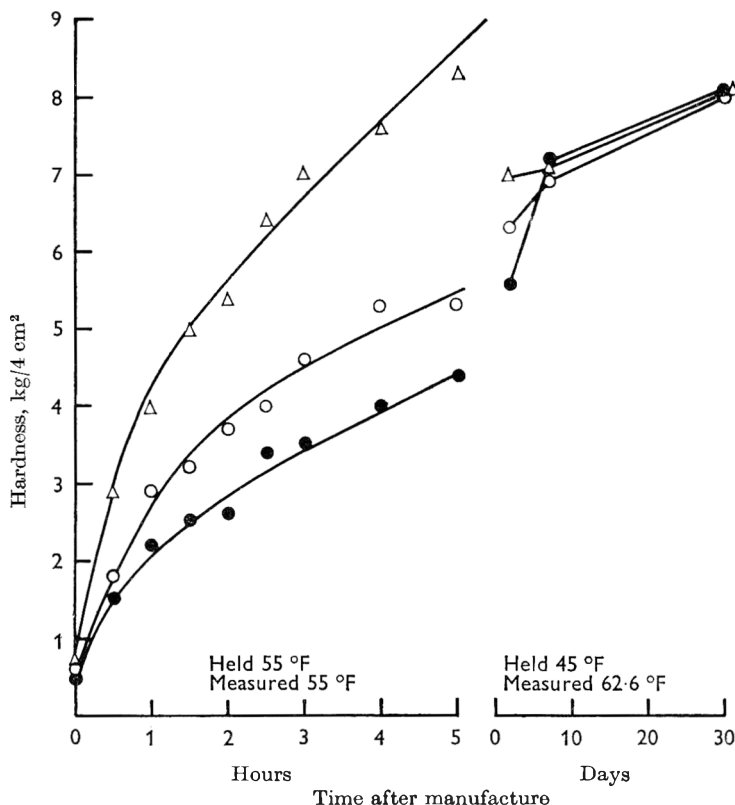


Fig. 5. Setting curves for butter from cream pasteurized by different methods. ●, Churning 1; ○, churning 2; △, churning 3.

Churning 2. The cream was pre-cooled in a plate heat exchanger to 39–40 °F, held for only 8 sec and then reheated in the same equipment to 65 °F. The remainder of the treatment was the same as for churning 1.

Churning 3. The pre-cooling step was omitted; otherwise the temperature treatment was the same as that for churnings 1 and 2.

The setting rates at 55 °F (Fig. 6a) for the 3 modifications of the Alnarp cream-pre-cooling and cooling methods showed small but consistent differences, those for the butter made from the pre-cooled cream, churnings 1 and 2, being lower than those for the butter made from the non-pre-cooled cream, churning 3. The setting rates during storage at 45 °F and the final hardness values of all churnings were almost alike.

The setting and final hardness values of these butters were much lower than those found for butters made at approximately the same time of the year from cream given the cooling and churning procedures in New Zealand factories (Fig. 1, churning 2 and 3; Fig. 5, churning 2 and 3).

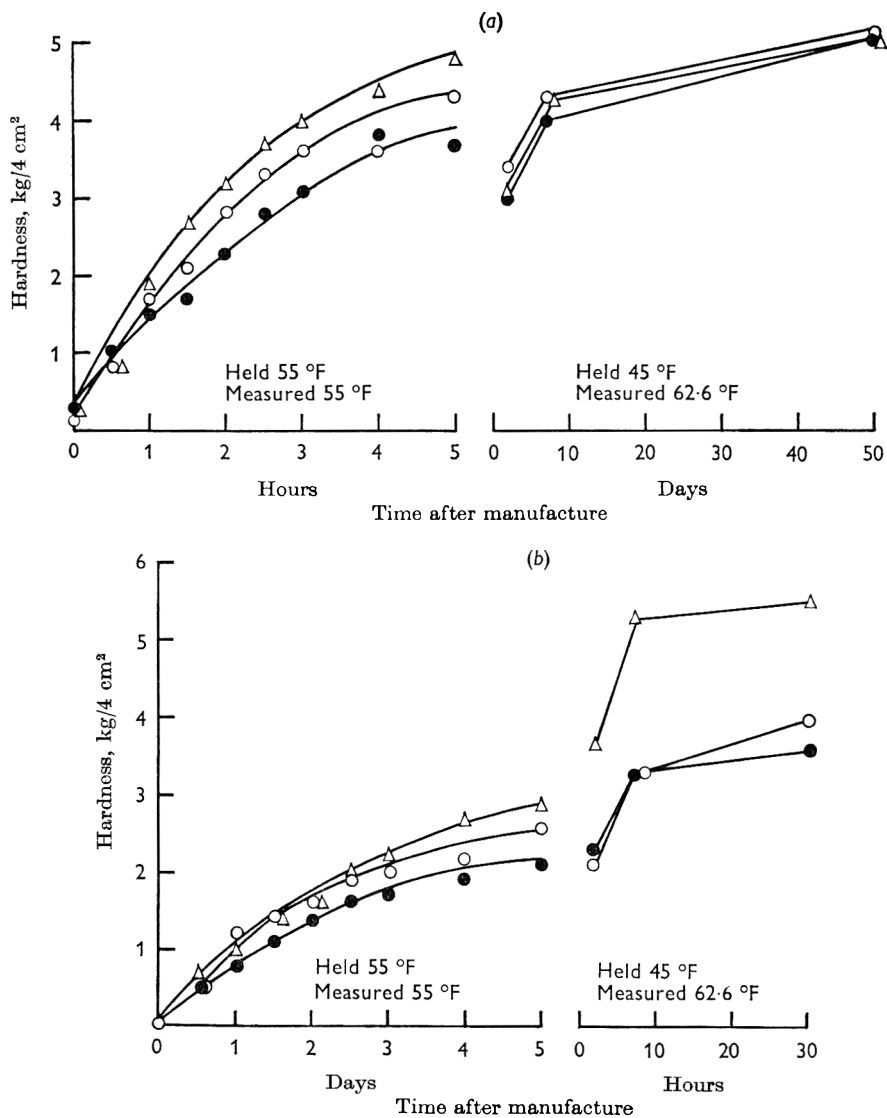


Fig. 6. Setting curves for butter from cream given various pre-cooling treatments (see text). (a) Vacreator-treated cream; (b) plate-pasteurized cream. ●, Churning 1; ○, churning 2; △, churning 3.

(b) Cream pasteurized in a plate heat exchanger

Except for the method of pasteurization of the cream (plate pasteurization at 135 °F with a holding time of 10 sec) the cream treatment was the same as that of the Vacreator-treated cream (section (a)).

The setting rates and hardness values, given in Fig. 6b, show that the setting rates at 55 °F for all churning were lower than those for Vacreator-treated cream receiving

the same thermal treatment (Fig. 6*a*). The butter made from the pre-cooled cream was also softer, especially churning 1, which was pre-cooled for 2 h at 45 °F. The setting and hardness values of the butter stored at 45 °F were very similar for churnings 1 and 2, which were made from cream receiving pre-cooling treatments. The hardness of the butter made from non-pre-cooled cream (churning 3), however, was higher throughout the storage time at this temperature.

DISCUSSION

The results obtained in this investigation show that the setting rates and final hardness values of the butter made in New Zealand were much higher than those reported for other countries where hardness values have been expressed in comparable (Kruisheer & Den Herder) units. Canadian investigators, de Man & Wood (1958), reported a setting hardness of only 2 kg at the end of 6 h at 55 °F and a seasonal range of hardness from 1.5 kg for summer butter to 3.2 kg for winter butter when measurements were made at 62.6 °F. In the present investigation butter made from cream cooled and churned under normal factory conditions (Fig. 2) had hardness values of 4.0 kg in spring and 8.3 kg in summer after 5 h setting at 55 °F. The same butters after 30 days at 45 °F had hardness values at 62 °F of 5.6 and 7.5 kg, respectively. In a recent Swedish survey, Olsson & Swartling (1962) report that 95.7% of the butter made from cream with an iodine value of 31.0–33.9 falls in the hardness range of 2.3–6.2 kg. Hardness values found in the present investigation were in the upper end of this range unless the butter was made from plate-pasteurized cream or from cream that received a thermal treatment that reduced hardness.

The principal differences between butter factory practices in New Zealand and those in most other butter-producing countries are in the methods of pasteurization and cooling of the cream. In New Zealand butter factories cream is pasteurized and deodorized in a Vacreator or in some other unit using direct steam heating. After pasteurization the cream is normally cooled in a plate heat exchanger to a temperature above the churning temperature. Further reduction of temperature in the holding vats, which may be of 3000-gal capacity, is limited by the amount of refrigeration that can be applied, and rarely exceeds 5–6 deg F.

The results shown in Fig. 1 indicate that some reduction in setting rate and final hardness is brought about by performing the last stages of cooling slowly in a vat instead of very rapidly in a heat exchanger, but these values are still considerably higher than those obtained on butter made from cream cooled slowly by a modified Alnarp procedure. These results could be anticipated from the findings of Andersen (1949), de Man & Wood (1959*b*) and Tverdokhlebov (1962), who have shown by dilatometric techniques that rapid cooling of milk fat greatly increases the content of crystalline fat.

The very high setting rates obtained when the cream was rapidly cooled to a low temperature to permit churning 30–60 min after pasteurization (Fig. 3) also indicate a high content of crystalline fat. Such rapid cream-cooling rates and short holding times before churning are uncommon in New Zealand but are used in other countries at the peak of the production season when cream storage facilities are limited. In a number of replications of this cooling method, the setting rate at 55 °F fluctuated considerably. This was most apparent in the results shown in Fig. 4 and leads to

speculation that changes in butterfat crystal form may occur under these conditions, when the time between the rapid cooling of the cream and the final working of the butter is much shorter than in normal buttermaking. The observation that butter made in this way lacked plasticity and had a texture described as brittle or carrotty lends further support to this view.

Vacreator treatment of cream markedly increased the setting rate of butter held at 55 °F (a normal temperature at the end of the working process) after the completion of working. This was especially true at high intensities of steam treatment and accounts for the very rapid setting of butter observed throughout this investigation. The method of pasteurization also affected the results obtained by pre-cooling and non-pre-cooling of cream. Dolby (1959) reported that contrary to the results reported by Samuelsson & Pettersson (1937) and Olsson (1948) pre-cooling under New Zealand conditions did not reduce the hardness of butter. The results obtained in the present study confirm this finding when the cream was pasteurized in a Vacreator. However, Alnarp pre-cooling procedures were found to be effective in reducing the final hardness of butter made from cream pasteurized in a plate heat exchanger.

Dolby (1953) has shown that Vacreator treatment of cream has 2 effects on the milk fat globules:

1. A subdivision of some of the globules which occurs where the mixture of steam and cream reaches a very high velocity in passing from one section of the Vacreator to another.

2. A clumping effect caused by boiling of the cream under reduced pressure. The clumping effect was much less than that found with flash-pasteurized cream and, while the fat clumps formed in this cream were readily observed in the butter, that from Vacreator-treated cream did not show any such uneven texture. Higher intensities of steam treatment in the Vacreator caused increases in the numbers of small globules and decreases in the numbers of clumps.

In the present experiments the highest setting rate was found in butter from cream which had been given a high-intensity Vacreator treatment. It appears therefore that the effect of Vacreator treatment on setting rate may be due to subdivision rather than to clumping of fat globules.

When butter made from Vacreator-treated cream was examined by polarized-light microscopy the fat crystals were consistently found to be smaller than those seen in butter made from plate-pasteurized cream.

The large milk fat globules containing crystalline fat, frequently seen in the butter made from plate-pasteurized cream, were absent in all examinations of butter made from Vacreator-pasteurized cream. These results suggest that the reduction in size of fat globules resulting from Vacreator treatment has an effect on the size of fat crystals formed in the globules.

The marked differences found in the physical properties, setting and final hardness of butters made from Vacreator- and plate-pasteurized cream warrant further investigation into the causes of these differences.

The senior author is grateful for the facilities that were made available for conducting this investigation and also for the assistance received from the staff of the Institute.

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A simple laboratory-scale HTST milk pasteurizer

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SUMMARY. A simple, quick, batch-type method for the laboratory-scale HTST pasteurization of milk is described and details of construction, operation, cleaning and sterilization of the apparatus are given. The heating and cooling curves approximate closely to those of commercial HTST milk-pasteurizing plants and the end-product, as measured by residual phosphatase, is similar. The method has a relatively high sample throughput and is suitable for the routine pasteurization of large numbers of milk samples of up to 300 ml in volume. Other possible applications of the method are discussed.

Pasteurization of liquid milk is usually achieved commercially by the high-temperature short-time (HTST) process. In the United Kingdom, it is required (The Milk (Special Designation) Regulations, 1963) that milk treated in this way shall be heated to, and held at, a temperature of not less than 161 °F for at least 15 sec. It is common practice, however, in order to study the effects of pasteurization, for laboratories to treat samples by a holder method in which the milk is heated to and held at 145 °F for 30 min (Clegg, Egdell, Thomas, McKenzie & Cuthbert, 1950; Franklin, 1965*a*). This method is used because of the lack of a suitable means of reproducing the HTST process in the laboratory. It was shown by Franklin (1965*b*) that the bactericidal efficiencies of laboratory holder and HTST pasteurization are not always equivalent and vary with different bacterial strains. Therefore, where the aim is to reproduce the end-product of commercial HTST pasteurization, a laboratory-scale HTST treatment should be used and various published methods capable of achieving this were referred to by Franklin (1965*c*). These methods, however, do not provide a laboratory HTST process capable of replacing the laboratory holder method for routine examination of large numbers of milk samples in control laboratories. Some are complex and more suited to research, pilot plant scale or demonstration applications; others give a poor reproduction of the complete commercial HTST process or necessitate the treatment of volumes of milk which are too large to be practicable or too small to yield results representative of the bulk.

It is considered that any method with its associated apparatus to be readily acceptable for routine application should ideally satisfy the following special requirements: (i) be capable of subjecting the milk to time-temperature conditions similar to those occurring in commercial plants, including the heating-up and cooling-down processes; (ii) be capable of treating quantities of milk sufficiently large to ensure that they are representative of the bulk but small enough to allow tests on milk

of individual producers. (It has been shown (Franklin, 1965*c*) that milk samples of $> \frac{1}{2}$ pint are necessary before reproducible results after pasteurization can be expected.)

In commercial continuous flow HTST pasteurization different particles of milk receive slightly different treatments because of differences in flow velocities and other effects and consequently an empirical approach of ensuring that all particles receive a certain minimum treatment is practised. Any given set of operating conditions will result in an end-product consisting of a mixture of slightly differently heated particles. In at least one property, i.e. phosphatase destruction, the overall quality of the product can be conveniently measured and related to the operating conditions of the plant. Provided a laboratory method has closely similar rates of heating and cooling as well as time of holding, and results in similar phosphatase destructions to those obtained with a commercial plant over a range of treatment temperatures, it is reasonable to assume that the 2 methods are equivalent. Phosphatase destruction curves have been used to assess laboratory HTST pasteurizers by MacWalter & Wright (1962) and Franklin (1965*c*). It is not considered essential that a laboratory method should be of a continuous flow type with its associated difficulties of maintaining constant flow, establishing steady operating conditions when only small quantities of milk are available, cleaning and sterilization of pumps and wear of moving parts. Moreover, a batch process would also yield a product composed of particles of milk which have been heated to slightly differing extents but which have all received a certain minimum treatment.

With these considerations in mind, the following apparatus and method suitable for the routine laboratory HTST pasteurization of milk was developed.

DESIGN OF APPARATUS

(A) *Pasteurizing unit.* This is made of stainless steel, has a capacity of 300 ml and is shown opened to reveal some of the internal features in Plate 1. A drawing with description and dimensions is given in Fig. 1. The gasket can be cut from suitable sheet material, e.g. silicone rubber or neoprene, to enable sterilization by autoclaving if desired, but because of difficulties encountered in obtaining such material of the required thickness, satisfactory gaskets were moulded from 'Escorubber' white silicone moulding paste SR 600 (Esco (Rubber) Ltd., Seal Works, Seal Street, London, E. 8) reinforced with single glass fibres taken from scrim (type GS; Holt Products Ltd., New Addington, Surrey) as follows. About 95 ml of the rubber paste is mixed with 0.5 ml non-toxic catalyst. A little is then poured into a rectangular groove of the dimensions of the finished gasket milled in a 0.5-in. thick sheet of Perspex. About 18 individual strands of fibreglass each equal to the length of the perimeter of the mould grooves are coated with rubber and laid in the mould, which is then slightly overfilled with more rubber paste. A Perspex sheet is pressed on to the groove forcing out the surplus paste without entrapping air, and is retained in position for 48 h with clamps or weights. After removing the gasket from the mould the edges are trimmed with a scalpel and the bolt holes made with a cork borer.

(B) *Heating bath.* This is shown containing the pasteurizing unit in Plate 2 and

is a water-bath (Model SB 3; Grant Instruments (Cambridge) Ltd, Barrington, Cambridge) with the depth increased by 2 in. to give a working volume of 21 in. \times 12 in. \times 11 $\frac{3}{8}$ in. The bath is fitted with a 1 kW heater for normal operation and a 1 $\frac{1}{2}$ -kW heater for boosting purposes. The 1 kW heater is controlled by a mercury contact thermometer and mercury relay which in a covered bath enables the temperature to be controlled within ± 0.05 °C. Forced water circulation ensures uniformity of temperature at all points in the bath and it is important to ensure by regular inspection that this circulation is not impaired for any reason. The only difficulties of this nature encountered have been caused by fouling of the impeller by cotton wool, or other fibrous material, gaining access to the water and by sagging of the false bottom due to the weight of the pasteurizing unit. The latter difficulty was overcome by placing small additional supports under the centre of the false bottom, taking care that they did not interfere with the water flow.

It is essential for treatment reproducibility that the temperature of the water should be controlled to an accuracy greater than is possible in an open bath of this type because of rapid local cooling at the surface. At a working temperature of about 161 °F, evaporation losses in an open bath are also excessive. Use of a lid is impracticable because of the height of the pasteurizing unit and the frequency of removal that is necessary. The problem was overcome, therefore, by the use of 20 mm diam. 'Allplas' polypropylene spheres (Capricorn Industrial Services Ltd, 49 St James's Street, London, S.W. 1) to cover the water surface (Plate 2), thus reducing heat and water losses considerably without impairing the movement of the heater in and out of the bath.

(C) *Cooling bath.* This is the smaller bath shown in Plate 2; it is constructed in copper with internal dimensions 25 in. \times 9 in. \times 16 in. The bath is fitted with inlet and outlet tubes to allow the continuous flow of cooling water and giving a working depth of 10 $\frac{1}{2}$ in.

METHOD OF OPERATION

The hot water heaters are switched on, the water is allowed to attain the required temperature, and the booster heater is then switched off. The pasteurizing unit is placed in the water so that all except the handle, funnel and part of the inlet and outlet tubes are submerged (see immersion level indicated by I in Fig. 1), and allowed to attain water temperature (about 1 min). It is important that the unit is positioned parallel to the sides of the bath so as not to interfere with the end-to-end system of water circulation necessary to maintain uniformity of temperature. A $\frac{1}{2}$ -pint volume of milk to be treated is then poured into the funnel F (Fig. 1) from a beaker in one rapid steady movement so that the entire volume passes into the space between the plates of the unit in < 2 sec. The funnel is then unscrewed from the septum M and removed together with the captive washer W. The flanged sleeve L, possibly soiled with raw milk from the end of the funnel F during removal, is also withdrawn, leaving all metal surfaces above water level free from milk, thereby ensuring that the treated milk cannot be contaminated with undertreated milk residues during subsequent manipulations. The inlet tube is then closed with a sterile rubber bung, the outlet tube having been closed from the start with a sterile non-absorbent cotton-wool plug or a loose-fitting metal cap.

At the end of the treatment time the pasteurizing unit is quickly transferred to the cooling bath, where a rapid decrease in milk temperature occurs. Operators, after very little practice, quickly achieve a high degree of uniformity of transfer time of 5 ± 0.5 sec. Slight variations in transfer time have little effect since they comprise only a very small proportion of the total heating cycle. When sufficiently cooled the apparatus is removed from the bath and the sample poured via the outlet tube O into a suitable container.

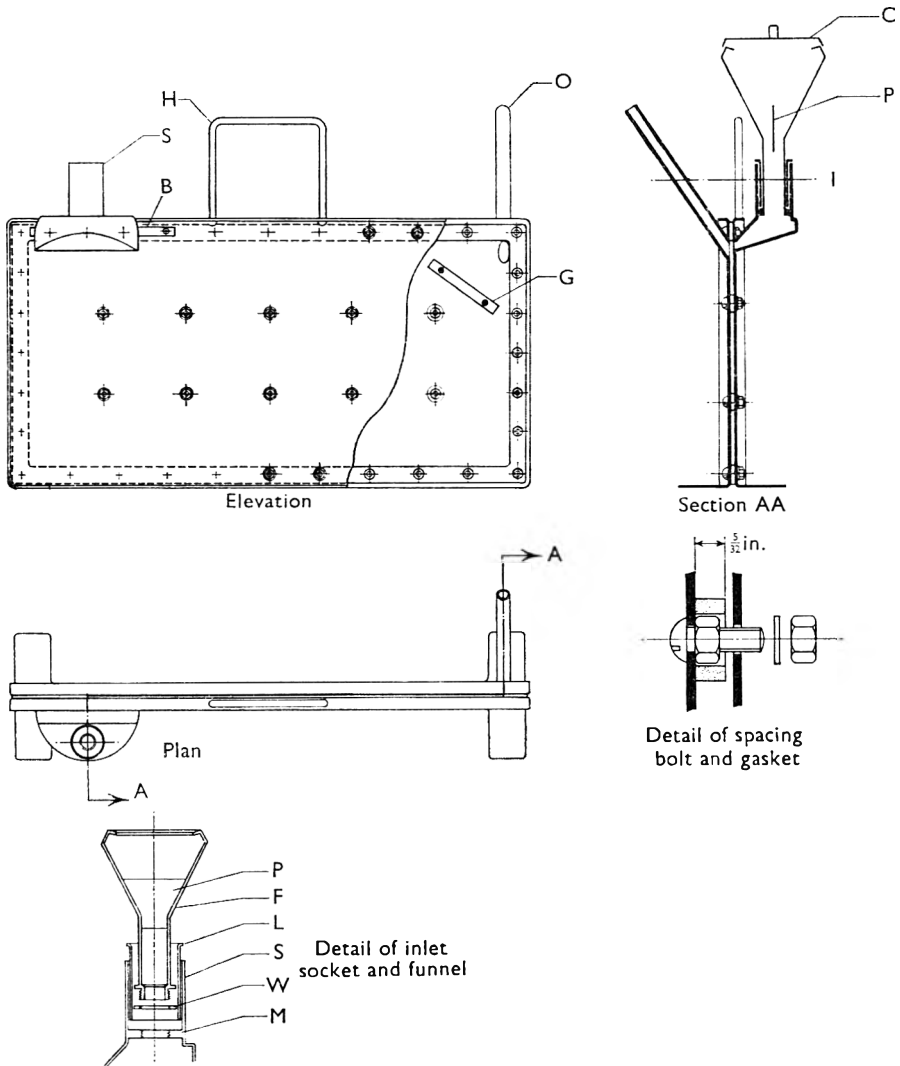


Fig 1. For legend see opposite.

ASSESSMENT OF PERFORMANCE

Half-pint quantities of milk were treated as above at temperatures from 157 to 163 °F for periods of 60, 65, 70 and 75 sec, the times taken from the instant when the milk disappeared from the funnel until the commencement of transfer of the unit to

the cooling bath. A polythene-insulated nickel-constantan thermocouple, calibrated against an N.P.L. certificated thermometer over the range 75–175 deg F, and placed about centrally in the milk, was used to measure the temperature reached by the milk, the reference junction being placed in crushed ice. The thermoelectric potentials were measured by means of a hand-operated potentiometer.

Residual phosphatase in the treated milks was determined by the method of Aschaffenburg & Mullen (1949) and a typical set of results is shown in Fig. 2. These are compared with typical phosphatase destruction curves for commercial plants (MacWalter & Wright, 1962) and with a laboratory-scale continuous flow HTST pasteurizer (Franklin, 1965*c*). It can be seen that a treatment time of 70 sec gives phosphatase values which agree very closely with those of laboratory and commercial continuous flow plants. Raw milk temperatures within the range covered by normal refrigeration (40 °F) and atmospheric temperatures were found to have little or no effect on the resulting end-product.

Thermocouples were also used as above to determine the water-milk temperature differential at the end of the heating period and to ascertain the shape of the heating and cooling curves. The results show (Fig. 3) that with a treatment time of 70 sec the water-milk differential at milk temperature 161 °F is about 1 deg F. To heat the milk to 161 °F therefore, it is necessary to set the hot water-bath to operate at 162 °F.

The heating and cooling characteristics of the apparatus using 70-sec treatments are compared with those of a typical commercial HTST plant (Ashton, 1950) in Fig. 4, from which the general similarity of the treatments is evident. More rapid cooling can be achieved using iced water but for routine treatment cooling in cold mains water is probably adequate.

From the above results it is recommended that, to reproduce the usual commercial pasteurization treatment, $\frac{1}{2}$ -pint quantities of milk should be given a 70-sec treatment

Fig. 1. Construction of the pasteurizing unit. Dimensions in inches; metal parts of stainless steel.

Elevation and plan. Side plates of 0.048 polished sheet, flanges 0.5 with corners welded, overall 19.75 × 9.875, feet 1.5 × 1.0 welded on to bottom flanges; silicone or other suitable rubber gasket 13.375 × 9.625 overall, width 0.5, thickness 0.156 with holes 0.25 diam. to fit spacing nuts; peripheral and inboard bolts 4 BA (shank diam. 0.142) all fitted to one side-plate with nuts 0.125 screwed up tightly to act as spacers, with a washer and second nut to draw up the other side plate (fixing nuts cannot be used near inlet socket S and are replaced by a loose bar B 5.25 long × 0.375 × 0.125 with the lower outer edge chamfered with 4 holes, tapped 4 BA and corresponding spacer nuts drilled out 4 BA clearance, allowing a screw-driver to be used to draw up side plates); handle H, 3.5 high, of rod 0.25 diam. fixed to flange of one side-plate with screws; outlet tube O, 0.375 int. diam. × 6.5 long with surge bar G, 3.13 × 0.375 × 0.125, screwed and cemented with epoxy resin across entrance to prevent milk surging high into outlet tube on filling the unit.

Detail of centre spacing bolt and gasket. Gasket 0.156 thick by 0.688 diam. surrounding spacer nut. Detail for peripheral bolts, similar.

Section AA and detail of inlet socket and funnel. Inlet socket S, 2.188 high × 1.0 int. diam. × 0.063 wall thickness, closed at lower end by septum M. 0.188 thick with central hole 0.688 diam. tapped 20 threads/in; flanged sleeve L 0.905 int. diam. and 1.813 long is loose fit in S; funnel F with 0.865 diam. flange, 0.25 from lower end of the spigot, which is 0.75 outside diam. × 2.25 long and threaded 20 threads/in below the flange with a threading recess to house loosely and hold captive a threaded soft aluminium washer W, 0.844 diam. × 0.063 thick; int. diam. of funnel spigot, 0.563 for lower 0.313 and 0.688 for remainder; body of funnel, 4.5 maximum diam. × 3.5 high, with bold anti-splash lip, cover C, and anti-swirl plate P which is a push fit into the bore of the spigot of the funnel; inlet socket S is connected to one side plate of the unit by a generous transition piece which is welded in place forming an entrance slot 4.0 long × 0.25 wide; depth of immersion of the unit in use is indicated at I.

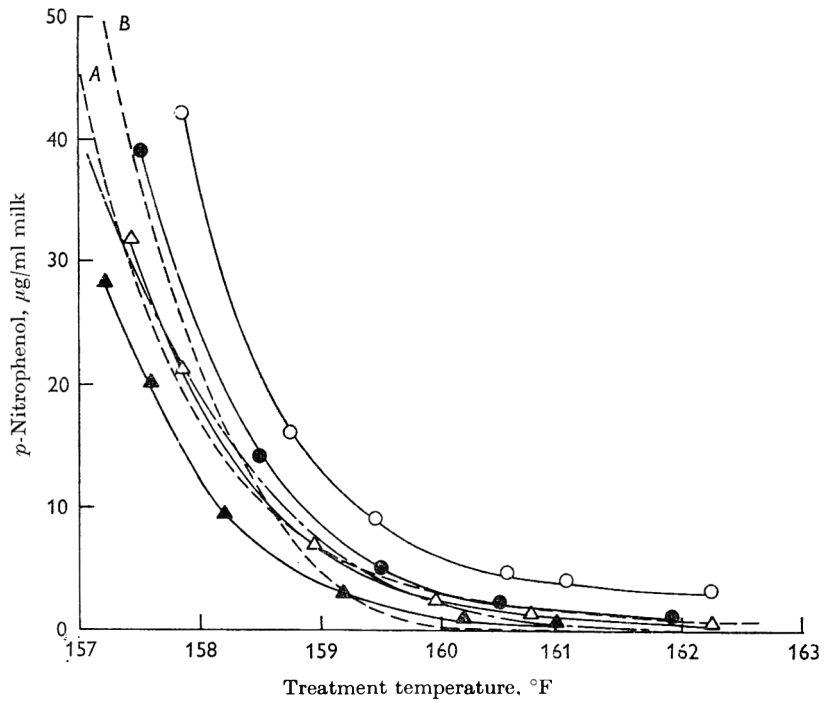


Fig. 2. Phosphatase destruction curves for milk subjected to different treatments in the laboratory-scale HTST batch pasteurizer. — Laboratory HTST batch pasteurizer (treatment time, sec: ○, 60; ●, 65; △, 70; ▲, 75). --- Astell laboratory HTST continuous flow pasteurizer (from Franklin, 1965c). - - - , Commercial HTST pasteurizers *A* and *B* (from Mac Walter & Wright, 1962).

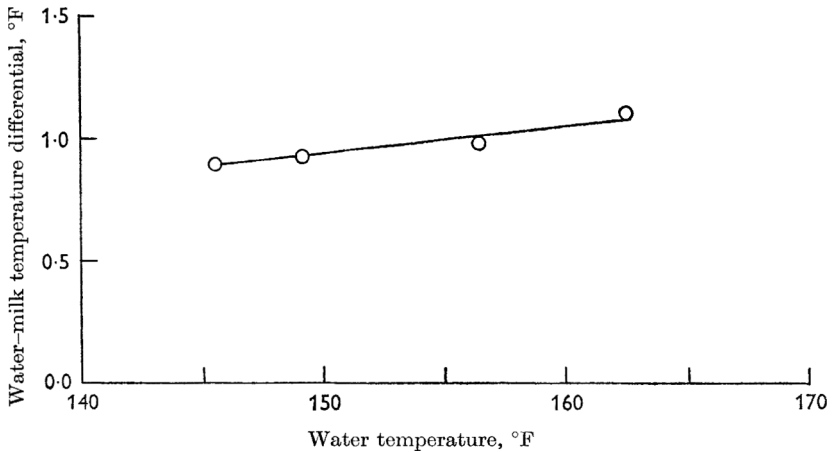


Fig. 3. Water-milk temperature differentials for a laboratory-scale HTST batch pasteurizer. Half-pint quantities of raw milk at an initial temperature of about 50 °F were used and measurements made after 70 sec treatment.

in a water-bath set at 162.5 °F to give a milk temperature maximum of 161.5 °F, i.e. providing a safety margin of 0.5 deg F compared with the legal requirements. Most commercial dairies tend to operate their pasteurizing plants at temperatures slightly in excess of the legal minimum. The treatment temperature in the laboratory process may be varied, of course, if it is required to reproduce the effect of commercial pasteurization at other temperatures.

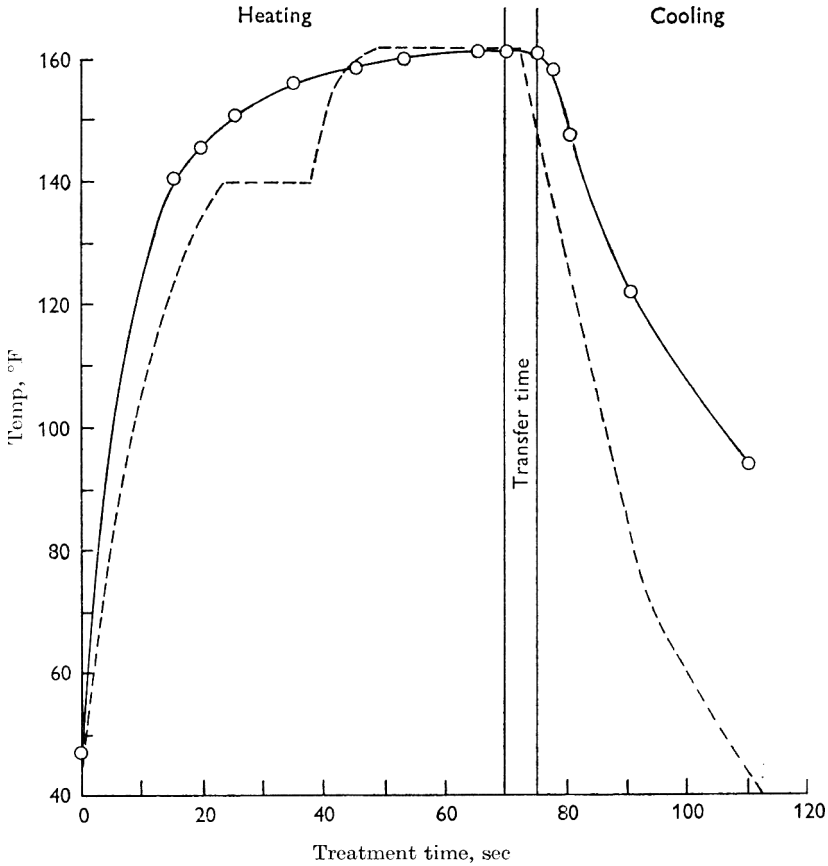


Fig. 4. Heating and cooling curves for a laboratory-scale HTST batch pasteurizer. ○, laboratory HTST batch pasteurizer; - - -, commercial HTST pasteurizer (from Ashton, 1950).

CLEANING AND STERILIZING PROCEDURES

Unlike a laboratory-scale continuous flow HTST pasteurizer, such as described by Franklin (1965*b, c*), in which extended operation can result in a considerable build-up of milk solids in the heater section, cleaning of the pasteurizing unit described here between samples and at the end of the day is simple because of the absence of milk solids deposition during the short treatment time necessary. Rinsing with hot water only between treatments seems to be satisfactory but a more efficient method should be used at the end of the day. Several methods were tested and found to be satisfactory and the following, being easy to apply and efficient in function, are given as examples.

Method 1. Rinse with hot tap water; drain; fill with 1% ODC detergent (manufactured by Reddish Detergents Ltd. and consisting of a mixture of alkalis, polyphosphates and organic sequestering agents) at 180–190 °F and soak for 2 min; drain; rinse with water.

Method 2. Rinse with hot tap water; drain; fill with 0.2% HNO₃ at 130–140 °F and soak for 2 min; drain; rinse with water.

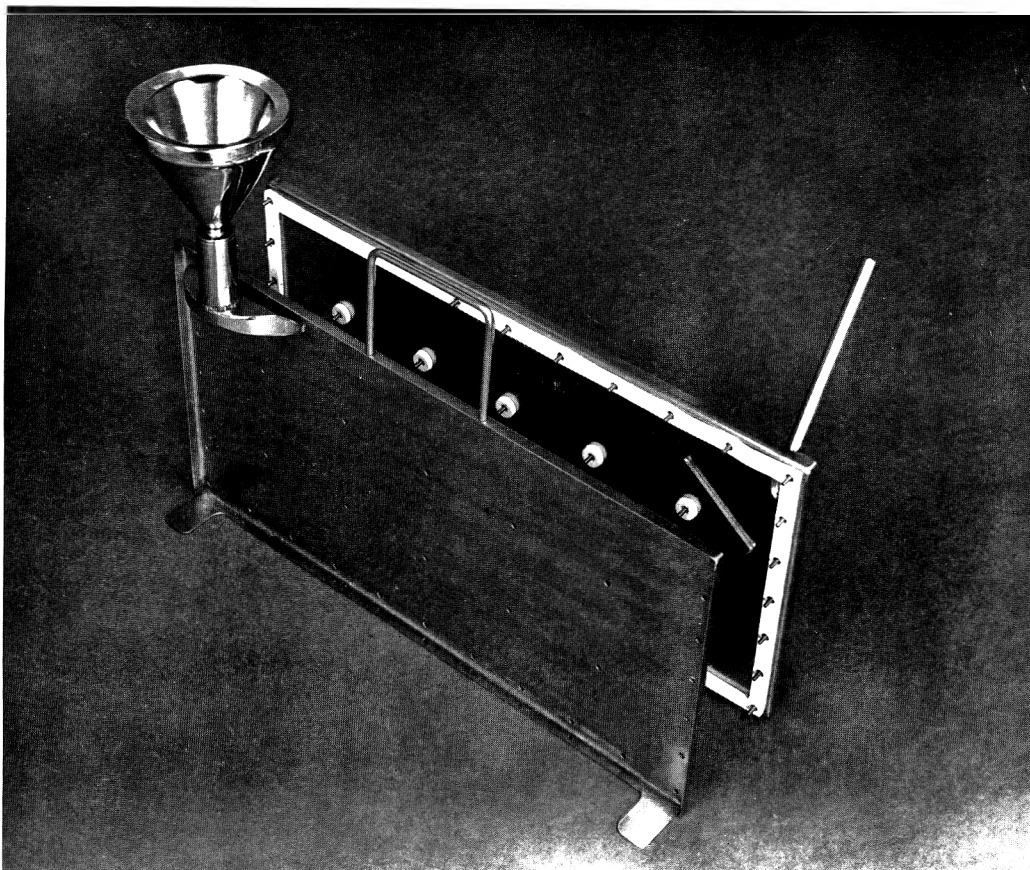
When method 2 is used, it is advisable to give the apparatus a dilute caustic soak periodically. No build-up of deposit or development of any defect as a result of cleaning was observed during 6 months regular cleaning using method 2.

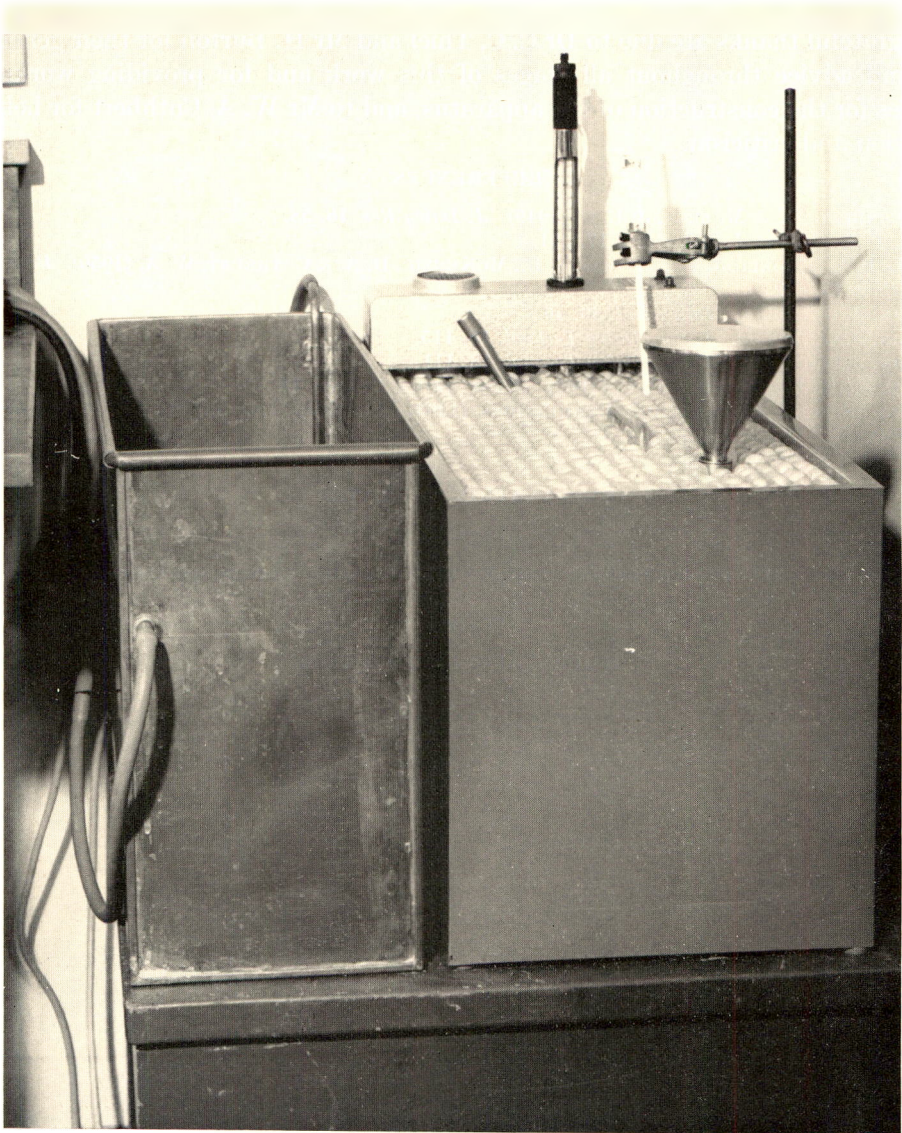
Disinfection of the plant can be achieved by increasing temperatures and contact times during cleaning, by using suitable chemical disinfectants, or preferably by steaming the unit at atmospheric pressure after normal cleaning. Sterility can be attained by autoclaving the entire pasteurizing unit at 15 lb/in² for 20 min provided the gasket and washers are made of the recommended material, and the inlet and outlet are plugged with non-absorbent cotton wool to prevent recontamination during cooling.

DISCUSSION

The method provides a simple rapid means of subjecting milk samples to a treatment closely resembling commercial pasteurization as measured by time-temperature curves and phosphatase destruction. The sample treatment time is about 2 min, but with between-sample rinsing the throughput is about 6 samples/h. The use of an additional steaming treatment to disinfect reduces this to about 4 per h but if two, or preferably three, pasteurizing units are used in conjunction with the one set of water-baths the treatment rate can be increased to about 12 samples/h.

The method is highly adaptable. Although it has been shown (Franklin, 1965*a*) that minimum milk quantities of $\frac{1}{2}$ pint are necessary to obtain keeping-quality results that are reasonably representative of the bulk, much smaller quantities might be sufficient for other purposes. These could be treated in the full-scale plant but a scaled-down version of the apparatus could be used if more convenient. During development of the method a very simple prototype of 30-ml capacity was shown to be capable of yielding similar phosphatase destruction curves under the same treatment conditions. Treatment of volumes larger than $\frac{1}{2}$ pint would necessitate correspondingly larger pasteurizing units with larger water-baths which might be inconvenient and unpractical. This size difficulty might possibly be overcome by the use of corrugated plates in the unit or even cylindrical ones but the latter would require carefully arranged water circulation to prevent local heating or cooling effects. The capacity of the heater can be increased by enlarging the gasket thickness, but this would necessitate an appropriate increase in treatment time or in the water-milk temperature differential or in both. This might result in an undesirable departure from the general shape of the heating profile in commercial plants and would increase the individual milk particle treatment variability. A more satisfactory means of treating larger volumes, because of the ease of operation and high sample throughput of the method, is to treat replicate $\frac{1}{2}$ -pint quantities followed by bulking. Without the necessity of between-sample cleaning and disinfection, treatment rates of > 1 gal/h could thereby be achieved.





The method might be adaptable for more rapid uniform heating by reducing the gasket thickness, and in this form could conceivably be used for studies of the heat resistance of bacteria particularly with short treatment times. Ease of manipulation and sterilization also makes the apparatus suitable for studies with pathogens.

My grateful thanks are due to Dr C. C. Thiel and Mr H. Burton for their generous help and advice throughout all stages of this work and for providing workshop facilities for the construction of the apparatus, and to Mr W. A. Cuthbert for helpful discussion and criticism.

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EXPLANATION OF PLATES

PLATE 1

Laboratory-scale HTST batch pasteurizer opened to show gasket, washers, spacers and surge bar.

PLATE 2

Heating and cooling water-baths.

Reviews of the progress of dairy science

Section A. Physiology. Cattle in a hot environment

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(Received 16 May 1965)

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The object of this article is to review the literature on the effects of heat on various structural and functional features of cattle. Since knowledge of the relative importance of single meteorological elements in producing heat stress is still incomplete, and since heat stress depends on the combined action of several meteorological elements, the subject is subdivided into sections on animal structures and functions rather than into sections on the effects of single meteorological elements.

HEAT PRODUCTION

The effect of high environmental temperatures on metabolic heat production depends on the way the heat stress is applied. If it is applied in an acute way, i.e. if the animal is exposed for a short period to severe heat, the metabolic heat production rises; if, on the other hand, heat stress is applied chronically, i.e. if the animal is exposed for a prolonged period to mild heat, the heat production tends to fall.

Short exposure to severe heat

Kibler (1960), when exposing heifer calves of 3 dairy breeds for 5-h periods to air temperatures* rising from 20 to 44°, found oxygen consumption to rise from 83 to 107 l/h, while respiratory volume increased by 95 l/min and rectal temperature by 1.1°. McLean (1963*b*) found that the heat production of bull calves did not change when temperature was increased over the range 15–40° at low humidities, but that it increased in an atmosphere of 35° at high humidity. Rogerson (1960), working with steers, also failed to find a change in heat production in the temperature range 20–40°. However, when increasing the hay ration from 3 to 6 kg/day, heat production at 40° increased by about 40%. Exposure of Jersey and Holstein cows to high temperatures and humidities resulted in an initial increase in heat production. This increase was accompanied by a rise in body temperature (Johnston, Hamblin & Schrader, 1958). An increase in heat production during acute heat stress may be attributed to the Van't Hoff effect and to the increased metabolic cost of breathing. It represents a partial breakdown of homeothermy rather than an adaptive change.

Long exposure to mild heat

Decreases in metabolic heat production during chronic exposure to heat, known to occur in man (Martin, 1930; Scott MacGregor & Loh, 1941), are now well established

* Except where otherwise stated temperatures are given in °C.

in cattle. When the same animals referred to in the previous paragraph (Kibler, 1960) were exposed to temperatures gradually rising from 10 to 35°, their oxygen consumption gradually declined from 110 to 85 l/h, even though respiratory volume increased by 80 l/min and rectal temperature by 1.2°. In lactating Jersey and Holstein cows heat production decreased in response to temperatures rising above 21–27° (Kibler & Brody, 1949) as well as during diurnal temperature cycles representing 'Imperial Valley conditions' (15–43°) and 'Midwest hot conditions' (21–38°) (Kibler & Brody, 1956). Yeck & Stewart (1959) showed that with environmental temperature increasing from –12 to 32° and with relative humidity ranging from 55 to 70%, heat production decreased by about 2 kcal per lb of body weight per h for each deg F change in temperature. Although animals of all breeds and categories investigated responded to chronic exposure to heat by decreasing their heat production, the environmental temperature at which this decrease began varied considerably; it was 21, 24 and 35° in lactating Brown Swiss, Holstein and Brahman cows, respectively, 35° in Brown Swiss heifers and 38° in Brahman heifers (Worstell & Brody, 1953). Finally, the same cows that on exposure to heat had suffered an initial rise in heat production (Johnston *et al.* 1958) responded to a prolonged exposure with a decline in heat production, even though the temperature and humidity of the air were higher. The decrease in heat production in response to chronic exposure to heat represents a thermoregulatory adjustment of the animal which results in an improvement of its thermal balance in a hot environment.

Thyroid activity

The mechanisms responsible for the thermoregulatory adjustment have not been fully elucidated, but there is evidence that thyroxine, which is well known to act as a regulator of cellular oxidation, is involved.

Employing various methods, all based on the use of radioactive iodine, numerous workers have shown that chronic exposure to heat depresses thyroid activity in cattle. It was observed in calves, heifers and cows of various breeds and over different temperature ranges by Johnson & Kamal (1958), Johnson & Ragsdale (1960), Thompson *et al.* (1963), Johnson & Kibler (1963), Blincoe & Brody (1955), and Premachandra, Pipes & Turner (1960). In general, it was considered (Johnson & Kibler, 1963) that environmental conditions which caused rectal temperature of cattle to rise by 0.6° or more evoked significant depressions in thyroid activity. These changes were associated with changes in various other body functions: feed intake and body weight both decreased (Thompson *et al.* 1963; Johnson & Kibler, 1963), heat production declined (Blincoe & Brody, 1955), and the plasma levels of 17-hydroxycorticosterone increased (Thompson *et al.* 1963). The findings suggested that a reduced feed intake—resulting from the decrease in appetite in a hot environment—accounts for at least part of the reduced activity of the thyroid. It has in fact been shown that starvation reduces thyroid activity in cattle (Blincoe & Brody, 1955; Kibler, 1960).

Since the magnitude of response to heat of the thyroid gland appears to depend on its original level of activity, it is relevant to note the genetic variation existing in normal thyroid activity. Normal thyroid activity has been found to be higher in Hereford cattle than in Brahman cattle (Howes, Feaster & Hentges, 1962), twice as

great in Jersey calves as in Holstein and Brown Swiss calves (Johnson & Ragsdale, 1960), and 67% higher in dairy cattle than in beef cattle (Pipes, Bauman, Brooks, Comfort & Turner, 1963).

HAIR COAT

The hair coat, representing the boundary between the body and its climatic environment, may profoundly influence an animal's thermal balance.

The number of hair follicles per unit of skin area (follicle density) is fixed at birth. Thus, with increasing age (Carter & Dowling, 1954) or, more specifically, with increasing body weight (Turner, Nay & French, 1962) follicle density becomes smaller. The weight-adjusted follicle density represents an inherent character which is stable throughout an animal's life (Turner *et al.* 1962). The same authors found follicle density to be higher in male calves than in female calves and about 20% higher in Brahman crosses than in European-type cattle. According to Hafez, Badreldin & Shafei (1955) follicle density is about 6 times as high in cattle as in buffaloes.

The thermoregulatory role played by the hair coat in a warm environment is two-fold: it affords a certain degree of protection against radiant heat from the sun, and it interferes with the dissipation of heat from the animal's surface.

Protection against heat gain

The 2 principal characters of the hair coat which determine the absorption of radiant heat are colour and texture. The hair coat of brown cattle may absorb about 3 times as much radiant heat from the sun, during a 14-h summer day, as is produced by their metabolism during that period. White cattle absorbed only two-thirds of the amount absorbed by brown cattle (Riemerschmid, 1943). These absorptivities were estimated by measuring the reflected energy of the total spectrum with the aid of a Moll-Gorczyński solarimeter. The reflexion of visible radiation from different-coloured coats was given as 15% from cream-coloured Afrikaner cattle, 11% from light-coloured Jersey cattle, 10% from red Afrikaner and 4% from dark-coloured Jersey cattle (Bonsma & Pretorius, 1943). Under Australian conditions, white- and smooth-coated Zebu cattle were found to have a reflectance of 0.40 cal/cm² min. Comparative values for black smooth Angus cattle were 0.10, for red smooth Shorthorns 0.22, and for red woolly Shorthorns 0.20 (MacFarlane, 1958). Measurements with a selenium photocell and appropriate filters showed Brown Swiss cattle in Switzerland to reflect 10% in the visible spectral range and 25% in the red and in the beginning of the infra-red range (Cena & Courvoisier, 1950). In comparing reflectance values reported by different workers, it is important to realize that the result obtained depends on the technique used. Ideally, instruments which are non-selective with respect to the natural spectral range should be used. Furthermore, as has been pointed out (Stewart, Pickett & Brody, 1951) caution should be exercised when estimating absorption from reflectance values. It does not necessarily follow that a reflectance from the coat of, say, 20% means an absorption by the animal body of 80%. An appreciable fraction of the incident radiation may be absorbed by the hair only (and not by the skin) and re-radiated to the environment as long-wave radiation. Indeed, it has been shown for the sheep (Priestley, 1957) that absorption of radiant heat raises the surface temperature to such a degree that most of the

absorbed energy is re-dissipated to the environment by convection and long-wave radiation.

There is evidence to show that heat may cause changes in the colour of the coat. Hair samples of Brown Swiss and Brahman cattle that were exposed for several months in a climatic room to temperatures rising from 18 to 35° became gradually more reflectant to radiation. This rise in reflectance was more rapid and occurred at a lower environmental temperature in the Brahman than in the Brown Swiss cows (Stewart *et al.* 1951). Since under natural conditions high temperature is normally associated with high intensities of solar radiation, the authors inferred from these results that by an evolutionary coupling process the hair reacts to rising temperature as if radiation were present. In subsequent experiments (Stewart & Brody, 1954) it was found that the reflectance of Holstein, Jersey and Brahman hair increased with rising temperature when the animals were exposed for 1 week at a time to radiation intensities of 5, 40, 90, 130 and 180 Btu/ft² h, at air temperatures of 7, 21 and 27°. Bonsma & Pretorius (1943) noted that dark-coloured dairy cattle exported from England to South Africa became lighter in colour after a few months, and that coats of indigenous breeds of cattle reflected more light in summer than in winter. Schleger (1962) also found that summer coats were lighter in colour than winter coats. This, however, was true only in non-lactating cows; in calves and lactating cows the summer coats were darker than the winter coats. These findings, as well as colour changes in general, were discussed by the author in the light of endocrine function.

The few investigations dealing with the texture of the coat as a characteristic influencing the absorption of solar radiation indicate that its effect is relatively small compared with the effect of the colour of the coat (Riemerschmid & Elder, 1945; MacFarlane, 1958). Dowling (1959*a*) expressed the view that medullated hair fibres might be more effective in reflecting infra-red radiation from the sun than non-medullated hair fibres.

Interference with heat dissipation

Much attention has been given both by field and by laboratory workers to the hair coat acting as a partial barrier to the dissipation of heat from the body. The total insulation of the hair coat of dairy calves was proportional to the hair weight per unit area of skin (Berry & Shanklin, 1961). Clipping the coat of calves had a beneficial effect on their thermal balance (Bianca, 1959*c*) in an environment of 40° probably due to an improvement in cutaneous evaporation. Clipping the coat of heifers in an atmosphere of 32° did not result in a decrease in rectal temperature but brought about some alleviation of heat strain, as evidenced by a reduction in respiratory activity (Berman & Kibler, 1959). An accurate method has been described by Blincoe (1956) which allows the measurement of the density of the hair coat to be made without clipping. Preliminary measurements indicated that hair coat density tended to decrease with rising environmental temperature.

As expected certain types of coats interfere more with heat loss than others. Hair that is short, thick and medullated forms a smooth coat which does not readily felt and therefore has a minimal effect on heat loss. By contrast, hair that is thin, long, non-medullated and frequently curled forms a woolly coat which felts easily and therefore interferes markedly with heat loss (Bonsma, 1949; Dowling, 1959*a, b*). The type of hair coat is partly genetically determined, *Bos indicus* cattle having shorter

and lighter coats than *B. taurus* cattle (Hayman & Nay, 1961). However, both species undergo seasonal changes in hair coat. Dowling (1959*a*) showed that Shorthorns and various Shorthorn crosses in Queensland shed their highly insulating winter coat in spring and early summer and grew a coat containing thicker, shorter and more medullated hair fibres. A high incidence of medullated hair fibres in the coat was considered of primary importance for a high rate of heat dissipation. Between the incidence of medullation and the animal's ability to control rectal temperature a high positive correlation was found. Yeates (1955), by artificially shortening or lengthening the hours of daylight, was able to produce in Shorthorn calves winter-type coats in summer and summer-type coats in winter. Dowling & Nay (1960) came to the conclusion that the hair follicles of cattle undergo 2 resting and 2 active phases within a year, peaks of follicle activity occurring in spring and autumn. The winter coat, which consists of long and thin hair, was shown to be not merely an elongation of the summer coat, which consists of short and thick hair, but an entirely new coat. Significant differences between winter and summer hair coats have been described by Dowling (1958*a*) for Hereford steers in Australia and by Berman & Volcani (1961) for Holstein and Holstein \times Syrian cattle in Israel.

Significance of the hair coat as an indicator of an animal's constitution and condition

The work discussed does not leave any doubt that a heavy, furry hair coat interferes with heat loss and that it is directly responsible for at least part of the hyperthermia developing in animals exposed to heat. However, in recent years evidence has been accumulating which suggests that the nature of its coat and the performance of an animal under heat stress may be inter-related also in an indirect way, some of the qualities of the coat being related to the physiological status of the animal, notably with regard to endocrine function, which in turn has a bearing on an animal's response to heat stress and possibly also to other types of stress. Thus, Turner (1962) found that differences in heat tolerance and body-weight gains of calves in Australia were more dependent on their inherent coat type (smooth or woolly) than on their actual coat cover. When all the animals had been clipped, the smooth-coated animals performed better in a hot environment than the woolly-coated animals. This was also true in winter when there was no heat stress problem. The superiority of smooth-coated animals was attributed partly to a more efficient sweating mechanism, as suggested by the work of Nay & Dowling (1957) and Dowling (1958*b*), and partly to non-thermoregulatory qualities, among which a high efficiency of energy conversion was speculated to be of primary importance. For the assessment of an animal's coat type, Turner & Schleger (1960) and Schleger & Turner (1960) have developed a coat-scoring system. Although a subjective method, the coat score was found to give consistent results and to have a heritability of 0.63. In a hot environment coat score was well correlated with rectal temperature and respiratory rate. The coat score was considered superior to Bonsma's felting test (Bonsma, 1949) with respect to repeatability and heritability as well as in its correlation with skin temperature and gain in body weight.

A study by Schleger (1962) with red beef cattle in Australia suggests that not only the type (texture) of coat but also its colour may have a significance in relation to

heat stress. They found that dark animals, which with respect to the absorption of solar radiation should be at a disadvantage, tended to be slightly more heat tolerant than lighter-coloured animals. This indicated that the darker animals had physiological characteristics which favoured an efficient heat balance, and that these characteristics counteracted the disadvantage of a higher absorption of radiant heat. Again, the inference was that the character of the coat, in this case the intensity of its pigmentation, was more important as an indicator of constitution than as a factor directly influencing heat tolerance.

It is interesting to note that animals in poor health tend to have a heavy, heat-retaining type of coat. Minett (1949) found cessation of normal shedding, high respiratory rates and high rectal temperatures among the sequelae of foot-and-mouth disease in Indian cattle. Likewise, Maqsood, Ishaq & Anwar (1958) have described a 'heat intolerance syndrome' in cattle following an attack of foot-and-mouth disease in Pakistan, again involving failure of shedding, increased respiratory activity and body temperature. Histological examination of the thyroid glands of these animals indicated an increased production of thyroxine. Administration of thiouracil improved the condition; oral administration of thyroxine aggravated it. From these observations it would appear that the disease caused a high thyroid activity with a concomitant increase in heat production and a retainment of a heavy coat, factors which in turn would adversely affect the animal's thermal balance even under conditions of mild heat stress.

In conclusion, it is important to recognize clearly that the nature or condition of the coat is related to the thermal balance of the animal (*a*) directly by modifying heat gain from solar radiation and heat loss by convection and evaporation, and (*b*) indirectly by reflecting the overall state of health of the animal.

SIZE, FORM AND STRUCTURE OF THE BODY

In a hot environment a small animal has a thermoregulatory advantage over a large but otherwise similar animal, because of its greater surface area per unit of body mass. For the same reason a slender animal with large body appendages, such as the dewlap and ears, has an advantage over a compact animal with small appendages but with otherwise similar features. However, the extent to which such geometrical effects become manifest depends on numerous functional factors, notably on the animal's heat production and on the blood flow and sweating capacity of its skin. Since the structural and functional features of the animal cannot readily be separated one from another, the significance of body size and body form *per se* on thermoregulation in cattle is still a matter of controversy. Furthermore, there is the complication that extreme heat (with air temperatures above skin temperature and with a high radiant heat load from the sun) has an opposite effect to less severe heat.

It is unlikely that body size plays an important role. The geographical distribution of cattle breeds does not clearly show that body size declines with rising environmental temperature. In some of the tropical regions small cattle may be found not because they are more efficient in their heat dissipation, but because they are more resistant to certain diseases and to a low standard of nutrition. Furthermore, the

young animal, which by being small has the geometrical advantage of having a large surface-to-mass ratio, is not more heat tolerant than the adult animal of the same breed; on the contrary, it is less heat tolerant (Bonsma, 1949; Klemm & Robinson, 1955; Walker, 1957). The superior thermal balance in a hot environment of the adult animal seems to be the result of a higher sweating rate (Klemm & Robinson, 1955) and of a lower heat production per unit body weight (Kibler, 1957).

Whether or not the well-documented superiority in heat tolerance of Indian-type cattle over European-type cattle is due, at least in part, to their body appendages is not yet clear. Using the surface integrator technique, McDowell, Lee & Fohrman (1953) failed to find a significant difference in the ratio of surface area either to body weight (W) or to $W^{2/3}$ between Jersey cows and Red Sindhi-Jersey cross-bred cows. Yet the heat tolerance was markedly higher in the cross-breds. An extensive cross-breeding experiment in the U.S.A. led to the conclusion that crossing animals of European breeds with animals of the Red Sindhi breed did not have a significant effect on body surface area, the larger body appendages of the Red Sindhis apparently being offset by their more compact body form (McDowell, Johnson, Schein & Swett, 1959). Amputation of the dewlap (McDowell, 1958) or of the hump (McDowell, McDaniel & Hooven, 1958) did not appear to depress the heat tolerance of Red Sindhi bulls.

These findings indicate that a high surface-to-mass ratio in cattle is not essential for tolerating heat. There is, however, evidence to suggest that the relative surface area does play some part in the animal's thermal balance. Mice reared in a warm environment developed longer tails than mice reared in a temperate environment, and amputation of the tail depressed their heat tolerance (Harrison, 1958). Brahman cattle were found to have a 12% greater surface area than Jersey cattle of the same weight (Kibler & Brody, 1950*b*). In Haryana bulls the skin of the hump had a higher sweat gland volume than the skin in other body regions, and the rate of evaporation was 50% higher from the hump than from the lumbar back region (Chowdhury & Sadhu, 1963). An intensive study with calves of 6 breeds (Johnson, Ragsdale, Sikes, Kennedy, O'Bannon & Hartman, 1961) revealed that the combined surface area of ears, dewlap and navel flap expressed as a percentage of total surface area was 11% in Brahman, 9% in Santa Gertrudis and 6% in Shorthorn animals, and that heat tolerance in these breeds declined in the same order. Shorthorn calves reared at 27° had a higher ratio of appendage surface to total surface than Shorthorn calves reared at 10°, which might indicate a thermal adjustment. The high heat tolerance of Brown Swiss calves as compared with the poor heat tolerance of Holstein calves was associated with a large surface area per unit of heat production.

Finally, there are 2 peculiarities of the internal body structure which have been suggested as possible explanations for the difference in heat tolerance between *B. taurus* and *B. indicus* cattle. Increasing the proportion of Red Sindhi inheritance in Jersey and Holstein cross-breds had the effect of reducing the size of the digestive and certain other internal organs independently of empty body weight (Swett, Matthews & McDowell, 1961). It was speculated whether this finding would explain the lower resting heat production of *B. indicus*, and also whether it would indicate a higher efficiency of food conversion. The other observation concerns the deposition

of body fat. Boran cattle (*B. indicus*) stored less of their total body fat under the skin than did *B. taurus* cattle (Ledger, 1959). In consequence heat dissipation from the periphery would be less interfered with in *B. indicus*.

BLOOD AND CIRCULATION

The role played by the blood and its circulation in the body of the heat-stressed animal is most complex. Haematological changes may indicate mobilization of defence and establishment of new equilibria, as well as breakdown of body functions and deterioration.

Blood volume

There are relatively few references on the effects of high environmental temperatures on blood and plasma volumes. Reynolds (1953) did not find any change in the plasma volume of a heifer kept under natural conditions at temperatures between 10 and 32°. Dale, Burge & Brody (1956), exposing dry and lactating Jersey cows and lactating Holstein cows to daily temperature rhythms of 15–43° and of 21–38°, found that serum and blood volumes increased by 20–30%. The increases were most noticeable in the lactating Holsteins. Increases in plasma and blood volumes, although smaller, were observed also by Bianca (1957) in calves repeatedly exposed to 45° for 5 h/day and compared with control calves kept under thermoneutral conditions. Plasma and blood volumes of buffaloes in India were reported to be higher in summer than in winter (Murti & Mullick, 1961).

Several workers have indicated that *B. indicus* cattle have higher blood and plasma volumes than *B. taurus* cattle. The volumes of plasma, erythrocytes and whole blood were significantly higher in Brahman cattle than in Hereford cattle (Howes, Hentges, Warnick & Cunha, 1957; Howes, Hentges & Feaster, 1960, 1963). Since all these values were expressed per unit of body weight it would be of interest to know whether Brahmans and Herefords were comparable with respect to lean body mass. It is conceivable that a higher fat content of the body or a larger fill of the gastrointestinal tract may be partly responsible for the lower ratios in European-type cattle.

Heart rate

The seemingly contradictory findings that heart rate responds to heat exposure either by a rise or by a fall may be largely explained by the fact that heart rate is positively correlated with metabolic rate (Blaxter, 1948; Kibler & Brody, 1949; Blaxter & Wood, 1951; Roy, Huffman & Reineke, 1957). Thus, during exposures to severe heat, heart rates of calves were found to increase (Bianca, 1953; Beakley & Findlay, 1955*e*; Whittow, 1962; Bianca & Findlay, 1962; Ingram & Whittow, 1963). At very high body temperatures, about 41° and above, the high respiratory activity may be a factor contributing to cardiac acceleration (Bianca, 1958). The direct mechanism which elicits the increase in heart rate of cattle exposed to severe heat is not yet known.

During chronic exposure to mild heat, on the other hand, heart rates of cattle of various breeds have been shown to decline (Worstell & Brody, 1953). This decline in heart rate was associated with decreases in feed consumption and in the production

of metabolic heat and of milk. The environmental temperatures at which heart rate began to decrease were 27° in lactating Jersey and Holstein cows, 29° in lactating Brown Swiss cows, and 35° in lactating Brahman cows (Worstell & Brody, 1953). When environmental temperature was raised to 32–38° (thereby creating conditions of acute heat stress), the heart rates of the same animals began to rise.

Circulation

Although structural features of the blood vessels of cattle tend to assist preservation of heat in a cold environment rather than dissipation of heat in a warm environment, it is possible that arteriovenous anastomoses in the skin of ears, forehead and cheek (Goodall, 1955) as well as in the teat (Nisbet, 1956) play a role in the defence against heat.

Beakley & Findlay (1955*c*) observed that at air temperatures between 15 and 20° the temperature of the ear of calves rose sharply from about 17 to about 36°, indicating a sudden and large increase in blood flow, probably due to the action of arteriovenous anastomoses. Thompson, Worstell & Brody (1953) measured very large differences in skin temperatures of various body regions when cows were exposed to low environmental temperatures. At air temperatures of –11° the skin temperature of a Jersey cow was near freezing temperature on the hoof cleft, but 29° on the milkwell. Whittow (1962), working with calves, recorded a large variation in the temperature of the skin of the extremities when the environmental temperature was in the range –5 to +25°. This variation was considered to reflect changes in blood flow. At air temperatures above 25° the skin temperatures of the extremities and those of the trunk were similar. Arterial blood pressure of calves was found to increase with increasing environmental temperature as well as with local heating of the hypothalamus and with infra-red irradiation of the skin (Ingram & Whittow, 1963). This increase in blood pressure was not due to an increase in cutaneous vascular resistance in the extremities since it was usually associated with an increase in the skin temperature of the extremities. In a study of climatic effects on the cardiovascular system of cattle Pichaicharnarong (1960) observed that the carbon dioxide content of the venous blood collected from the right atrium was significantly higher than that collected from the right ventricle, and that during thermal polypnoea the arteriovenous oxygen difference increased owing to a decrease in the oxygen content of the venous blood. Cardiac output changed with body posture but did not respond to heat in an unequivocal fashion.

Erythrocytes

The haematocrit value and the haemoglobin concentration in the blood seem to fall or rise depending on the severity of the heat load imposed on the animal.

Acute exposure of Ayrshire calves to humid heat (35° dry bulb, 33° wet bulb) (Bianca, 1953) and to dry heat (45° dry bulb, 28° wet bulb) (Bianca, 1957) caused increases in haemoglobin concentration and in haemocrit value, respectively. Subjecting Jersey and Red Sindhi–Jersey cross-bred heifers to an atmosphere of 40° dry bulb, 33° wet bulb did not have appreciable effects (Rusoff, Schein & Vizinat, 1955), possibly because the heat load was not sufficiently high for adult animals of these breeds.

Chronic exposure to heat resulted in decreases in haematocrit; Holstein cows kept

at a temperature of 32° had lower haematocrit values than control cows, and yearling Angus heifers exposed to 38° for 7 weeks showed a fall in haematocrit values from 40 to 29% (Weldy, McDowell, van Soest & Bond, 1964). The magnitude of this change leads one to suspect that an age effect was involved as well. An inverse relationship between air temperature and haemoglobin levels was also reported for steers (Murty & Mullick, 1960) and buffalo bulls (Raghavan & Mullick, 1962) in India.

Species and breed comparisons have revealed that Zebu-type cattle in general have higher values for the concentration of erythrocytes in the blood than European-type cattle (Blincoe *et al.* 1951; Rusoff, Frye & Scott, 1951; Rusoff, Johnston & Frye, 1955; Evans, 1963; Howes, Shirley & Hentges, 1963; Howes, Davis, Loggins & Hentges, 1961), and it has been suggested that this character might be an index of their superior heat tolerance. It would appear, however, that such a relationship, if established at all, would be incidental rather than causative. There is evidence to show that Zebu and taurine cattle may differ also with respect to the composition of the erythrocytes. Investigators in Florida found that Brahman cattle, compared with Hereford cattle, had a higher concentration of sodium (123 versus 113 m-equiv./l) in the erythrocytes and a lower concentration of potassium (13.8 versus 18.4 m-equiv./l). Evans in Australia (1963) confirmed this difference in erythrocyte character between *B. indicus* and *B. taurus* in an extensive study involving 10 different herds. He also made the interesting observation that a rising concentration of potassium in the erythrocytes was associated with a rising coat score (Turner & Schleger, 1960). Since well-adapted animals have a low coat score, he suggested the possibility of selecting for low erythrocyte potassium concentration among European-type stock introduced into semi-tropical areas. According to Crockett, Koger & Chapman (1963), who examined the blood of 939 animals, Brahmans and Brahman crosses have haemoglobin types A, B, AB or AC, whereas Angus, Herefords and Angus-Hereford crosses have almost exclusively type A.

Various blood and plasma constituents

A great variety of blood and plasma constituents have been studied both in temperate-zone breeds of cattle exposed to heat and in cattle genetically adapted to life in hot regions. Changes in blood constituents specifically relating to changes in respiratory activity of the heat-stressed animal are discussed on p. 310.

Goberdhan (1955) investigated the inorganic constituents in the blood and urine of dairy cows subjected to increasing thermal stress. When the environmental temperature was raised from 7 to 21° there was a tendency to retain sodium, potassium, calcium, phosphate, chloride and carbonate, as evidenced by the decreased excretion of these constituents in the urine and their increased concentration in the blood. When the temperature was further increased to 27° the concentration of chloride in the plasma increased but the potassium, sodium and sulphate levels decreased. In general, the changes in the concentrations of the constituents appeared earlier in the smaller Jerseys than in the larger Holsteins. Kamal, Johnson & Ragsdale (1962), on the basis of results obtained from long-term heat exposures of Brown Swiss, Holstein and Jersey cattle, came to the conclusion that effects of heat on the animal showed better in the composition of the urine than in that of the blood.

Plasma electrolyte concentrations changed only little and in the opposite direction from those of the urinary electrolytes.

More pronounced changes have been found for other blood constituents of cattle exposed to heat: cholesterol decreased (Brody, 1949; Blincoe & Brody, 1951; Diven, Page, Erwin & Roubicek, 1958), and creatinine increased (Blincoe & Brody, 1951). Serum glutamic-oxaloacetic transaminase rose and fell in close association with the diurnal temperature changes (Page, Erwin & Nelms, 1960). Where animals of various breeds were exposed to heat the levels of glucose in the blood consistently declined (Riek & Lee, 1948*a*; Brody, 1949; Diven *et al.* 1958; Kamal *et al.* 1962) but this decline was probably due to the concomitant fall in feed consumption. It is unlikely that the respiratory activity, which is greatly increased in the heat-stressed animal, is a causative factor; because under conditions of excessive heat, where respiratory activity was maximal, blood glucose concentration of calves rose sharply (Bianca & Findlay, 1962). This sharp rise, which began at a rectal temperature of about 41°, may be the result of a stimulation of the sympathico-adrenal system, since it is accompanied by a similar rise in heart rate (Bianca & Findlay, 1962) and in haematocrit value (Bianca, 1953). Plasma levels of adrenal glucocorticoids of cows decreased during a 9-week period at 29° (Bergman & Johnson, 1963). Heat-induced changes were also observed in the levels of various vitamins in the blood; ascorbic acid levels decreased in cows (Blincoe & Brody, 1951), but did not show clear effects in heifers (Singh & Merilan, 1957). Riboflavine levels in the blood of heifers were highest in July, August and September, and the levels of niacin and thiamine in the blood of Shorthorn heifers were distinctly depressed in an atmosphere of 27° (Singh & Merilan, 1957).

In view of such changes in blood composition in response to a hot environment, several workers have made comparisons between the blood composition of European-type breeds and that of Zebu-type breeds. Serum alkaline phosphatase activities were about twice as high in immature Brahman cattle as in European-type cattle; in cross-breds they were intermediate (Kunkel, Stokes, Anthony & Futrell, 1953). In Israel, serum albumin levels were found to be higher in Damascene cattle than in Holstein-Friesian cattle (Perk & Lobl, 1959). Since the albumin fraction of the plasma is responsible for most of the effective osmotic pressure, this result suggested that the blood of the Damascene cattle has a higher water-retaining capacity which in a hot dry area may be an important feature. A study conducted in Arizona (Erwin, 1960) showed that in Brahman cows the serum levels of carotene, vitamin A, albumin, α -globulin and β -globulin exceeded those for Angus cows. Various blood constituents in African breeds of cattle have been reported by Smith (1959*a, b*) and by Gourlay (1959).

EVAPORATION FROM THE SKIN

The source of the moisture evaporated from the skin

In a cool environment cutaneous evaporation is low and can be accounted for solely by the diffusion of moisture through the skin. In a warm environment, however, it may be so high that an additional source of moisture must be postulated. There is now ample indirect and direct evidence to show that the additional source is the water in the sweat glands, and the earlier belief that cattle do not sweat is no

longer tenable. The evidence for the occurrence of sweating is based on a variety of findings. The evaporative weight loss observed in Jersey cows and calves exposed to heat was always much greater than that which could be accounted for by respiratory evaporation alone (Riek & Lee, 1948*a, b*).

At environmental temperatures up to about 20° the rate of cutaneous evaporation in calves was remarkably uniform over the whole body surface; at higher temperatures, however, distinct regional differences developed (McLean, 1963*a*). In adult cattle cutaneous evaporation began to rise sharply at an environmental temperature of about 18°, comparable to the outbreak of sweating in man at a temperature of around 29° (Kibler & Brody, 1950*a*). Sweat prints were obtained whose distribution corresponded to that of the sweat glands (Ferguson & Dowling, 1955; Taneja, 1959*b*). Iontophoresis with formaldehyde, a procedure considered to incapacitate the sweat glands, markedly reduced cutaneous evaporation in various breeds of cattle (McDowell, McMullan, Wodzika, Lee & Fohrman, 1955; McDowell, McDaniel, Barrada & Lee, 1961). Heating of the hypothalamus of calves was followed by a progressive increase in cutaneous evaporation (Ingram, McLean & Whittow, 1961). Later, the observation was made in calves that during the early part of heat exposure cutaneous evaporation increased in distinct steps and that this occurred simultaneously in different regions of the body, an observation that suggested a secretory process (McLean, 1963*a*).

The quantitative relationship between the diffusion component and the sweating component of moisture loss from the skin is still unknown. Experiments with oxen deprived of water and exposed to heat (Bianca, 1964) suggested that the ratio of diffusion moisture to sweating moisture under conditions of apparently maximal cutaneous evaporation was about 1:7. A similar ratio has been obtained in animals in which sweating had been inhibited by drugs (Findlay & Robertshaw, 1965).

It is possible that the sebaceous glands contribute to cutaneous evaporation, but no figures are available on this potential source of moisture.

The number and volume of the sweat glands

The number of sweat glands corresponds to the number of hair follicles (Yamane & Ono, 1936; Findlay & Yang, 1950) and is fixed at birth. Thus, with increasing size of the animal, as a result of normal growth or of a high level of nutrition, the number of sweat glands per unit area of skin decreases (Findlay & Yang, 1950; Dowling, 1955*a*). The number of sweat glands per unit area of skin was found by Nay & Hayman (1963) not to be significantly different in mature Ayrshire, Guernsey, Jersey, Australian Illawarra Shorthorn and Friesian cattle but it was higher in *B. indicus* than in *B. taurus* (Dowling, 1955*b*; Nay & Hayman, 1956; Taneja, 1960). It is important, however, to realize that sweat-gland density varies considerably within each breed with consequent overlapping of the ranges for different breeds.

More important than the number of sweat glands seems to be their volume. Sahiwal Zebu cattle and Jersey cattle had virtually the same number of sweat glands per unit area of skin, but the Sahiwals had much larger sweat glands resulting in a 340% greater total sweat gland volume per unit area of skin (Pan, 1963). Similarly,

higher sweat-gland volumes were found for cattle sired by a Texas Zebu bull than for cattle sired by a Shorthorn bull from Scotland (Nay & Dowling, 1957). A rough calculation of the storage capacity for sweat in 1 m² of skin gave figures of 40 ml for European-type animals possessing very small sweat glands, and 480 ml for Zebu-type animals possessing very large sweat glands (Nay, 1959). A large storage volume for sweat would give an animal that is introduced into a hot environment an initial advantage. Depending on the mode of functioning of the sweat gland (as yet not known) it might give it also a lasting advantage during long-term exposure. This would certainly be in line with the finding that high sweat-gland volumes are associated with high heat tolerance (Nay, 1959; Walker, 1960; Nay & Dowling, 1957). Sweat-gland size and shape were found to vary not only between animals but also even between various body regions of the same animal (Pan, 1963). The sweat glands of the mid-side position (between the 10th and 11th rib) showed the closest relation to the average for the sweat glands from all the body regions. Comparative studies should therefore be made by using samples from an animal's mid-side position (Pan, 1963).

Regional distribution of cutaneous evaporation

At environmental temperatures in the range 15–20° cutaneous evaporation in calves is small and similar in all body regions investigated (McLean, 1963*a*).

At high environmental temperatures cutaneous evaporation varies significantly between various body regions. This was demonstrated in Holstein–Syrian cows (Berman, 1957; Volcani & Schindler, 1954); in Jersey and Red Sindhi–Jersey cows (McDowell, McMullan *et al.* 1955; McDowell, McDaniel *et al.* 1961; in Shorthorn, Santa Gertrudis and Brahman calves (Kibler & Yeck, 1959); and in Indian Zebras (Chowdhury & Sadhu, 1961). In spite of the great variety of breeds used in these studies, there was a common general pattern of regional distribution of cutaneous evaporation: evaporation rate tended to be high in the upper surfaces and low in the under surfaces of the body. The high rate of evaporation from the parts of the body exposed towards the sky would have the advantage of counteracting the heat load imposed on them by direct solar radiation.

Of particular importance in this regard seems to be the hump. In Zebras of the Haryana breed the hump has been reported to contain sweat glands which are larger and lie nearer to the surface of the skin than in other body regions (Chowdhury & Sadhu, 1963). From this it was speculated that solar radiation would readily activate the sweat glands in the hump and that evaporation from the hump would be assisted by the air movement around this prominent appendage. Among the body appendages of American Brahman cattle the rate of evaporation was highest in the hump, intermediate in the dewlap and lowest in the navel flap (Kibler & Yeck, 1959). The observation made on Holstein–Syrian cattle under field conditions, that black areas of the coat tended to have higher rates of evaporation than white ones, is interesting but needs confirmation (Berman, 1957).

Relation of cutaneous evaporation to respiratory evaporation

At low environmental temperatures the evaporation from the skin and that from the respiratory passages are approximately equal (Kibler & Brody, 1950*a*; McLean,

1963*b*). At high environmental temperatures cutaneous evaporation becomes much greater than respiratory evaporation (Kibler & Brody, 1950*a*; McLean, 1963*b*; Weldy & McDowell, 1962; Kibler, Yeck & Berry, 1962). The air temperature at which they begin to differ is around 15° in Holstein and Jersey cattle (Kibler & Brody, 1950*a*). When temperature was elevated above this level cutaneous evaporation rose sharply to a maximum of about 150 g/m² h while respiratory evaporation gradually rose to about 50 g/m² h (Kibler & Brody, 1950*a*). In calves of 3 breeds reared at 10° cutaneous evaporation accounted for 55–72% of the total evaporation; in similar calves reared at 27° it accounted for even 64–82% (Kibler & Yeck, 1959). Also, in adult cattle when exposed to heat, the skin may contribute as much as 80% to the total moisture evaporated from the animal, the remaining 20% coming from the respiratory passages (Yeck & Stewart, 1959). It is evident from the results quoted that in the heat-stressed animal cutaneous evaporation may be 5 times greater than respiratory evaporation.

Since sweating lowers the skin temperature and since it is the skin temperature which largely governs respiratory frequency, certainly in mild heat (Bligh, 1957*b*; Firdlay & Ingram, 1961), it would be expected that a high sweating rate is associated with a relatively low respiratory frequency, and a low sweating rate with a relatively high respiratory frequency. Such an inverse relationship of sweating and panting (and thus of cutaneous and respiratory evaporation) has been established in Zebu-type cattle (Kibler & Yeck, 1959) and in growing Ayrshire calves (McLean, 1963*a*).

Factors affecting cutaneous evaporation

Some of the changes in evaporation reported in this section refer to total evaporation, but in view of the relatively small part played by respiratory evaporation these changes in total evaporation may be assumed to reflect predominantly changes in cutaneous evaporation.

Environmental temperature

The response of cutaneous evaporation to changes in environmental temperature is well documented. Holstein and Jersey cows showed a tenfold increase in evaporation (25–250 g/m² h) when the temperature was raised from –18 to 38°. Evaporation rate varied with surface area rather than with body weight. A rough comparison indicated that between 32 and 38° cows evaporate about 2 lb moisture/h, which is virtually the same amount as that evaporated at this temperature by man, whose body weight is about a tenth that of the cow (Thompson, McCroskey & Brody, 1949). The rate at which evaporation rises with rising environmental temperature is not uniform. In European-type cows it was described as slow and linear from –18 to 10° and rapid and exponential from 10 to 29°. Above 29° uncertain variations were recorded indicating that a maximum was being approached (Thompson, McCroskey & Brody, 1951). This S-shaped evaporation curve in response to rising environmental temperature seems to be characteristic. The reason why it was not observed in Ayrshire calves in the temperature range 15–40° (McLean, 1963*b*) must have been that in these animals the phase of sharp rise in evaporation rate did not begin until an environmental temperature of about 25° had been reached, so that the upper portion of the S-curve was not revealed.

When cows are subjected to radiant heat, cutaneous evaporation may rise at relatively low air temperatures. When the intensity of artificially produced radiation was raised from a low level to about 500 kg cal/m² h, cutaneous evaporation increased at air temperatures of 27, 21 and even 7° (Kibler & Brody, 1954). Experiments conducted with cows exposed in a hygrometric tent to various diurnal temperature rhythms indicated that the time required for evaporation rate to adjust to relatively short-term changes in air temperature is generally less than 2 h (Yeck & Kibler, 1956).

Air humidity

Air humidity affects cutaneous evaporation in 2 different ways. Increasing the air humidity depresses evaporation from the skin by reducing the water vapour pressure gradient between the skin and the air. This effect, which is a purely physical one, has been clearly demonstrated by McLean (1963*b*); raising the air humidity at 20-min intervals from 8 to 35 mmHg caused local cutaneous evaporation of calves to decrease linearly from 150 to 60 g/m² h. However, this decrease in cutaneous evaporation augments the heat stress on the animal, thereby stimulating a compensatory increase in cutaneous evaporation provided maximum evaporation has not yet been reached. Thus, under certain conditions, cutaneous evaporation may remain unaffected by rising air humidity, or even increase in response to it.

Thompson *et al.* (1953), using Jersey, Holstein, Brown Swiss and Brahman cows, did not find any effect of high humidity on evaporation rate at environmental temperatures of -11 and 4°; a depressing effect was, however, observed at 24, 29 and 35°. McDowell, McDaniel, Barrada & Lee (1961) obtained a humidity-induced decrease in cutaneous evaporation in Holstein cows only at a temperature as high as 35°.

It is clear that a high air humidity at a high environmental temperature acts as a powerful heat stress factor. Various attempts have been made to evaluate the relative importance of air humidity and air temperature in causing heat stress in cattle. Barrada (1957) expressed the combined effect of temperature and humidity by constructing 'lines of equal effect' on psychrometric charts. Bianca (1962*a*) determined weighting factors for dry and wet bulb temperature, and his findings indicated that the effect of wet bulb temperature was approximately twice as large as that of dry bulb temperature (65% wet bulb and 35% dry bulb). The fact that in man the wet bulb temperature effect exceeds the dry bulb temperature effect by a factor of about 6 (Provins, Hellon, Bell & Hiorns, 1962) is probably caused by the large difference in the capacity for evaporation of moisture in the 2 species.

Air movement

A third climatic factor which influences cutaneous evaporation is air movement. Its effect is dependent on the environmental temperature. Thompson, Yeck, Worstell & Brody (1954) placed propeller-type fans above cows and determined evaporation in the temperature range -8 to 35°. At -8° no effect was observed; at 10° the effect was uncertain; at 15 and 27° increasing air movement reduced evaporation from the animal. This reduction in evaporation was thought to be due to the greatly increased convective cooling which reduced the homeothermic need for heat dissipation by evaporation. At very high environmental temperatures, of course, the temperature

gradient between the animal and the surrounding air becomes too small for convective cooling to have an appreciable effect.

Non-climatic factors

There is evidence to show that the rate of cutaneous evaporation is greater in the adult than in the young animal. With increasing age calves of various breeds, when exposed to heat, showed increases in the rates of cutaneous evaporation (Taneja, 1958*b*; McLean, 1963*b*) while the rate of respiratory evaporation remained unaltered or even declined. In Shorthorn, Santa Gertrudis and Brahman calves the percentage of heat dissipated by cutaneous evaporation increased after about 6 months of age. This increase was more rapid in the animals reared at 27° than in those reared at 10° (Kibler & Yeck, 1959). A similar trend was observed in Brown Swiss, Holstein and Jersey calves (Kibler *et al.* 1962).

Clipping an animal's hair coat has been reported to depress evaporation (Kriss, 1930; Berman & Kibler, 1959; McLean, 1963*b*). In these instances the environmental temperature was below body temperature, so that the decrease in cutaneous evaporation was probably the direct result of the improved non-evaporative cooling brought about by the removal of the hair coat. On the other hand Berman (1957), working under probably hotter conditions with 221 Holstein-Syrian cross-bred cows in Israel, found that clipping increased cutaneous evaporation to a highly significant degree. Indirect evidence for an augmentation of cutaneous evaporation caused by clipping has been obtained in calves exposed to 40° (Bianca, 1959*c*).

Finally, it is known that an increase in cutaneous evaporation in calves may be produced by local heating of the hypothalamus, by infra-red irradiation of the pump (Ingram, McLean & Whittow, 1963), and by physical exercise (Hayman & Nay, 1958).

Genetic differences in cutaneous evaporation

Work conducted mainly in Australia and America has established genetic differences, both of sweat-gland structure and cutaneous evaporation. The number of sweat glands per unit area of skin is higher in Zebu than in animals of various European-type breeds (Dowling, 1955*a*; Nay & Hayman, 1956). In Jerseys it was found to be only very little below that of Sahiwal Zebu (Pan, 1963). The sweat glands of *B. indicus* cattle are characterized by their greater length, greater diameter, their sac-like appearance with only few convolutions, and their large volume. Sweat glands of *B. taurus* cattle, on the other hand, are normally short, small in diameter, fairly convoluted and have a small volume. The same authors have also observed that in *B. indicus* the sweat glands are situated more closely to the skin surface than in *B. taurus*. Compared with these differences between species, the differences between breeds are small, although Nay & Hayman (1963) have described significant differences in sweat-gland volume among 5 European-type breeds in Australia.

In general, the structural differences between sweat glands are associated with functional differences in the sense that *B. indicus*-type sweat glands have a higher capacity for producing sweat than *B. taurus*-type sweat glands. This superiority in sweating, however, may not manifest itself under conditions of low heat stress, because a large proportion of the body's heat can be dissipated by convection and

radiation. Thus, Brahman calves compared with Shorthorn calves had lower rates of evaporation in mild heat, but higher ones in severe heat (Kibler & Yeck, 1959). Yeck & Kibler (1958) found that the ratio of evaporation at 27° to evaporation at 10° in calves of 6 breeds of cattle increased in the order: Shorthorn, Holstein, Jersey, Brown Swiss, Santa Gertudis, Brahman. In the same order the animals ranked with respect to rising heat tolerance. Allen (1962) found that for a given rectal temperature Zebu cattle sweated less than Jersey cattle. He considered that this enabled the Zebus over a part of each day and during most months of the year to lose 40–50% less water from the skin than the Jerseys.

The above results underline the importance of differentiating between the inherent capacity to produce sweat and the amount of sweat actually produced in response to a given heat load (which reflects the thermoregulatory requirements for sweating).

EVAPORATION FROM THE RESPIRATORY PASSAGES

This section deals with the major effects of heat stress on respiratory activity. It also includes some secondary effects of heat-induced over-ventilation.

Frequency, depth and volume of breathing

Respiratory evaporation is a function of the vapour pressure of the air and of respiratory ventilation (minute volume).

The changes in ventilation and in respiratory evaporation produced by heat stress are practically identical (Worstell & Brody, 1953). Ventilation in turn is the resultant of the frequency and the depth of breathing (respiratory rate and tidal volume).

Heat is well known to augment the respiratory activity of cattle. Respiratory rate has been shown to start to rise at environmental temperatures of 16° in lactating Jersey, Holstein and Brown Swiss cows, and at 24° in Brahman cows. Corresponding figures for the beginning of an increase in ventilation were (in the same order of breeds) 24, 18, 16 and 32° (Worstell & Brody, 1953). With rising environmental temperature the 3 respiratory variables do not increase in the same way. Up to environmental temperatures of approximately 40° respiratory rate at first rises sharply and later more slowly (Worstell & Brody, 1953). Maximum respiratory rates are about 200/min in cows (Riek & Lee, 1948*b*) and about 250/min in calves (Bligh, 1957*b*). This rise in respiratory rate is accompanied by a corresponding fall in tidal volume (Riek & Lee, 1948*a*; McDowell, Lee, Fohrman & Anderson, 1953; Findlay, 1957; Bianca & Findlay, 1962). Since the change in respiratory rate exceeds the change in tidal volume, the resultant of both, i.e. the ventilation, increases (Worstell & Brody, 1953; Findlay, 1957; Bianca & Findlay, 1962). Ventilation may be as high as 300 l/min in cows (Worstell & Brody, 1953) and 120 l/min in 9-month-old calves (Bianca & Findlay, 1962).

High air humidity greatly enhances the effect of high air temperature on respiration. Riek & Lee (1948*a*) concluded from hot room experiments with Jersey cows that an increment in humidity of 0.4 grains/ft³ had the same effect as an increase in temperature of 1 deg F. Beakley & Findlay (1955*d*), working with Ayrshire calves, found that air temperatures of 30 and 35° at a high humidity were equivalent in their effect on respiratory rate to air temperatures of 33 and 46° at a low humidity. Barrada (1957) has plotted both respiratory rate and ventilation of cows as a function

of the temperature and humidity of the air. From the 'lines of equal effect' so obtained, it is evident that the effect of humidity increases systematically with increasing temperature.

Under conditions of severe heat (normally produced by the combination of high temperature with high humidity), where body temperature rises continuously, the response of frequency and depth of breathing is biphasic: in a first phase the frequency rises while the depth falls. In a second phase the reverse changes occur (Findlay, 1957; Bianca & Findlay, 1962). Throughout both phases, ventilation rises more or less continuously. The biphasic respiratory response is evident in young animals, but less so in adult animals. The change-over from the first to the second phase occurs at a rectal temperature of about 40.5° (Findlay, 1957). It is not known whether this relationship is incidental or causative. There is some evidence that the rectal temperature at which the change in respiratory pattern occurs may increase progressively during the course of acclimatization of an individual animal (Bianca, unpublished observations).

Thermoregulatory significance of respiratory activity

The cooling effect of respiratory evaporation may be directly measured. Ingram & Whittow (1962) observed that in a hot dry atmosphere an increase in respiratory frequency of calves led to a cooling of the blood (as evidenced by a widening of the temperature difference of the blood in the jugular vein and in the bicarotid trunk). Since Bligh (1957*a*) failed to detect a temperature difference between the blood in the bicarotid trunk and that in the pulmonary artery of calves exposed to heat, it may be concluded that the main cooling effect of respiratory evaporation does not take place in the lungs but in the upper respiratory passages.

As discussed in the previous section the contribution of respiratory evaporation to total evaporation is much smaller than that of cutaneous evaporation (under extreme conditions it is only one-fifth or one-sixth of the total). This suggests that respiratory activity is not the decisive factor in the control of body temperature when cattle are subjected to heat stress. Indeed, it is well established that high respiratory activity under conditions of heat stress is 'a measure of the inadequacy of the quantitatively more important cutaneous evaporation to maintain a balance' (Riek & Lee, 1948*a*). McDowell, Lee, Forhman & Anderson (1953) found that in an atmosphere of 40° dry bulb and 33° wet bulb Jersey cows had a higher ventilation than Jersey-Red Sindhi (F_1) crosses, and yet, in spite of the additional cooling derived from the increased ventilation, the Jerseys suffered a much greater increase in rectal temperature than did the crosses. Thus, 'the high respiratory activity was an attempt to compensate for a poor heat balance brought about by some other cause'. An inverse relationship between ventilation and rectal temperature, and therefore with heat tolerance, has also been demonstrated for calves (Bianca, 1962*b*).

There is still the unresolved question, to what extent the net effect of respiratory cooling is reduced by the heat generated by the respiratory muscles. Work on man (Liljestrand, 1918; and many later authors) and also on the dog (Albers, 1961) has shown that, with increasing respiratory minute volume, oxygen consumption does not rise linearly but exponentially. Rossier & Bühlmann (1959) found that hyper-ventilating men had a critical rate of ventilation of 130-140 l/min beyond which the body did not profit any further from a rise in ventilation because the extra oxygen

taken up was consumed mainly by the respiratory muscles. It is feasible that breathing in severely heat-stressed cattle (with body temperatures at 41° or above) is performed at an increased calorific cost, since in calves heart rates (Bianca, 1958) and blood lactic acid concentrations (Bianca, 1955) have been found to increase significantly during this phase.

Secondary effects of heat-induced over-ventilation

A high rate of ventilation may cause the elimination from the lungs of an excessive amount of carbon dioxide. This results in the first place in a carbon dioxide deficit in the blood (Dennis & Harbaugh, 1946; Blincoe & Brody, 1951). Under more severe conditions of heat, where compensatory mechanisms are unable to prevent the pH of the blood from rising, the acid-base status of the animal becomes disturbed. A respiratory alkalosis has been shown to develop in cows (Dale & Brody, 1952; Barrada, 1957) and in calves (Bianca, 1955; Bianca & Findlay, 1962). It is characterized by a low carbon dioxide content of the blood plasma and a high pH of the blood and the urine. The rise in urinary pH is considered to represent a renal compensation consisting in a diminished rate of re-absorption of bicarbonate by the renal tubules. Direct evidence of an increased bicarbonate content of the urine in cows exposed to heat has been presented by Barrada (1957).

The magnitude of the acid-base disturbance increases with increasing heat stress. Under conditions of dry heat no major changes were observed in Holstein cows up to air temperatures of about 43°, but very pronounced changes occurred at 54°, involving values for blood pH as high as 7.83 (Barrada, 1957). Bianca & Findlay (1962) compared the effects of 'severe' and of 'mild' heat on the acid-base status of calves. Their findings suggest that, as long as equilibrium conditions of body temperature and respiratory activity can be maintained ('mild' heat), respiratory alkalosis does not seem to constitute a serious hazard in the heat-exposed animal.

Apart from the observations of Riek & Lee (1948*b*) that heat-stressed calves showed weakness of the hind limbs (at rectal temperatures above 41.1°) and the finding of Riek & Lee (1948*a*) and Bianca & Findlay (1962) that with rising body temperature the concentration of calcium in the blood of calves tended to fall, there is no evidence that cattle develop a hypocalcaemic tetany in response to a heat-induced over-ventilation. This is in contrast to man, in whom, according to Peters & Van Slyke (1946), a rise of blood pH to only about 7.6 is sufficient to induce tetany.

WATER EXCHANGE

Leitch & Thomson (1944) have made an extensive survey of the various factors involved in the water economy of cattle. They calculated that a cow producing 48 kg milk/day, in order to maintain thermal balance, would have to evaporate 30–40 kg water/day. They concluded that under hot climatic conditions animal production may be limited by the capacity of the animal to dissipate heat rather than by its capacity to hold and digest feed in the intestinal tract.

Effects of heat on water consumption

Cattle exposed to conditions of rising temperature may develop the habit of spilling water and sprinkling it over their body (Ragsdale, Thompson, Worstell & Brody,

1951). This results in falsely high figures for water consumption. But, even if allowance is made for spillage, the water consumption of cattle exposed to heat varies greatly from one animal to another (Thompson, Worstell & Brody, 1949). One Jersey cow has been reported to have increased her water consumption from 50 to 195 l/day when the environmental temperature was raised from 10 to 38°, while under similar conditions other cows even decreased their water consumption (Worstell & Brody, 1953).

The amount of water drunk by normal cattle in a hot environment is governed by 2 main factors: the severity of the heat and the amount of dry matter eaten. Increase in water consumption with rising environmental temperature is well documented. Calves of 3 dairy breeds drank more at 27 than at 10°, the difference being largest in Holsteins (13.4 l/day), intermediate in Brown Swiss (6.6 l/day) and smallest in Jerseys (1.4 l/day) (Johnson, Ragsdale & Yeck, 1960). Raising air temperature from 10 to 27° produced an increase in water consumption also in Jersey and Holstein cows (Ragsdale, Worstell, Thompson & Brody, 1949) and field observations in Texas with cows of these 2 breeds revealed a highly significant linear correlation between air temperature and water consumption (Harbin, Harbaugh, Neeley & Fine, 1958). Brahman and Brown Swiss heifers also increased their water consumption with rising environmental temperature (Ragsdale *et al.* 1951). Under comparable conditions of heat, Zebu-type cattle have been observed to drink less water than European-type cattle of the same size (French, 1939; Ittner, Kelly & Guilbert, 1951; Hungate, Phillips, MacGregor & Hungate, 1958).

The mechanism responsible for heat-induced increases in water consumption seems to involve the hypothalamus, since warming the pre-optic area and rostral hypothalamus of the goat with thermodes evoked a large increase in water consumption, an observation which supports the thermostatic theory of the regulation of water intake (Andersson & Larsson, 1961).

Effects of feeding on water consumption

The rise in water consumption with rising temperature does not manifest itself if the rising temperature depresses feed intake and with it the milk secretion to such an extent that the decreased metabolic requirements for water outweigh the increased homeothermic requirements. Indeed, under such conditions there is a decrease in water consumption with rising temperature, as shown for Jersey and Holstein cows in the temperature range 27–35° (Ragsdale *et al.* 1949), and for Brown Swiss cows at temperatures above about 29° (Ragsdale *et al.* 1951). The finding that Brahman cows, kept under the same conditions as the Brown Swiss cows, did not decrease their water consumption, but actually increased it, is explainable by the fact that their food intake and their milk production, which was low to begin with, declined only a little. It is likely that the depression in water consumption observed in cows subjected to high humidity at high temperature is also largely due to a lowering of feed intake (Ragsdale, Thompson, Worstell & Brody, 1953).

To allow for the effect of food intake several workers have related the water consumption to the dry matter intake. An excellent condensed account of the changes of this ratio with rising ambient temperature has been given by Winchester & Morris (1956). When plotting water consumption per unit of dry matter intake of *B. taurus* cattle against environmental temperature, a curve was obtained which

remained level between -12 and 4° , but which rose at an accelerated rate between 4 and 38° . *B. indicus* cattle showed a similar curve but the water consumption per unit of dry matter eaten was always lower for any given temperature. Later work has confirmed that *B. indicus* cattle consume less water than *B. taurus* cattle, not only absolutely but also relatively to feed intake (Phillips, 1960; Horrocks & Phillips, 1961; Payne, 1963). Corresponding differences were also found between various breeds of *B. taurus* cattle. Holstein calves had higher water consumptions than Brown Swiss and Jersey calves, whether expressed per animal, per unit of feed intake or per unit of skin area (Johnson, Ragsdale & Yeck, 1960). Thus, high heat tolerance was always associated with a low water consumption, and low heat tolerance with a high water consumption.

Several workers found water consumption to be affected by the composition of the feed. Water consumption of cows grazing in Trinidad was inversely related to the water content of the grass (Wilson, Barratt & Butterworth, 1962). Steers on high protein rations drank 26% more water than steers on low protein rations (Ritzman & Benedict, 1924). Similarly, raising the crude protein content of the feed induced *B. taurus* and *B. indicus* cattle to increase their water consumption (Payne, 1963).

Prediction of water consumption

The dependence of water consumption on environmental temperature and dry matter intake has been used for making predictions of water consumption. Winchester & Morris (1956) constructed tables for various categories of cattle covering the temperature range $4-32^{\circ}$. There was, in general, a good agreement between the estimated and actual water consumption. Mullick (1959) and Negi & Mullick (1960), on the basis of a long-term study with cattle and buffaloes in India, recommended that in summer the animals should be given 3.5-5 times more water than feed dry matter (weight for weight), in winter 2.5-3.5 times more. Harbin *et al.* (1958) presented an equation for the prediction of water consumption of grazing cattle from environmental temperature alone.

Ways of using water for cooling

It is obvious that the cooling effect on the animal of the water consumed depends on the way the water is being used in the body. If the water drunk is cool, a high water consumption may lead to an appreciable cooling of the body by conduction. Steers which, after a period of water restriction, drank 50 l of cold water (14°) experienced a precipitous fall in rectal, skin and subcutaneous temperature of about 1.7° (Bianca, 1964). The heat-induced increase in water consumption (145 l./day) of a Jersey cow (Worstell & Brody, 1953) would require the dissipation of over 3600 kcal/day to heat the water from 16° to body temperature (41°). However, a much greater cooling effect would be achieved if a high proportion of the water drunk were to be evaporated from the skin. In this respect Brown Swiss and Jersey calves seem to be superior to Holstein calves. Thus, by evaporating a larger percentage of the water they consumed, the Brown Swiss and Jersey cattle made more efficient use of the water as a cooling medium (Kibler *et al.* 1962).

Similar observations apply to the elimination of water in the faeces. Since half the water consumed may leave the body in the faeces (Leitch & Thomson, 1944) the

observation that under comparable conditions the faeces of Zebu cattle contain less water than that of European-type cattle (Quarterman, Phillips & Lampkin, 1957) is important in relation to water economy.

Effects of water restrictions

Restricting cows on pasture to drink water only twice daily had no effect on their yields of milk and milk fat (Campbell, 1958). This finding is not surprising since heifers have been shown to be able to drink at one time all the water they need for a day (Leitch & Thomson, 1944). Payne (1963), working with identical cattle twins in Tanganyika, found that 4 days of water deprivation reduced the output of water in urine and faeces, and that this effect was more pronounced in *B. indicus* than in *B. taurus* cattle. Ayrshire steers which were deprived of drinking water for 4 days showed decreases in hay consumption, faeces excretion, urine excretion, insensible weight loss, body weight, heat production, respiratory minute volume, plasma potassium concentration and in urinary potassium output. At the same time there were increases in haematocrit, plasma solids, blood urea, plasma sodium, plasma chloride and in the output of urinary sodium (Bianca, Findlay & McLean, 1965). Reducing the water consumption of Hereford and Zebu steers to half the normal amount resulted in a slower passage of the digesta, and an increased absorption of water from the terminal section of the gut (Phillips, 1961*b*). According to Payne (1963), in cattle that are on a very low level of feeding, deprivation of water for not too long a period may even have a beneficial effect. He found that on a ration containing 4% crude protein steers had a negative nitrogen balance, and that when they were then deprived of water for 4 days the nitrogen balance improved. From this, Payne concluded that water deprivation could enable cattle to remain in protein balance at a much lower level of crude protein than had been accepted for normally watered animals.

There is some evidence to suggest that under conditions of water deprivation cattle may, within limits, save water even at the expense of homeothermy. In an atmosphere at 40° water deprivation of steers for 4 days caused a decline in respiratory rate and a delay in the outbreak of sweating, with a resulting increase in body temperature (Bianca *et al.* 1965; Bianca, 1965). Dehydration brought about by adding sodium chloride (1.5% on average) to the drinking water of heifers also affected thermoregulation unfavourably (Weeth, Hunter & Piper, 1962). Rapid rehydration had no ill effects when dehydration had been brought about by withholding drinking water (Bianca, 1964) but caused prostration in some of the animals dehydrated with salt water (Weeth *et al.* 1962).

ALIMENTATION

Feed intake in a hot environment

Worstell & Brody (1953) have cited environmental temperatures at which feed consumption begins to decline: 21, 24 and 27° in lactating Holstein, Jersey and Brown Swiss cows; 35° in lactating Brahman cows as well as in Brahman and Brown Swiss heifers. Since, in the cows, the decrease in feed intake was greater than the decrease in milk production, there was a loss in body weight. At an environmental temperature of 32° feed consumption of lactating Holstein cows was depressed by 20%

(Davis & Merilan, 1960), and at 40° feed intake of Holstein and Jersey cows virtually stopped (Ragsdale, Brody, Thompson & Worstell, 1948). At body temperatures above 40° rumination in Illawarra Shorthorn cows ceased (Robinson & Klemm, 1953). Calves of different breeds kept under conditions of thermoneutrality (10°) and of mild heat (27°) varied considerably in their response: Shorthorn, Holstein and Jersey calves all consumed less feed at 27 than at 10°. With Brown Swiss calves there was no change, and Brahman calves, up to 8 months old, even ate more at 27 than at 10° (Johnson, Ragsdale & Yeck, 1958, 1960). Similar differences were obtained for heifers. In an atmosphere of 39° Jersey heifers reduced their feed intake while Zebu heifers maintained their appetite (Allen, Pan & Hayman, 1963). A diurnal temperature rhythm of 4–21° ('Mid-West optimal') was without effect on feed consumption of cows, but one of 21–38° ('Mid-West hot') produced a decrease in feed intake. The latter diurnal temperature rhythm was found to correspond in its effects on the animals to a constant temperature of 29° (Brody, Ragsdale, Yeck & Worstell, 1955). High air humidity was found to affect feed intake of cows only at air temperatures higher than 24° (Ragsdale *et al.* 1953).

The finding that voluntary feed intake of cattle falls with rising environmental temperature and that the beginning of this fall coincides with the beginning of the rise in body temperature (Worstell & Brody, 1953) conforms with the concept of Brobeck (1948) that the amount of food consumed is determined, at least partly, by the organisms' ability to dissipate the heat generated by the metabolism of food. It appears that appetite, the immediate regulator of food intake, responds to thermal stimulation. Brody, Dale & Stewart (1955) speculated that the rumen temperature itself might limit feed intake in the heat, since it was found that the temperature of the rumen could exceed the temperature in the rectum by as much as 2.2°. In a later paper Brobeck (1960) proposed that the hypothalamus acted as an integrator for regulating food intake and other functions involved in energy balance. Direct evidence in favour of Brobeck's thermostatic theory of the regulation of feed intake has been provided by Andersson & Larsson (1961). Warming the pre-optic area and rostral hypothalamus of goats with thermodes caused the hungry animals, which had just begun to eat with good appetite, to stop eating within 1 min.

Johnson, Wayman *et al.* (1961) prevented the heat-induced decline in food consumption by introducing food into the rumen through a fistula. They found that compared with control cows the fistula-fed cows responded differently to heat: they drank more water instead of less, they respired at a slightly higher rate and they experienced an increase in heat production instead of a decrease. They also put on weight and produced 2.6 lb more milk/day. This novel approach may prove a help in elucidating the complex interrelationship of feed intake and temperature.

Grazing performance

Under field conditions the depressing effect of heat on feed intake is evident from the shorter times the animals spend grazing. Observations on beef cattle in tropical Queensland (Larkin, 1954) showed that high temperatures reduced day-time grazing, restricted the total grazing time and caused the animals to spend long periods in the shade. The effects of heat on grazing time were more pronounced in animals of 3 European beef breeds than in Afrikaner cattle (Bonsma, Scholtz & Badenhorst,

1940). The time spent grazing was significantly correlated with the vapour pressure of the air, but not with its relative humidity (Miller & Frye, 1956). Reduced day-time grazing may be overcome, at least in part, by night grazing. However, Joblin (1960) found that night grazing was useful only under conditions of moderate grass shortage. On good and on very poor pastures night grazing did not improve weight gains.

As may well be expected the temperature thresholds for a decline in feed consumption are not the same in the field as in the climatic room, because of the modifying effects of other climatic factors that operate out of doors. Thus, Holder (1960) stated that environmental temperatures up to 30°, which are known to depress feed intake of cattle in climatic rooms, had no adverse effect on the grazing time of Jersey, Guernsey and Illawarra Shorthorn cows in New South Wales, and Seath & Miller (1946) found that solar radiation (in addition to high temperature) depressed grazing time.

Feed quality and digestion

There is evidence to show that in a hot environment a ration with a low fibre content has a beneficial effect on the animal's thermal balance and hence on its production. In Arizona a low fibre ration, as compared with a high fibre ration of approximately the same net energy content, was found to lower body temperature by 0.3°, respiratory rate by 14 respirations/min and to raise the yield of fat-corrected milk by 1.2 lb/day (Stott & Moody, 1960). Similarly, Leighton & Rupel (1960) observed that in warm weather a ration high in protein and low in fibre tended to keep body temperature, respiratory rate and heart rate low and milk yield high.

The digestibility of feed seems to increase slightly under conditions of mild heat stress. This was shown by Blaxter & Wainman (1961) in steers when the environmental temperature was raised from 4 to 35°, and by Davis & Merilan (1960) in cows exposed to an atmosphere of 32°. There are also reports which indicate that Zebu-type cattle are superior to European-type cattle in their capacity to digest feed, particularly if the feed is of poor quality (Howes, Hentges & Davis, 1963; Ashton, 1962; Phillips, 1961*a*). This difference has been related to differences in the rate of fermentation in the rumen. Zebu cattle were found to have higher fermentation rates than European cattle (Phillips, Hungate, MacGregor & Hungate, 1960; Hungate, Phillips, Hungate & MacGregor, 1960; Phillips, 1961*a*). *B. indicus* cattle differed from *B. taurus* cattle also with regard to the large intestine: samples taken from the gut within 2 h after death gave higher values for dry matter concentration and osmotic pressure in *B. indicus* than in *B. taurus* cattle.

Exposure of cattle to heat depressed the concentrations of volatile fatty acids in the rumen (Weldy, McDowell, van Soest & Bond, 1964). This depression was largely the result of a lowered concentration of acetic acid. The resulting decline in the ratio of acetic acid to propionic acid would have the effect of reducing the heat increment (Blaxter, 1962) and thus the heat load of the animal. The concentration of volatile fatty acids in the heat-exposed animals was, in fact, inversely related to rectal temperature and respiratory rate (Weldy *et al.* 1964).

TEMPERATURE REGULATION

Temperature regulation in mammals in general has been studied intensively and the work has been reviewed by numerous authors, e.g. by Thauer (1958), Hardy (1961), von Euler (1961) and Bligh (1965). Temperature regulation in the ox has received relatively little attention. This section deals with topographic variation, periodic fluctuations and with regulators of body temperature.

Body temperature

The temperature of the body surface has been measured under a variety of hot conditions by many workers. Thompson, Worstell & Brody (1951) determined skin and hair temperatures on 6 body areas of Holstein and Jersey cows in the temperature range -18 to 40° . Skin and hair temperatures, which at -18° differed by about 15° , became similar and merged with environmental temperature at 39° . The same authors (1952), extended their measurements to Brown Swiss and Brahman cows and heifers, obtaining essentially similar results. Skin and hair temperatures have also been determined in cattle exposed to various intensities of artificially produced radiation (Stewart & Brody, 1954) and in calves reared at 10 and 27° . Beakley & Findlay (1955*b, c*), who determined skin temperatures of calves in the temperature range 15 to 40° , presented an equation for the prediction of the mean skin temperature on the trunk from rectal temperature, environmental temperature and the absolute humidity of the air. Whittow (1962), also working with calves, recorded large variations in skin temperatures of the extremities when the environmental temperature was -5 to 25° . At environmental temperatures above 25° the temperatures of the extremities and those of the trunk were similar. Bianca (1964) observed that, during exposure of calves to heat, and following the rapid ingestion of large amounts of cold water, changes in skin temperatures were closely paralleled by changes in subcutaneous temperature.

Considerable emphasis has been placed on the measurement of deep body temperatures. Bligh (1955) tested in calves the validity of using rectal temperature as a measure of deep body temperature by comparing the temperature in the rectum with that of the blood in the bicarotid trunk. Under conditions of thermoneutrality and of mild heat stress rectal temperature was consistently 0.1 – 0.3° higher than carotid blood temperature. Under conditions of severe heat stress the 2 temperatures became identical and rose conjointly. Apart from the fact, therefore, that rectal temperature responds to abrupt changes in environmental temperature only after a short delay, changes in rectal temperature indicate changes of a similar magnitude in deep body temperature. Bligh (1957*a*) also showed that in the calf exposed to heat the blood in the pulmonary artery and in the bicarotid trunk had the same temperature. The temperature of the carotid blood may be obtained by measuring the temperature of the outer surface of the carotid artery with the aid of a thermocouple terminating in metallic gauze sewn around the blood vessel (Ingram & Whittow, 1961). The same workers (1962) recorded the temperature of the blood in the jugular vein and in the hypothalamus (1962, 1963) of the ox under a variety of thermal conditions. Temperatures in the vagina of dry cows have been reported by Kriss (1921). Finally, it has been shown that the temperature in the rumen of cattle may exceed that in the

rectum by as much as 2.2° (Dale, Stewart & Brody, 1954). The fact that this difference was reduced to 0.8° when the animals received no food indicates the involvement of heat-producing micro-organisms. Changes in rumen temperature in response to the ingestion of cold water have been reported by Cunningham, Martz & Merilan (1964).

Deep body temperature not only varies with different body areas; it also fluctuates from time to time. Patchell (1954), working with 3 pairs of monozygotic twins, found rectal temperature to have a maximum in the early evening (17–18 h) and a minimum in the early morning (4–6 h). This finding is in general agreement with earlier observations by Kriss (1921) and by Gaalaas (1945). The classification of 102 continuously recorded body temperatures of cows revealed distinct diurnal patterns (Wrenn, Bitman & Sykes, 1961): 67 % of the animals were biphasic in that they had 2 temperature elevations per day, 23 % were monophasic, 7 % polyphasic and 3 % aphasic. Ovariectomy and pregnancy did not seem to affect the incidence of those patterns. Increases in temperature have been found in the jugular blood (Ingram & Whittow, 1962) and in the brain (Findlay & Ingram, 1961) as a result of feeding, and in the rectum due to physical exercise (Dowling, 1956). Decreases in body temperature below the normal level have been reported for Zebu cattle during the night in the hot season (Hutchison & Mabon, 1954) and in calves acclimatized to heat (Bianca, 1959*a, b*). Body temperature has also been shown to change with the level of nutrition (Robinson & Lee, 1947) and to fluctuate with the oestrous cycle (Wrenn, Bitman & Sykes, 1958; King, 1963). Kaemmerer (1955) claimed that there is an apparent 7-day cycle in the body temperature of cows. These results suggest that deep body temperature can vary over a certain range without any apparent compensatory reactions being brought into play.

Regulators of body temperature

In recent years work has been conducted to define peripheral and central thermoreceptors responsible for the initiation and control of peripheral vasomotor activity, of sweating and of panting in the ox.

Peripheral vasomotor control

Very little is known about peripheral vasomotor control. Beakley & Findlay (1955*c*) found that at an environmental temperature of $15\text{--}20^{\circ}$ the ear temperature of calves rose suddenly by about 18° , which they attributed to an increased blood flow resulting from vasodilatation. Since in this range of environmental temperature deep body temperature was not elevated the vasodilatation may be interpreted to be due to the action of peripheral thermoreceptors. Localized irradiation of calves with infra-red rays caused an immediate rise in the temperature of the subcutaneous tissues by $5\text{--}9^{\circ}$ (Ingram & Whittow, 1962), indicating a peripheral control of vasodilatation. However, it has also been shown that heating the hypothalamus produces a rise in skin temperature (Ingram & Whittow, 1962). Thus peripheral vasomotor control seems to depend on at least 2 sets of thermoreceptive structures.

Control of sweat-gland secretion

Ferguson & Dowling (1955) produced sweating in heifers by injecting adrenaline intradermally. This finding was later confirmed by Taneja (1959*a*), Findlay &

Jenkinson (1964) and Findlay & Robertshaw (1964). Noradrenaline did not have an effect (Taneja, 1959*a*) except when given at a dosage higher than that used for adrenaline (Findlay & Robertshaw, 1964). Acetylcholine and acetyl- β -methylcholine had no effect on cutaneous evaporation (Findlay & Robertshaw, 1964). Intravenously applied, adrenaline also stimulated sweating (Findlay & Jenkinson, 1964; Ingram *et al.* 1963; Findlay & Robertshaw, 1964; Bianca, 1964), and sweating could be suppressed by the injection of Bethanidine, a drug which blocks adrenergic neurone transmission but has no adrenolytic activity (Findlay & Robertshaw, 1964). Thus sweating in cattle appears to be a process which is controlled by an adrenergic mechanism. It has further been shown that thermal sweating is stimulated by sympathetic nerve fibres since it did not occur on an area of skin that had been sympathetically denervated (Findlay & Robertshaw, 1964). So far no histological evidence has been found for the presence of nerve fibres in the immediate vicinity of the sweat glands (Jenkinson, Sen Gupta & Blackburn, personal communication). Under conditions of mild heat stress, with rectal temperature only slightly elevated (39–39.5°) the adrenal medulla does not seem to be involved in thermal sweating since denervation of the adrenal medulla did not affect cutaneous moisture evaporation (Findlay & Robertshaw, 1964). The full elucidation of sweat-gland control requires more work, especially concerning the immediate cause of glandular stimulation.

Even less is known about the mode of functioning of the sweat glands. The older concept that sweat secretion was the result of a necrobiotic discharge has been repudiated. Sweat glands of calves were found full of a colloidal material before, as well as after, heat exposure of the animal (Findlay & Jenkinson, 1960). The actual size of the full gland did, however, decrease after stimulation by heat and adrenaline (Findlay & Jenkinson, 1964) and by exercise (Hayman & Nay, 1958).

Control of thermal panting

Riek & Lee (1948*a*) noted that, in cows exposed to various conditions of heat stress, respiratory rate began to rise before rectal temperature. Also Barrada (1957) found that the air temperature at which an increase occurred was significantly lower for respiratory rate than for rectal temperature, and Bligh (1957*b*) recorded a marked rise in the respiratory rate of calves before there was an increase in the temperature of the blood in the bicarotid trunk when the air temperature was abruptly raised from 20 to 40°. These findings, together with the observation that infra-red irradiation of the skin causes the respiratory rate to rise before there is a rise in the temperature of the blood or the brain (Findlay & Ingram, 1961), indicate that the thermal stimulus for the initiation of panting comes from the periphery. However, local heating of the hypothalamus of calves also elicits panting, at least when body temperature is above about 40° (Findlay & Ingram, 1961). It was therefore concluded that thermal polyпноea is controlled by a peripheral stimulus as long as body temperature is within its normal range, but that central receptors become of major importance when body temperature rises above about 40°.

It is clear from these results that the control of the various thermolytic processes depends on thermoreceptors in the skin and in the brain. Thermoreceptors in other parts of the body, however, cannot be ruled out at present. More information is also needed on the complex interrelationship of peripheral and central control. Bligh

(1964/5) after reviewing the literature, put forward the thesis of a 'two-tiered' control of mammalian homeothermy. This control would consist (1) of a coarse control functioning as an 'emergency over-ride mechanism' by activating thermal defence mechanisms at body temperatures somewhere between 40 and 41° at the upper level and at 35–36° at the lower level, and (2) of a fine control to within 0.5–1°. The coarse control may depend on the stimulation of deep body thermoreceptors, and the fine control on the stimulation of both peripheral and deep body thermoreceptors.

HEAT TOLERANCE

In a comprehensive publication entitled *Manual of Field Studies on the Heat Tolerance of Domestic Animals*, Lee (1953) has dealt with methods for estimating heat tolerance, with factors that influence it and also with the interpretation of such studies. Heat tolerance in cattle and other species of domestic animals has been reviewed by Yeates (1956*a*). Turner (1958) has described work in Australia designed to elucidate genetic characters which are components of heat tolerance of cattle. Bianca (1961) has discussed heat tolerance in cattle, dealing in particular with its concept, its measurement and its dependence on modifying factors.

Criteria and methods of assessment of heat tolerance

Field tests

The most widely used test for determining an animal's heat tolerance is the 'Iberia heat tolerance test' by Rhoad (1944), in which heat tolerance is expressed as an increase of rectal temperature above a level of 38.3°.

Most of the numerous field tests for assessing the 'adaptability' of cattle to a hot environment depend in their interpretation largely on the behaviour of rectal temperature: the water expenditure test (Rhoad, 1940), the water deprivation test, the felting test, and the walking test (Bonsma, 1949), the coat score (Turner & Schleger, 1960; Schleger & Turner, 1960) the test for cooling efficiency following exercise (Dowling, 1956), and the coefficient of adaptability (Benezra, 1954).

Field tests for heat tolerance have the disadvantage that the environmental conditions under which they are conducted are not standardized. Strict comparisons, therefore, are valid only between animals tested at the same place at the same time.

Laboratory tests

Lee & Phillips (1948) published what they termed a laboratory analogue to the Iberia heat tolerance test ('*R*-values'), based on measurements of rectal temperature under standardized hot conditions.

Barrada (1957) graded heat tolerance by plotting the reaction of rectal temperature to various combinations of dry and wet bulb temperature on a temperature-humidity chart ('lines of equal effect').

Yeck & Kibler (1958) used the ratio of total evaporation at 27° to that at 10° to predict heat tolerance of calves of 6 different breeds.

Bianca (1963) concluded from experiments in which calves were subjected to 10 different combinations of temperature and humidity that rectal temperature attained after exposure to heat for 5 h was a better criterion of heat tolerance than either the magnitude or the rate of increase of rectal temperature.

Kamal *et al.* (1962) have proposed a 'biochemical index of heat tolerance' in cattle which is based on the retention of nitrogen in a 27° environment as compared with that in a 10° environment. Heat-tolerant animals show a small decline and heat-intolerant animals a large decline in nitrogen retention between the two temperatures. The same authors also speculated on the possibility of using decrease in total body ^{40}K (which is directly related to tissue protein) as a criterion of heat tolerance.

McDowell, Matthews, Lee & Fohrman (1953), when testing repeatedly the response of rectal temperature of cows to standard hot conditions, found that this response varied with the time of the year, showing a maximum in February, a second but smaller peak in August and a minimum in May–June.

Many of the above laboratory methods for assessing heat tolerance, although providing useful information on the state of the heat-stressed animal, are too elaborate to serve as a routine test. Since most of them ultimately rely on rectal temperature as an indicator of the strain experienced by the animal, it seems that deep body temperature, if properly used, is the best single physiological criterion of heat tolerance in cattle.

Climatic heat stress factors

The principal climatic factors causing heat stress are temperature, humidity and solar radiation. Wind acts as a partial heat stress factor only on the rare occasion when environmental temperature exceeds body temperature.

Temperature and humidity

Most workers have related heat tolerance to various combinations of temperature and humidity. Worstell & Brody (1953) presented critical environmental temperatures in the range 10–40° (at relatively low humidities) above which marked changes occurred in rectal temperature and other physiological variables of cattle. Beakley & Findlay (1955*a*) stated that in an environment at 40° and at high humidity the rectal temperatures of calves rose linearly at a rate of approximately 3°/h. They also gave a multiple regression equation to describe the behaviour of rectal temperature in dry heat. Cargill, Stewart & Johnson (1962) expressed the combined effects of temperature and humidity in terms of a 'discomfort index', normally used for man. Bianca (1963) found that the order of heat tolerance of calves was essentially the same in each of ten environments having different combinations of dry bulb and wet bulb temperatures. His results also suggested that the degree of severity of heat stress was not important in discriminating between animals on the basis of their heat tolerance. Quazi & Shrode (1954), who conducted heat-tolerance tests under field conditions in Texas, observed that cross-bred cattle ($\frac{1}{2}$ Jersey $\frac{1}{2}$ Brahman) were more affected by changes in air humidity than pure-bred Holstein and Jersey cattle. This is probably due to the higher sweat production of the cross-breds, as discussed previously (p. 307). in the section on evaporation from the skin.

Solar radiation

Under outdoor conditions solar radiation may be a powerful heat stress factor. In Texas, Williams, Shrode, Leighton & Rupel (1960), studying physiological responses of heifers of various dairy breeds, that were either exposed to direct solar radiation or protected from it by a roof, found that solar radiation affected body temperature

when air temperature was below 32°. Respiratory rate responded more to solar radiation than to any of the other meteorological factors measured. It was further shown that rectal temperature and respiratory rate were almost as reliable as indicators of heat tolerance when measured in the shade as when measured in the sun. Similar experiments with Holstein and Jersey cows also indicated that solar radiation caused rectal temperature and respiratory rate to rise. Buffaloes seem to respond most sensitively to direct solar radiation. Exposure to sun at air temperatures ranging from 23 to 43° raised rectal temperature, respiratory rate and heart rate of buffalo cows (Badreldin & Ghany, 1952). Murrah buffaloes, when compared with Haryana cattle, exhibited a greater increase in rectal temperature, respiratory rate and heart rate when exposed to the sun; they were, however, less stressed in the shade (Mullick, 1960). A depression of heat tolerance following the exposure to solar radiation has also been described in buffalo calves (Bhatnagar & Chaudhary, 1961). Atmadilaga (1959), studying heat tolerance in Indonesian cattle, considered that in general a 1-h exposure to direct solar radiation was sufficient to establish animal differences in heat tolerance.

On the other hand Shrode, Quazi, Rupel & Leighton (1960) stated that, under conditions prevailing in Texas, air temperature was the most important climatic variable with respect to summer heat stress in cattle. They came to this conclusion after having measured air temperature, vapour pressure, solar radiation and wind velocity and having found that almost as satisfactory an explanation of the variation in rectal temperature, respiratory rate and heart rate could be achieved with air temperature as the only independent variable, as when all 4 climatic variables were included.

Factors which modify heat tolerance

The expression of an animal's genetic potentiality for heat tolerance depends on a number of modifying factors. The relation of heat tolerance to acclimatization, clipping and to many aspects of nutrition is discussed in other sections. In this section reference is made to several other modifying factors.

Age

To decide to what extent heat tolerance is affected by age, one ought to know more about the dose/response relationship of animals of different age groups. For it is not certain whether a heat response of a given magnitude has the same physiological significance in the young organism as it has in the adult organism (Bianca, 1961). However, in the absence of this knowledge, the same concept of heat tolerance has to be applied when judging the heat performance of cattle of different age groups. Riek & Lee (1948*b*) found that the responses to heat of 8-week old Jersey calves differed from those of Jersey cows; the initial rise of rectal temperature and respiratory rate was more rapid and the equilibrium values attained by these 2 variables were higher. Klemm & Robinson (1955), working in Australia, observed an increase in heat tolerance in various breeds of cattle from 2 to 12 months of age, as judged by reductions in the rise of rectal temperature and respiratory rate. Similar increases in heat tolerance with advancing age have been reported for Jersey and Sindhi-Jersey cross-breds in Louisiana from 8 to 24 months of age (Schein, McDowell, Lee & Hyde, 1957), and for various African breeds of cattle from 1 to 2 years of age (Walker, 1957).

Heat tolerance of cattle was found to increase especially after the second year (Bonsma, 1949) and to remain reasonably stable at ages of 4 years and above. Whether heat tolerance decreases in the old animal, as might be expected, is not known. When comparing the age/heat-tolerance relationship of various breeds it is important to bear in mind that the chronological age of an animal need not be identical with its physiological age. Tropical breeds tend to mature later than breeds of temperate regions.

Level of production

A high level of production is associated with a high heat production and thus depresses heat tolerance. This is particularly true with regard to milk production: lactating animals were less heat tolerant than non-lactating animals (Worstell & Brody, 1953); the response of rectal temperature to a hot environment increased with rising milk yield in Jersey cows (McDowell, Lee, Fohrman, Sykes & Anderson, 1955) and in both Jersey and Sindhi-Jersey cross-bred cows (Schein *et al.* 1957). It is of interest to note that if the cows were grouped according to milk yields of 15, 25, 35 and 45 lb/day the respective increases in rectal temperature were higher in the Jersey cows than in the Sindhi-Jersey cross-bred cows, the figures for the lowest and for the highest groups being: 1.44 versus 0.39°, and 1.72 versus 1.00°. Similarly, Red Sindhi-Holstein (F_1) cross-bred cows proved more heat tolerant than Jersey and Holstein cows giving similar levels of milk production (Johnston *et al.* 1958).

The depressing effect of a high level of production on heat tolerance is not so clearly evident in beef cattle. Weight gain and heat tolerance of beef steers in Mashonaland were not closely related (Quartermain & Oliver, 1963). This negative result was, however, obtained under conditions where feed was available day and night and where shade was provided. Statistical analysis of the results of a 9-year survey conducted in Louisiana revealed that the correlation between heat tolerance (determined by Rhoad's method) and body weight development was not significant. The use of heat tolerance ratings as aids to the selection of beef cattle was therefore discontinued (Vernon, Damon, Harvey, Warwick & Kincaid, 1959).

Feeding, state of health, and excitement

The work by Yeates (1956*b*) with Shorthorn heifers indicates that a high level of nutrition over a prolonged period need not necessarily interfere with heat tolerance, but that a high rate of feeding for a few days before heat tolerance is measured, either in fat or lean cattle, depresses heat tolerance. This finding stresses the importance of a standard feeding routine when testing animals for heat tolerance.

Heat tolerance may also be depressed by a low state of health. The disorder of 'chronic panting' which has been observed in India and Pakistan as a sequel to foot-and-mouth disease interferes with temperature regulation, probably owing to defective functioning of endocrine glands (Minett, 1949; Maqsood *et al.* 1958).

Finally, it may be generally recognized, but perhaps not always taken fully into account, that emotional excitement may raise body temperature, thus interfering with heat tolerance. The excitable, brisk animal, as compared with the tranquil, docile animal, may thus easily be underrated in its capacity for tolerating heat.

*Genetic variation in heat tolerance**Differences between species*

The superiority in heat tolerance of tropical over European cattle has been clearly demonstrated by Rhoad (1940). A comparison made under field conditions in Louisiana between Brahman, Aberdeen Angus and various crosses between them gave the following results for rectal temperature: 4/4 Brahman, 38.5° (i.e. normal); ½ Brahman, 38.8°; ¼ Brahman, 39.7°; 4/4 Aberdeen Angus, 40.0°. A smaller rise in deep body temperature during exposure to heat was also characteristic of ½ Sindhi-½ Jersey cows as compared with pure-bred Jersey cows, namely 1.9 versus 3.1° (McDowell, Lee, Fohrman & Anderson, 1953). Likewise, the degree of tolerance to heat (tested in a climatic room) was directly related to the amount of Red Sindhi inheritance in the Red Sindhi-Jersey cross-breeds. The cross-breeds were also more heat tolerant than the Jerseys when compared at the same level of milk production (Schein *et al.* 1957). Under a variety of combinations of high dry bulb and wet bulb temperatures, Red Sindhi-Holstein heifers proved significantly more heat tolerant than pure Holstein heifers (Johnston & Frye, 1953). Also Red Sindhi cross-bred bulls were more heat tolerant than pure-bred Holstein and Brown Swiss bulls (Johnston, Naelapaa & Frye, 1963). In South Africa, Bonsma (1949) showed that Afrikaner cattle could withstand heat better than cattle of various British beef breeds. He also found that the mortality rate shortly after birth was 8% in the indigenous breed but 35% in the British breeds. In a comparative study made in Egypt (Badreldin, Oloufa & Ghany, 1951), buffaloes had lower values for rectal temperature, respiratory rate and heart rate than Shorthorn, Jersey and native cows. Finally, the work conducted in the Climatic Laboratory of the University of Missouri provides ample evidence of *B. indicus* cattle being more heat tolerant than *B. taurus* cattle. Summary reports of the Missouri work have been published by Worstell & Brody (1953) and Yeck & Stewart (1959). In the earlier experiments comparisons were between Brahman cattle on the one hand and Holstein and Jersey cattle on the other. The high heat tolerance of the Brahmans was ascribed to their high surface/mass ratio, to their lower heat production and to their low initial levels in cardiorespiratory functions (Worstell & Brody, 1953). In subsequent experiments the comparisons were extended also to Santa Gertrudis cattle (*B. indicus* × *B. taurus*) and to Brown Swiss and Shorthorn cattle (both *B. taurus*).

Differences between breeds, types and individuals

A comparison conducted under field conditions in Louisiana at temperatures ranging from 18 to 34° showed Jersey cows to be more heat tolerant than Holstein cows (Seath & Miller, 1947*a*). Probably as a consequence of this, the Holstein cows but not the Jersey cows tended to lie in mud and water. In Australia, Jersey cows were considered more heat tolerant than Illawarra Shorthorn cows (Robinson & Klemm, 1953). A newly developed herd of white Afrikaner cattle has been claimed to have a high heat tolerance (Bramley, 1960). Differences in heat tolerance have been demonstrated between smooth-coated and woolly-coated British beef breeds in South Africa (Bonsma, 1949) as well as between Shorthorns with highly medullated hair and Shorthorns with non-medullated hair in Australia (Dowling, 1956). In

Rhodesia, Walker (1957) investigated the heat tolerance of Afrikaner, Angoni, Barotse and Tonga cattle in relation to sweat-gland density. Under conditions prevailing in Indonesia, Atmadilaga (1959) found Bali cattle to be the most heat tolerant of several breeds. Seath (1947) estimated the heritability of heat tolerance (as expressed by rectal temperature) in dairy cattle at 15–30 %.

The establishment of clear differences in heat tolerance between breeds or types of cattle is often made difficult by the great variation existing between individuals within each breed or type. A large individual variation in heat tolerance has been noticed and commented on by most workers in this field, e.g. by Barrada (1957), Beakley & Findlay (1955*a*) and Bianca (1959*a, b*, 1963). Such differences are important for the selection of heat-tolerant animals from within a population.

ACCLIMATIZATION

Acclimatization may be said to occur when an animal, in response to repeated or continuous exposure to an environment hotter than that normally experienced, develops functional or structural changes which increase its ability to live in a hot environment without distress. There is ample evidence of heat acclimatization in man but relatively little in cattle.

Short-term changes

Calves accustomed to normal atmospheric temperatures in Scotland were kept in an atmosphere of 45° dry bulb and 28° wet bulb for a period of 5 h on each of 21 successive days. On the first exposure rectal temperature, heart rate and respiratory rate were increased and breathing was laboured but with successive exposures the magnitude of these changes became less (Bianca, 1959*a*). Most of the acclimatization occurred during the first 10 days. Under more stressful atmospheric conditions (40° dry bulb, 38° wet bulb temperature), which severely limited any form of heat loss from the animals, the tolerance time, i.e. the number of minutes for which the animals could withstand the hot atmosphere before reaching a rectal temperature of 42°, increased on average from 70 to 110, i.e. by 57 %, over a period of about one week. It was also found that a high acclimatization effect was associated with a satisfactory overall gain in body weight and with only a small loss in body weight during each exposure to heat (Bianca, 1959*b*). Indirect evidence suggested that the observed acclimatization involved a decrease in metabolic heat production. Kibler & Brody (1949) observed in cows a continued decline in heat production during a 4-week period at 10° which followed a colder period with temperatures below freezing point. Brody, Ragsdale *et al.* (1955) obtained acclimatization effects with regard to feed consumption and milk production in Jersey and Holstein cows after the animals had been subjected for about 1 week to a diurnal temperature rhythm of 21–38°. Johnston, Hindery, Hill & Guidry (1961), working with yearling heifers of 3 breeds at temperatures between 24 and 35°, found that dry matter intake and weight gain declined during the first 20 days in the heat, but that the values recovered during the following 20 days. This recovery of productive function was achieved with an increase in body temperature and respiratory activity.

Long-term changes

When conducting repeatedly standardized heat-tolerance tests on Jersey and Sindhi \times Jersey cattle in Louisiana and Maryland, Schein *et al.* (1957) made the observation that the animals tested in the hot climate of Louisiana were significantly less affected by the standard heat treatment than the animals tested in the temperate climate of Maryland, and also that this lessened heat response was more pronounced in the cross-breds than in the pure-breds. This finding suggests that heat acclimatization occurred in the animals kept in Louisiana. Also in Louisiana, exposure of 10 Holstein heifers to temperatures of 24–35° caused heat production, rectal temperature and respiratory rate to decline after a transient increase (Thompson *et al.* 1963). The decline appeared to be the result of compensatory adjustments brought about by alterations in thyroidal and adrenocortical function. A transient increase and subsequent decline in heat production in response to prolonged exposure to heat has been reported also by Johnston *et al.* (1958). Recently, Berman, Amir & Volcani (1963), working with lactating Israeli-Holstein cows, found that at air temperatures of 23–28° animals given food *ad lib.* experienced only a small and non-significant heat increment of lactation. They concluded that the animals had gradually become adapted to summer heat by changes in hair coat and by reducing their resting metabolic rate. The work of Kamal *et al.* (1962) stresses the importance of an animal's thermal history. Rearing calves in a warm environment (27°) improved their later heat tolerance, whereas rearing them in a cool environment (10°) improved their later cold tolerance. Since the heat-acclimatized animals became more sensitive to cold and the cold-acclimatized animals more sensitive to heat, this also meant that the whole zone of thermoneutrality had been shifted, upwards in the heat-tolerant group and downwards in the other. It is noteworthy that all these acclimatization changes occurred although the animals had been 'thermally equalized' for 1 month before the heat- and cold-trials were conducted. The authors interpreted this as a demonstration of the stability of the acclimatization acquired in early age. It might be argued, however, that the period of 'thermal equalization' was too short for complete de-acclimatization to take place.

There is evidence of seasonal acclimatization to heat. McDowell, Matthews *et al.* (1953) showed that rectal temperature response of heifers to heat was greatest in February and smallest in May–June. The fact that the rectal temperature response had a second peak in August suggests that the long-continued summer heat had brought about a state of deterioration, characterized by a lowered heat tolerance. Bianca (1962*b*) found that calves which were tested for heat tolerance in July–September were more heat tolerant than calves tested in November–January, again indicating seasonal acclimatization. It is well established that seasonal acclimatization involves changes in the hair coat (Yeates, 1955; McDowell, Bond, McDaniel & Warwick, 1960; Berman & Volcani, 1961; Bedwell & Shanklin, 1962) and also in water consumption (McDowell *et al.* 1960).

GROWTH AND BEEF PRODUCTION

Two books have been published on beef production in hot regions and related problems: *Breeding Beef Cattle for Unfavourable Environments*, edited by Rhoad (1955), and *Crossbreeding in Beef Cattle*, edited by Cunha, Koger & Warnick (1963). In a review, Joubert (1954) has reported on breeding for beef in Africa, and Nelson (1959) has reviewed the 'effects of climate and environment on beef cattle'.

Effects of heat on growth rate

Hancock & Payne (1955) split up 8 sets of identical twins between New Zealand and Fiji and provided similar conditions of feeding and management in both places. Apart from an initial setback in the animals in Fiji due to transport and quarantine, an appreciable depression in growth rate occurred only when the temperature in Fiji was at its highest. At calving the Fiji animals were 84 lb or 9.6% lighter than the New Zealand animals. The retardment in growth of the Fiji animals was reasonably uniform in so far as all body measurements were affected except the belly girth, which was large in the Fiji animals owing to their drinking twice as much water as the New Zealand animals. O'Bannon, Cornelison, Ragsdale & Brody (1955) found that Brahman heifers grew more rapidly at 27° than at 10°, that Santa Gertrudis heifers grew equally well at both temperatures, and that Shorthorns grew far more rapidly at 10° than at 27°. The depression in growth rate suffered by Shorthorn cattle in an environment of 27° was paralleled by reductions in feed intake, thyroid activity and heat production, and at 16 months of age the Shorthorns lagged behind the animals of the other breeds by about 200 lb (Johnson, Ragsdale & Cheng, 1957). In a comparable study conducted with calves of 3 dairy breeds Johnson & Ragsdale (1959) showed that a temperature of 27°, compared with one of 10°, depressed the growth rate of Holstein and Jersey calves but not that of Brown Swiss calves. Holstein bulls gained weight at environmental temperatures below 29°, but lost weight at higher temperatures (Casady, Legates & Myers, 1956). In Australia Brahman cross-bred cattle were superior to cattle of British breeds with respect to weight for age. However, British cattle which had been selected specifically for adaptability and performance suffered little setback (Dowling, 1960). A growth study conducted at 3 American research stations indicated that, in general, up to 12 months of age Sindhi-Jersey crosses gained weight more rapidly than Jersey animals. This superiority of the cross-breeds continued to the age of 18 months and to the beginning of the first lactation only in the $\frac{1}{2}$ Sindhis and the $\frac{3}{8}$ Sindhis (McDowell, Johnson, Schein & Swett, 1959). In Texas, Cartwright (1955) concluded from results obtained with 365 head of beef cattle that selection should be based on summer weight gain rather than on heat-tolerance score.

In the years that have elapsed since Brody & Frankenbach (1942) demonstrated the importance of thyroxine in the growth of cattle, several workers have investigated thyroid function in relation to growth of cattle under hot conditions. In Queensland, Post (1963) compared in 177 grazing heifers and steers the weight gains and the levels of protein-bound iodine in the plasma: both variables became reduced in summer, and differences in protein-bound iodine levels were found to account for about 25% of the differences in weight gain between individual animals. Similarly, Kamal, Johnson &

Ragsdale (1959) showed that in calves of 3 dairy breeds exposure to 27° led not only to a fall in growth rate but also to a decrease in the level of butanol-extracted ¹³¹I in the plasma and to an increase in the level of the co-enzyme glutathione.

Beef production of different species and breeds in hot countries

When assessing the factors that determine beef production in hot countries, it is difficult to dissociate direct from indirect climatic effects and from effects that are not connected with climate. In the tropics, as in temperate climates, weight gain is affected by the quality of the grazing (Joubert, 1954; Maltos, Roux & de Alba, 1962), by feeding and management (Ittner, Guilbert & Carroll, 1954) and by heterosis (Ellis & Cartwright, 1963). Many more examples could be quoted. In view of this complex situation only brief reference will be made to a few reports.

In California during autumn, winter and spring, i.e. when heat stress was minimal or absent, Hereford steers and heifers exceeded Brahman × Hereford animals in weight gain, feed conversion efficiency and market grading (Carroll, Rollins & Ittner, 1955). In a comparative study conducted in Florida, Santa Gertrudis calves had the highest market grades, and Brahman and Hereford calves the poorest (Cobb, Burns & Koger, 1964). Several investigators showed Brahman cross-bred steers to have higher dressing percentages than steers of British breeds (Black, Semple & Lush, 1934; Butler, Reddish, King & Sims, 1956; Butler, Warwick & Cartwright, 1956; Arbuckle, 1958; Hewetson, 1962). This superiority of the Brahman cross-breds may, in part, be due to the lower weight of their digestive tracts (Butler, Reddish *et al.* 1956).

Preliminary investigations in Africa suggest that wild species may be more profitable than domestic livestock for the production of meat in the semi-arid tropics; the weight of lean meat in the carcass as a percentage of liveweight has been given as 46 for the Thomson gazelle and 32 for *B. taurus* cattle (Ledger, Payne & Talbot, 1961). The wild ungulates were considered superior to cattle because of their higher efficiency in feed conversion, their higher growth rates and killing-out percentages, their earlier maturation and age of reproduction (Talbot, Ledger & Payne, 1961). As a logical next step the domestication of wild species, in particular of the Eland antelope, the African buffalo, the Wildebeest, the Impala and of gazelles, has been suggested (Bigalke, 1964).

REPRODUCTION

There is evidence to show that reproductive processes undergo changes in direct response to high environmental temperatures. Reproduction in livestock under climatic stress has been reviewed or discussed by Hammond (1955), Ulberg (1958), Hafez (1959), Rollinson (1962) and Hart (1955).

Testis and scrotum

Reproduction in the bull

The vascular architecture of the testes has been described in mammals in general (Harrison & Weiner, 1949), and in the bull in particular (Kirby & Harrison, 1954; Kirby, 1953; Hofmann, 1960). The degree of convolution and calibre of the testicular artery, and particularly its relation to the veins of the pampiniform plexus, suggested that the vascular pattern of the testes has a thermoregulatory function. This is supported by experimental evidence.

The temperature of the scrotal surface of calves exposed to temperatures up to 40° remained consistently below the temperature of the surface of the trunk and of the rectum (Beakley, 1953). Guzsal & Haraszti (1961) recorded temperatures for various parts of the scrotum and testes, and found a temperature gradient of 4.2° from the proximal to the distal part of the scrotum. Temperature measurements in bulls in Israel suggested that it is the direct heating of the scrotum, rather than the general heating of the body, which is responsible for the reduction in fertility which occurs in summer (Schindler, 1957). Artificial insulation of the scrota of Hereford bulls raised scrotal skin temperature by about 1.7 deg F and thereby depressed sperm quality (Austin, Hupp & Murphree, 1961).

Semen production

The anatomical features of the testes and scrotum just described no doubt help to protect these structures against overheating but, if the environmental heat load is too high, spermatogenesis is adversely affected. Brown (1959) found the semen quality of Jersey and Holstein bulls in Texas to vary inversely with environmental temperature. In India the quality of Kumauni bulls' semen was lowest from August to October, when temperature and humidity were highest (Mukherjee & Bhattacharya, 1952). Similarly, the quality of buffalo semen was worst in summer and the oxygen consumption of the semen varied significantly with the season (Sen Gupta, Misra & Roy, 1963). Also bulls of 4 European breeds in Indiana produced low-quality semen in summer (Erb, Andrews & Hilton, 1942). Of the semen samples from bulls kept in a 'cooled' climatic room at 27°, 91% were suitable for use in artificial insemination, whereas the corresponding figure for semen from bulls kept in a barn under natural conditions prevailing in Louisiana was only 47% (Patrick *et al.* 1954). Later experiments at the same place also indicated that a heat-induced decline in semen quality could be reduced by special housing and various managerial practices (Patrick, Kellgren, Johnston & Branton, 1958). Increasing the cooling power of the atmosphere with the aid of large fans had a beneficial effect on semen quality in the summer (Bielanski, Janowski & Wojtacha, 1961).

Continuous exposure of Guernsey bulls in a climatic room to temperatures up to 37° depressed initial sperm mobility and sperm concentration. The volume of the ejaculate and the sex drive were not appreciably impaired (Casady, Myers & Legates, 1953). The quality of the sperm of Red Sindhi cross-bred bulls, when subjected to temperatures cycling between 40 and 28°, was less affected than that of similarly treated Holstein and Brown Swiss bulls. According to Asaj & Vergles (1961), bulls in Yugoslavia, after exposure to direct solar radiation for 1½ months, produced ejaculates without spermatozoa. In Israel it was found that the state of sexual activity of bulls, as indicated by the state of the seminiferous tubules, changed directly with thyroid activity (Volcani, 1954).

Fertility

The poor semen quality of bulls exposed to heat is reflected in low male fertility (expressed in terms of 'non-return rates'). In Washington fertility was lowest in September (Erb & Waldo, 1952), and in Texas it was lowest during July and August

(Brown, 1959). Johnston & Branton (1953) found fertility of dairy bulls in subtropical Louisiana lowest when the vapour pressure of the air was highest (up to about 24 mmHg), which occurred in August and September. It is of interest that the onset of semen production in young bulls may be accelerated by a high level of feeding and retarded by a low level of feeding during calthood, but that the ultimate fertility does not seem to be affected (Bratton, Musgrave, Dunn & Foote, 1959, 1961). The average useful life, which may be taken as an indicator of fertility, was given as almost 9 years in Afrikaner bulls and just over 3 years in Shorthorn and Hereford bulls in South Africa (Bonsma, 1949).

Reproduction in the cow

Oestrus

Climatic room studies (Dale, Ragsdale & Cheng, 1959) revealed that in an environment of 27° Brahman heifers reached puberty at a mean age of 463 days and that Santa Gertrudis and Shorthorn heifers matured more rapidly (290–440 days). Since of these 3 breeds the Brahmans were the fastest growers, it was concluded that their late sexual maturation was a direct temperature effect, rather than an indirect nutritional effect.

High environmental temperatures seem to cause a shortening of the duration of oestrus: in Holstein and Jersey cows in Louisiana oestrus was reported to last for only 12–13 h, which is 5–6 h shorter than the norm in a temperate climate (Branton, Hall, Stone, Lank & Frye, 1957). Also Poston, Ulberg & Legates (1962) found some difficulty in detecting oestrus in times of hot weather, and Hall, Branton & Stone (1959) suggested that in hot areas oestrus should be looked for more frequently than twice daily.

Regarding the oestrous cycle, Bond, McDowell, Curry & Warwick (1960) observed that exposure to 32° induced the oestrous cycle in 5 out of 6 Shorthorn heifers to cease after about 5 weeks exposure to heat, but that by the 21st week at 32° all the heifers had re-established their normal oestrous cycles. By this time they also had shed their winter coats.

The results of over 46000 first inseminations of cows in Germany suggested an influence of the weather on oestrus, a turn from fair to bad weather resulting from the inflow of warm and moist air masses having a particularly unfavourable effect (Brezowsky & Haeger, 1959).

Conception rate

Stott & Williams (1962) obtained evidence of a low rate of fertilization and a high rate of embryonic mortality in Holstein cows during high temperatures in summer. The critical time for the damage to occur appeared to be the time of mating. In buffaloes in India 89% of all conceptions took place in the cooler part of the year between September and March (Basu, 1962). An extensive survey in Germany indicated that conception rate was enhanced under conditions of low barometric pressure (Müller & Lenz, 1957), that it was highest at byre temperatures around 12°, and that it was depressed when the absolute humidity in the byre was high or the light intensity low (Müller & Kurtz, 1958).

Pregnancy

In Red Sindhi × Jersey cows each 25% of Red Sindhi inheritance increased the length of the gestation period by approximately 3 days; and up to 75% Red Sindhi inheritance could be used without delaying the age of first calving beyond that normal for pure-bred Jerseys (McDowell, Fletcher & Johnson, 1959). In South Africa, Afrikaner cattle were reported to have an average gestation period of 295 ± 0.3 days and Hereford cattle one of 287 ± 1.0 days (Joubert & Bonsma, 1959). Cows of British breeds in South Africa produced calves in summer that were 20% lighter than calves born in winter. This seasonal difference in calf size did not occur in well-adapted indigenous breeds (Bonsma, 1948). The finding by Taneja (1958*a*) that exposure of Australian Illawarra Shorthorn cows to 40° dry bulb, 30° wet bulb temperature did not interfere with pregnancy and the birth-weight of calves in 11 out of 12 animals, was interpreted as an indication of a high state of adaptation to heat.

MILK PRODUCTION

In studies on the effects of climate on milk production effects of non-climatic factors such as stage of lactation, age, nutrition and management may be either controlled or eliminated by the experimental design or by statistical procedures. However, as has been discussed (p. 313), with rising environmental temperature there is a decrease in voluntary feed intake, although plenty of good feed may be available. It may thus be expected that a hot environment, apart from affecting milk production directly, will cause changes in milk yield and milk composition that are comparable to those caused by under-feeding or even by starvation.

The general problem of milk production in hot areas has been discussed by Payne (1957), Johnston, McDowell, Shrode & Legates (1959) and Lee (1957). Hancock (1954) has reviewed work on 'direct influences of climate on milk production' and Yeck (1959) has reviewed 'environmental research with dairy cattle'. A summary report by Yeck & Stewart (1959) on the climatic work conducted at the University of Missouri up to 1959 discusses the effects of controlled hot environments on milk production of cattle.

*Milk yield**Hot room studies*

Effects of temperature. Regan & Richardson (1938) observed in Holstein, Jersey and Guernsey cows a drop in milk yield from 29 to 17 lb/day when the temperature was increased from 4 to 35°. Riek & Lee (1948*a*) working with Jersey cows in the temperature range 29–43°, failed to find a decrease in milk yield. This negative result may have been due to the experimental procedure (7-h exposures twice a week). In a report summarizing the work conducted in the climatic laboratory at Missouri before 1953, Worstell & Brody (1953) stated that milk yield declined at temperatures above 29° in Jersey, Holstein and Brown Swiss cows and above 35° in Brahman cows, but it should be noted that the general level of milk production was much lower in the Brahman cows than in the cows of the 3 European breeds. The optimal temperature for milk production was considered to be around 10°, a rise in temperature above 10° being much more detrimental to milk production than a comparable fall below 10° (Ragsdale *et al.* 1949). In a later study (Johnson, Hahn, Kibler & Merilan, 1962) it was

noted that the response of milk yield to high temperature was dependent on heat tolerance and on the level of milk production: milk yield decreased in all the cows during the first 2 weeks at 29°. It recovered, however, during the following 7 weeks in 3 heat-tolerant cows, but not in 3 heat-intolerant cows. In the 3 highest milk producers milk yield fell by 449 lb, whereas in the 3 lowest producers during the same period it fell by only 151 lb. Similarly, the high milk yield of early lactation was more depressed by heat stress than the low milk yield of late lactation, namely by 7.9 lb/day compared with 2.5 lb/day at 32° (Johnson, Kibler, Ragsdale & Shanklin, 1960). Effects of diurnal temperature cycles (simulating naturally occurring conditions) were found to compare roughly with the effects of constant temperature equivalent to the average temperature of the diurnal cycles (Brody, Ragsdale, Yeck & Worstell, 1955). A temperature cycle 21–38° depressed milk yields of Holstein cows by about 20% and that of Jersey cows by about 8%. But after the first week under these conditions the magnitude of the depression became smaller, indicating acclimatization (Brody, Ragsdale, Yeck & Worstell, 1955). Rees (1964) in Tasmania found that constant temperatures above about 28° depressed milk yield in cows of various European breeds, but that temperature cycles simulating hot day conditions (32–38°) for 5½ h and cooler night conditions (24–29°) for 15½ h remained without effect on milk yield. Cows exposed to heat declined less in milk yield if they were fed through a rumen fistula at a controlled high level (–4.7 lb/day) than when they were fed *ad lib.* (–7.3 lb/day) (Johnson, Wayman, Kibler, Ragsdale, Berry & Merilan, 1961).

Effects of humidity. Effects of high humidity on milk yield become pronounced only at temperatures above 24°. At a temperature of 29° the milk yields of Holstein, Jersey and Brown Swiss cows were 97, 93 and 98% of the norm when the relative humidity was 40%, but were only 69, 75 and 83% of the norm, when the relative humidity was 90% (Yeck & Stewart, 1959). The norm was the milk yield at 18° corrected for the stage of lactation. In confirmation of the above findings, milk yields of 40 Holstein cows were seriously depressed by high humidity only above air temperatures of 27° (Johnson, Ragsdale, Berry & Shanklin, 1963). From experiments made under a variety of temperature/humidity combinations, it was concluded that changes in milk yield were in most animals not complete until about 10 days after the change of the environmental conditions (Johnson, Kibler, Ragsdale & Shanklin, 1960). Responses of milk yield to various combinations of temperature and humidity have been related to a 'temperature-humidity discomfort index' by Cargill *et al.* (1962) and Johnson, Ragsdale, Berry & Shanklin (1962).

Effects of wind. The beneficial effect of wind on milk production of cows exposed to heat was considered to be more pronounced the larger the cow, the higher the milk yield and the higher the wind speed (Brody, Ragsdale, Thompson & Worstell, 1954). The milk yields of Holstein cows in an environment of 35° dropped to 63% of its normal level when the wind speed was ½ m.p.h., but to only 79% when the wind speed was 10 m.p.h. (Yeck & Stewart, 1959).

Effects of radiation. Artificially produced radiation, when combined with high air temperature, depressed milk yield. At 27° the highest intensity of radiation used in the trials reduced the milk yields of Jersey cows to 79% and those of Holstein cows to only 57% of the normal level. There was, however, a very large individual variation (Brody *et al.* 1954).

Field Studies

Under field conditions it is exceedingly difficult to dissociate climatic and non-climatic influences on milk production. Johnston (1958) concluded from a series of combined air conditioning and feeding trials in Louisiana (Johnston, Stone, Smith, Schrader & Frye, 1957) that the fall in milk production during the summer was due mainly to a decline in the quantity and quality of the available forage. As long as feed consumption in a hot environment remained normal, milk production also remained high. Influences of various practices of management and feeding under hot conditions on milk yield have been discussed by Johnston *et al.* (1959) and Breidenstein, Johnston, Hindery & Rusoff (1960).

Realizing that the study of the effects of a hot climate on milk and other products requires a clear definition of the hot climate, Johnston *et al.* (1959) made an extensive survey of the summer weather conditions in the southern region of the U.S.A. by presenting graphically frequency distributions for air temperature, dew point and solar radiation.

A most dramatic example of the effect of heat stress on milk yield has been reported by Espe (cited by Yeck, 1959). During a heat wave at an exhibition in Seattle a record-producing Holstein cow with no change in her ration dropped her milk yield from 142 to 98 lb/day. Ten days after the return of cooler weather her milk yield recovered to 131 lb/day. In the experiment with identical twins (p. 326) the animals kept in New Zealand produced on average 44 % more milk than their twins kept in Fiji (Payne & Hancock, 1957). However, 2 of the Fiji animals gave almost as much milk as their corresponding twins in New Zealand, a finding which again stresses the great individual variation which may exist within a breed as regards the response to climate.

From data collected in field trials in Louisiana it was calculated that for each deg F increase in body temperature the dairy yield of fat-corrected milk of Holstein and Jersey cows decreased on average by 2.14 lb (Branton, Johnston & Miller, 1953). A study at Beltsville in Maryland (Lee, McMullan, McDowell & Fohrman, 1954) showed that the correlation between air temperature and milk yield was most marked when the temperature of the fourth and fifth preceding day was used. The authors also showed that the milk production of cows kept in open barns declined appreciably when the local mean shade temperature exceeded 22° for 2 successive days, and they presented an equation relating milk yield to mean shade temperature. In the Imperial Valley in California, where water and pasture crops are abundant, summer heat with temperatures up to 44° is the limiting factor for milk production. An investigation with Holstein cows by Ittner *et al.* (1954) revealed the following: grazing occurred early in the morning or in the evening; during the day most cows stood up (exposing all of their body surface to the air, and also facilitating respiratory movement); the greatest drop in milk yield (23 %) occurred in July; a rise in night temperature, which occurred when air humidity was high, clearly depressed milk production; and predominantly black animals had significantly higher respiratory rates than predominantly white animals when in the sun but not when in the shade. Under conditions of less thermal stress in Texas, exposure of Holstein and Jersey cows to solar radiation did not cause an appreciable fall in milk yield although various physio-

logical variables were affected (Harris, Shrode, Rupel & Leighton, 1960). An investigation with Holstein cows in Louisiana indicated that in a hot climate a preliminary evaluation of the production value of a cow may safely be based on the first or the second lactation yield (Martoyo, Branton, Farthing & Evans, 1963).

Genetic differences in milk yield

The establishment of genetic differences in milk yield between species, breeds and individuals is often made difficult by the lack of control of environmental factors. Mahadevan (1957), discussing the performance of dairy cattle in Ceylon, concluded that 'differences in the extent of variation in most economic characters between cattle reared in tropical and temperate countries are due to differences in husbandry rather than to any great inherent differences between tropical and temperate breeds of cattle'. By contrast, the work conducted in the climatic room at Missouri, admittedly involving only a small number of animals, indicated that even under identical conditions of feeding and management the milk yields of Brahman cows were consistently lower than those of cows of European breeds (Worstell & Brody, 1953).

There are contradictory reports on the usefulness of cross-breeding as a means of improving milk production in hot areas. The results with Red Sindhi Zebu cattle, which were introduced in 1946 to improve dairy production in the Gulf Coast region of the U.S.A., have not been favourable. Under conditions prevailing in Maryland, Georgia and Louisiana, cross-breeding with Red Sindhis did not improve, but rather reduced, the production of Holstein, Jersey and Brown Swiss cows (McDowell, Johnson, Fletcher & Harvey, 1961; Branton, McDowell, Frye & Johns, 1961). It was pointed out also that Zebus had characters which impaired their usefulness as dairy animals: their temperament, their slow rate of milking, their udder characteristics and feeding habits (McDowell, Johnson, Fletcher & Harvey, 1961). The suggestion was therefore made that milk production in these areas should be improved by selecting within European breeds and by improving nutrition. Selecting within European breeds may, however, be fraught with difficulty, since selection for heat tolerance may result in selection for inferior milk production (Branton, Johnston, Miller, Vizinat & Frye, 1955). On the other hand, cows with 50% Zebu inheritance appeared to be most suitable for milk production in Jamaica (Howe, 1949), and under the conditions prevailing in Costa Rica Zebu cross-breds performed better than pure European stock (de Alba & Solares, 1962). In a recent study in Georgia (Johnson, Johnson, Harvey, McDowell & Southwell, 1964) evidence was obtained that intercrossing various European breeds (Jerseys, Brown Swiss, Holsteins) led to increases in milk yield of up to 20% over the mean yields of cows of the pure-bred parental breeds. The finding by Mahadevan & Galukande (1962), that indigenous East African Zebu cows had only about half the potential for milk production of Indian Sahiwal cows, emphasizes the genetic variation that exists within the group of Zebu-type cattle.

It would appear that the question of whether crossing *B. taurus* and *B. indicus* leads to an improvement in milk production in hot regions cannot be answered categorically, but that the answer depends on the severity of the heat stress and on accompanying non-climatic factors, notably nutrition, management and control of disease. The higher the heat stress and the more unfavourable the accompanying conditions, the more it would be warranted to make use of Zebu inheritance.

*Milk fat**Milk composition*

The inverse relationship known to exist between milk yield and the fat percentage of the milk has been shown also under various conditions of heat stress. Harrlass (1941) recorded lowest values for fat percentages under summer conditions when milk yields were highest. Fat percentage was elevated at 35° environmental temperature in Jersey cows (Regan & Richardson, 1938), above 27° in Holstein and Jersey cows (Ragsdale, Thompson, Worstell & Brody, 1950) and above 29° in Brown Swiss and Brahman cows (Ragsdale *et al.* 1951). Cobble & Herman (1951), working with Jersey, Holstein and Brown Swiss cows, noted a slight decrease in fat percentage when the air temperature was raised from 10 to 32°. This decrease was followed by a sharp increase at higher temperatures. In Brahman cows, temperatures up to about 40° did not seem to affect the yield and composition of the milk. A study made in 10 herds in Germany (Saathoff, 1957) suggested an influence of the weather on fat percentage; a depression by polar air masses and a stimulation by maritime air masses.

As might be expected, the yield of milk fat of cows exposed to heat declines with declining milk yield. In his review, Hancock (1954) cited numerous earlier workers who all observed decreases in the yield of milk fat under hot environmental conditions. These findings are supported by more recent studies. The climate of Fiji, compared with that of New Zealand, had a depressing effect on the yield of milk fat (Payne & Hancock, 1957). Under hot-room conditions in Missouri the milk-fat yields of Holstein cows fell at temperatures above 27° (Richardson, 1961), and those of various cross-bred cows in Tasmania at temperatures around 28° (Rees, 1964). In the cross-breeding study in Georgia already mentioned (Johnson *et al.* 1964) the greater milk yield of the cross-bred cows was associated with a 21% greater yield of milk fat. A study of the fatty acid composition of milk fat under controlled high temperatures showed that any external heat load which raises rectal temperature to 39.4–40.5° may cause changes in the characteristics of the milk fat (Richardson, Johnson, Gehrke & Goerlitz, 1961). In particular it was found that under heat stress the content of lower fatty acids decreased, whereas that of palmitic and stearic acid increased.

Solids-not-fat

Most workers have reported that the solids-not-fat (SNF) content of the milk decreases in the heat-stressed cow. Regan & Richardson (1938) gave values of 8.26, 8.06, 7.88 and 7.58 at environmental temperatures of 4, 15, 27 and 35°. Parallel to this there was a decline in casein percentage. Decreases in the SNF percentage of the milk of cows of various breeds have been found to occur at temperatures higher than about 30° (Cobble & Herman, 1951; Rees, 1964), as well as in cows that had elevated body temperatures owing to various conditions of disease (King, 1955). According to a survey in Germany (Kiermeier & Renner, 1960) the protein percentage of milk before, during and after a heat wave averaged 3.56, 3.04 and 3.35. Protein percentages in the milk of cows of various breeds in the humid tropics have been reported by Bateman & de Alba (1961). The values ranged from 3.29 in Sindhi × Brown Swiss to 3.59% in Criollo cattle.

Other constituents and properties of milk

In the milk of heat-stressed cows the percentage of lactose seems to decrease slightly (Cobble & Herman, 1951; Richardson, 1961). Also there is a slight decrease in acidity (Rees, 1964) and a slight increase in pH (Regan & Richardson, 1938), and the salt balance is affected.

High environmental temperatures *per se* did not appear to reduce the carotenoid and vitamin-A levels in milk fat, since the decreases that were observed were closely associated with the heat-induced decrease in feed consumption (Stallcup & Herman, 1950). High temperature cycles had the effect of increasing the levels of ascorbic acid and riboflavine in the milk and of decreasing slightly the level of pantothenic acid (Singh & Merilan, 1959; Singh, 1957). Finally, there are reports indicating that high temperatures tend to raise the freezing point of milk; i.e. they tend to decrease the freezing-point depression (Regan & Richardson, 1938; Rees, 1964). Rees noted also that changes in osmotic equilibrium, as indicated by freezing-point depression and acidity levels, generally preceded changes in milk composition, and also that they returned more rapidly to normal. Under conditions of alternating temperature (5½ h at high temperatures and 15½ h at lower temperatures) there occurred similar changes in milk composition as under continually hot conditions but less pronounced. Since feed consumption and milk production in this work remained normal, these changes were interpreted as indicating disturbed physiological function rather than underfeeding (Rees, 1964).

Comment

From the results quoted in this and previous sections it is obvious that the decline in milk yield of cows exposed to heat is predominantly the result of a heat-induced reduction in voluntary feed consumption, i.e. an indirect climatic effect. Furthermore, the accompanying changes in the composition of the milk are essentially the same as those which are found when milk yield is depressed as a result of non-climatic factors. There is relatively little evidence about the direct effects of heat on milk yield and milk composition. For improving milk production in hot areas it is therefore important to supply sufficient food of the right kind and to select cows whose appetite does not readily decrease in response to heat.

MEANS OF ALLEVIATING HEAT STRESS

The importance of managerial measures designed to alleviate heat stress in cattle is emphasized by the statement that in 1958 51 % of the total cattle population of the U.S.A. lived south of the 24° isotherm (Ittner, Bond & Kelly, 1958). It has also been said (Brody, 1956) that vast amounts of money have been spent unnecessarily in protecting cold-tolerant European cattle against cold, and that it is more important to protect them against heat. Ittner *et al.* (1958) have made a most comprehensive study of alleviating measures under conditions prevailing in California, and Bond, Kelly & Heitman (1958) have given a catalogue of practical recommendations for the improvement of the environment of livestock in hot areas. Payne (1955) has reviewed the literature dealing with the effects of improved management of dairy cattle in the tropics. The subject has also received attention in reviews by Bond *et al.* (1958) and Nelson (1959), and in a book by Williamson & Payne (1959).

*Properties of shelters**Hot weather shelters*

Hahn, Thom & Bond (1962) have discussed the design of livestock shelters in relation to meteorological variables. Properly designed sun roofs reduced the radiant heat load on cattle by up to 50%; hay proved the 'coolest' of several materials tested for sun roofs (Ittner *et al.* 1958). Aluminium was best when painted white on top and black underneath (Bond, Kelly & Ittner, 1957). Shade provided by thorn trees was found slightly superior to shade provided by straw roofs for protecting calves from heat stress (Alim, 1962). For various climatic and managerial reasons 10–12 ft was considered to be the best height for sun roofs (Ittner *et al.* 1958). The sun roofs should certainly not be too low, because then they act as a shade from part of the cool sky, to which the animals can radiate heat, and provide a hotter surface in its place (Kelly, Bond & Ittner, 1957*a*). In work by Kelly, Bond & Ittner (1957*b*) the north sky had a temperature that was 6–9° lower than the temperature of the air near the ground and therefore could act as a 'heat sink'. The temperature and movement of the air were essentially the same in the sun and under a sun roof made of corrugated galvanized steel and painted white on top, but the radiant temperature (measured with a globe thermometer) was much lower under the sun roof than in the sun, 45 compared with 82° (Boren, Smith, Hodges, Larson & Cox, 1961). In the work of Ittner, Bond & Kelly (1955), when the pens for the animals were made of wire instead of wood a cooler environment was provided: the temperature of the air was 2·1° and that of the water 2·7° lower, and wind velocity around the animals was 1·3 mile/h higher. In an effort to take into account not only the meteorological factors but also the characteristics which influence radiant and convective heat exchange of a surface, the concept of 'sol-air-temperature' has been introduced and tested on skin specimens (Nelson, Mahoney, Berousek & Graybill, 1954). With the aid of evaporative coolers air temperature in shelters could be reduced, but the system had the drawback of increasing the air humidity (Nelson, Berousek & Mahoney, 1956). Finally, White & Isaacs (1961) have described a system for cooling livestock shelters with the aid of solar energy.

Effects of shelters on animals

Garrett, Kelly & Bond (1962), using daily dry matter intake and daily weight gain as criteria, decided that a sun roof area of 25–30 ft²/animal was adequate for beef cattle, but, to avoid overcrowding of the animals, Ittner *et al.* (1958) preferred an area of 60 ft².

There are several reports on the effects of shading on dairy cattle. Under summer conditions in New Zealand shading of Jersey cows was thought hardly worth while (Quartermain, 1960). A study in Oklahoma (Nelson, Mahoney & Berousek, 1961) showed that lactating dairy cattle seemed much more at ease in a shelter with an open front and in a closed shelter equipped with fans and an evaporative cooler than when kept without a shelter. The animals seemed to prefer shade outside to shade inside a shelter. There were, however, no statistically significant differences in milk yield between the 3 groups of cows. The authors calculated that it would require an increase in milk production of about 22% during the 4 hottest months of the year to warrant economically the use of a cooler in a cattle shelter. In Louisiana, Holstein

cows were more stressed in an open shed with an aluminium roof and air temperatures ranging from 21 to 36°, than in a barn conditioned to 17–22° but, again, the milk yields were not significantly different in the 2 groups (Johnston, Hindery, Turnipseed & Thompson, 1960). It would appear that in this work the heat stress on the animals was not high enough or lasting enough for sun roofs to have a beneficial effect on milk yield.

Beef cattle have been reported to benefit from shading. In Kansas, heifers kept in the shade, compared with heifers kept in the sun, gained significantly more weight, 2.2 compared with 1.99 lb/day and required less feed per unit of gain (Boren *et al.* 1961). According to McDaniel & Roark (1956) Hereford and Aberdeen Angus animals made greater weight gains on a pasture with natural shade than in a pasture without shade. The same was not true, however, of a pasture with artificial shade. The use of wire pens instead of wooden pens resulted in a significant increase in weight gain (Ittner *et al.* 1955). The importance of providing buffaloes with shade is clearly indicated by the work of Minett (1955) and Mullick (1960).

Showers and fans

Holstein and Jersey cows spent 3 times more time under a shower when the air temperature was in the range 33–36° than when it was in the range 27–29°. Sprinkling with water reduced their body temperatures and respiratory rates but did not increase their milk yields (Miller, Frye, Burch, Henderson & Rusoff, 1951). In a later study the milk yields of Holstein cows were slightly raised by sprinkling, while those of Jersey cows remained practically unaffected (Rusoff, Miller & Frye, 1955). Sprinkling followed by shade was more effective than shade alone in reducing various heat responses in Jersey cows (Seath & Miller, 1947*b*). The effect of sprinkling could be enhanced by fanning (Seath & Miller, 1948). The cooling effect of showers was more pronounced in water buffaloes than in cattle. Probably as a result of differences in hair density, buffaloes cooled mostly while under the shower, cattle mostly during the drying-off period. Behavioural studies suggested that buffaloes had a natural inclination to wallow when air temperature exceeded 29°. Artificial showers were considered more effective and more hygienic than wallowing (Minett, 1947). Numerous other workers have demonstrated the beneficial effect of showers on the thermal balance of buffaloes, e.g. Sinha & Minett (1947); Ragab, Ghany & Asker (1953); and Taneja & Bhatnagar (1960).

Observations made on over 600 European-type cows in Singapore showed that body temperatures could be kept practically normal by fanning the animals and sprinkling them once every hour (Dobinson, 1951). In California it was found that supplementing natural air movement with fans significantly lowered the body temperature and respiratory rate of Hereford steers but only when the animals were exposed to the sun, not when they were in the shade (Garrett, Bond & Kelly, 1960). Ittner, Kelly & Bond (1957) were able to increase the weight gains of Hereford steers by fanning them, but they also noted that at air temperatures above 39° fanning began to have a heating effect on the animals. Methods for keeping dairy bulls comfortable during summer weather in Louisiana have been investigated by Patrick *et al.* (1958).

Various other procedures

Cooling the drinking water of cattle to about 18° increased animal comfort and produced noticeable increases in weight gain. Since cooling water by mechanical refrigeration may be too expensive, several inexpensive ways have been suggested (Ittner *et al.* 1951, 1958). Refrigerated panels may act as radiant heat absorbers. Cows standing in a hot atmosphere have been found to radiate heat to cold panels to such an extent that respiratory rate and body temperature were reduced. The panel surface temperature which gave the greatest heat exchange was +3° (Shanklin & Stewart, 1958; Bedwell & Shanklin, 1962). An interesting way of cooling cows exposed to a hot atmosphere has been tried by Hahn, Johnson, Shanklin & Kibler (1963). Holstein cows in an atmosphere of 29° were supplied through a wide hood around the head with cool air at 10 or 16° for breathing. With this device it was possible to reduce the rise in rectal temperature to a minimum of 0.2° above normal and to keep milk production at 90% of its normal level.

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