

# Metabolism of Water, Sodium, Potassium, and Chlorine by High Yielding Dairy Cows at the Onset of Lactation<sup>1,2</sup>

N. SILANIKOVE,<sup>3</sup> E. MALTZ,<sup>4</sup> A. HALEVI,<sup>3</sup>  
and D. SHINDER<sup>3</sup>

Agricultural Research Organization, The Volcani Center,  
PO Box 6, Bet Dagan 50250, Israel

## ABSTRACT

We studied the balance of Na<sup>+</sup>, K<sup>+</sup>, Cl<sup>-</sup>, and water in six high yielding (>39 kg/d of milk) cows between wk 2 to 1 prepartum and at 2 and 7 wk postpartum during winter in Israel. Cows were fed complete diets; Na<sup>+</sup> and Cl<sup>-</sup> contents exceeded dietary recommendations, and K<sup>+</sup> content was equal to dietary recommendations. Milk yield was related positively and significantly to retention of Cl<sup>-</sup> and K<sup>+</sup>, indicating that ions that are the main constituents of sweat can limit the ability of cows to express full genetic potential. The highest ion retention was recorded for cows that had the highest dry matter intake and, hence, the highest ion intake. Retention of Cl<sup>-</sup> was highest for cows that were most efficient in retaining Cl<sup>-</sup> in the kidney. In hot climates, increasing the concentrations of ions in the diet of early lactation cows according to the actual dry matter intake could prevent or reduce the severity of ion deficiencies. Water turnover rate of the cows was dependent on dry matter intake, milk yield, and respiratory-cutaneous water loss. The milk-free water balance (water turnover rate minus water secreted in milk) could be very efficiently predicted for lactating and nonlactating cows by the following equation: milk-free water balance (kilograms per day) = digestible energy intake (megacalories per day) × 0.58 + respiratory-cutaneous loss (kilograms per day) × 0.97 (n = 18; R<sup>2</sup> = 0.97). This formula provides a tool to assess the evaporative-cutaneous water loss from feed and water intake measurements to evaluate the severity of heat stress.

(**Key words:** water, ions, metabolism, lactation)

**Abbreviation key:** FWI = free water intake, MFWB = milk-free water balance, RCW = respiratory-cutaneous water, WTO = water turnover.

## INTRODUCTION

The selection of dairy cows for high milk yield has so increased water output that the daily water turnover (**WTO**) rate of cows is among the highest recorded in mammals (16). Also, secretion of Na<sup>+</sup>, K<sup>+</sup>, and Cl<sup>-</sup> through milk has markedly increased (22). Water and ion balance are closely related: a surplus intake of ions increases the demand for water, and water lost during thermoregulation is accompanied by ion losses. The balance of Na<sup>+</sup>, K<sup>+</sup>, and Cl<sup>-</sup> in dairy cows was negative under the hot summer conditions of the Mediterranean region (22). At initiation of lactation, DMI is still limited. Therefore, in hot climates, increasing the concentrations of ions in the diet fed to early lactation cows according to actual DMI could prevent or reduce the severity of ion deficiencies.

The negative balance of Na<sup>+</sup>, K<sup>+</sup>, and Cl<sup>-</sup> was associated with marked reduction of their loss in excreta, particularly the loss of Na<sup>+</sup> and Cl<sup>-</sup> (22). The deficiency of Na<sup>+</sup>, K<sup>+</sup>, and Cl<sup>-</sup> might have limited cutaneous loss of these ions, reducing the efficiency of thermoregulation of the cows and perhaps even negatively affecting milk yield (22). Because the increase in milk yield in early lactation is greater than the increase in DMI, initiation of lactation per se probably is a factor in ion depletion (22). Unlike energy deficiency, ion deficiency at this stage cannot be compensated by body reserves. Consequently, ion depletion might obstruct the rate of increase in milk yield, and milk yield might be adjusted relative to ion availability.

A serial study of fluid and ion (Na<sup>+</sup>, K<sup>+</sup>, and Cl<sup>-</sup>) balance of cows during late pregnancy and early lactation was conducted from winter through spring when conditions were uncomplicated by summer heat load in order to compare water and ion metabolism of cows fed typical Israeli diets and to evaluate the

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<sup>3</sup>Institute of Animal Science.

<sup>4</sup>Institute of Agricultural Engineering.

TABLE 1. Ingredients and chemical analysis of diets fed 2 wk prepartum (period 1) and 2 wk postpartum (period 2) and 7 wk postpartum (period 3).

Ingredient	Period	
	1	2 and 3
	———— (% of DM) ————	
Wheat hay	100	. . .
Vetch hay	. . .	9.2
Corn silage	. . .	25.6
Concentrate mixture <sup>1</sup>	. . .	65.2
DM, % of Feed	83.2	59.3
CP <sup>2</sup>	9.92	18.21
ME, <sup>3</sup> Mcal/kg of DM	2.85	1.76
NDF	65.77	29.33
Ash	13.68	7.46
Na <sup>+</sup> <sup>4</sup>	0.68	0.30
K <sup>+</sup> <sup>4</sup>	1.62	0.95
Cl <sup>-</sup> <sup>4</sup>	1.44	0.57
Ca	0.27	1.13
P	0.10	0.60

<sup>1</sup>Contained (DM basis): 34% corn, 18% barley, 13% wheat bran, 12% soybean meal, 10% cottonseed meal, 6% gluten, 2% protected fat (Ca soap), 1% dicalcium phosphate, 1.8% CaCO<sub>3</sub>, 1.7% CaCl<sub>2</sub>, and 0.5% vitamin and trace minerals complex. The vitamin and trace minerals complex contained 4 million IU/kg of vitamin A, 0.8 IU/kg of vitamin D, 0.75 IU/kg of vitamin E, 0.36 g/kg of I, 6 g/kg of Fe, 6 g/kg of Mn, 3.2 g/kg of Cu, 0.08 g/kg of Co, 6 g/kg of Zn, and 0.08 g/kg of Se.

<sup>2</sup>Ruminally degradable protein for period 1 was 65% and 61% for periods 2 and 3 [based on Israeli and NRC (18) tables].

<sup>3</sup>ME = Metabolizable energy, calculated from OM digestibility and NRC (18) conversion factors.

<sup>4</sup>NRC recommendations for monovalent ions are K<sup>+</sup>, 1.00% of DM; Na<sup>+</sup>, 0.18% of DM; and Cl<sup>-</sup>, 0.20% of DM.

assumption that DMI during early lactation is a rate-limiting factor for adequate ion supply.

## MATERIALS AND METHODS

An experiment was conducted during winter and spring (December through May) using three pairs of pluriparous Israeli Holstein cows. Four weeks before expected parturition, each pair of cows was transferred to individual indoor stalls; diet was not changed. Daily feed and water intake and fecal and urinary excretion were measured individually during wk 2 to 1 prepartum (period 1) and at wk 2 (period 2) and wk 7 (period 3) postpartum. Sampling and management routines were identical to those described by Shalit et al. (22). Prepartum cows were fed wheat hay for ad libitum consumption, and 1.5 kg/d (DM basis) of the TMR were given to the lactating cows (Table 1). The TMR was prepared daily and fed at 0800 h; orts were collected before the provision of the fresh ration. For 1 wk before the study and during the balance study at wk 2 prepartum, cows received only hay for ad libitum consumption.

The procedures for measuring water intake; quantitative collection of urine and feces; and sampling and analysis of Na<sup>+</sup>, K<sup>+</sup>, and Cl<sup>-</sup> in water, urine, and feces were identical to those described by Shalit et al. (22). Total intake [free water intake (FWI) + metabolic water + feed moisture = WTO rate] equaled total water excretion [urine water + fecal water + respiratory-cutaneous water (RCW) loss] + water retention. From Woodford et al. (26), a retention of 1.3 kg/d of water could be calculated for the initiation of lactation. This value was used to estimate the experimental error that was associated with the estimation of RCW from the previous balance equation. The water balance was also presented as milk-free water balance (MFWB), the WTO rate minus the water secreted in milk. Obviously, for prepartum cows, MFWB is equal to the WTO rate. Thus, when prepartum and postpartum avenues of loss are compared as a fraction of MFWB, trends of adaptation can be identified easily (22).

Ambient temperature and relative humidity were measured throughout the balance period every hour by a data logger (21X; Campbell Scientific, Inc., Logan, UT) (22). Rectal temperature of each cow was measured in the morning (0800 to 1000 h), afternoon (1200 to 1400 h), and evening (1900 to 2200 h) on each day of the balance periods.

Variation was analyzed by the GLM procedure of SAS (21). Cow and period were the independent terms in the model. Statistical significance ( $P < 0.05$ ) between pairs of periods was assessed by Duncan's multiple range test. Relationships among variables were analyzed by linear and multiple linear regressions. The stepwise backward elimination procedure of SAS (21) was used to discard independent variables that were not significant predictors ( $P > 0.10$ ) of dependent variables. Correlation coefficients were considered to be significantly different from zero at  $P < 0.05$ .

## RESULTS

### BW, DMI, Milk Yield, and Body Temperature

The data summarized in Table 2 show that BW in periods 2 and 3 were similar. The DMI differed between periods; DMI was lowest in period 1 and was highest in period 3. Milk yields were similar in periods 2 and 3.

Mean night temperature was 12°C (within-day SD = 0.3°C; SD between days = 1.8°C), and mean day temperature was 14.2°C (within-day SD = 0.5°C; SD

TABLE 2. The BW, DMI, and milk yield (MY) of six cows 2 wk before calving (period 1), 2 wk postpartum (period 2), and 7 wk postpartum (period 3).

	Period			SEM
	1	2	3	
BW, kg	654 <sup>a</sup>	550 <sup>b</sup>	550 <sup>b</sup>	28
DMI, kg/d	7.2 <sup>a</sup>	16.8 <sup>b</sup>	22.2 <sup>c</sup>	0.9
MY, kg/d	. . .	39.4	41.5	1.8

<sup>a,b,c</sup>Within rows, means with different superscripts differ ( $P < 0.05$ ).

between days = 2.2°C). Relative humidity ranged between 85 and 93% throughout the trial.

No notable fluctuations in rectal temperature occurred among the morning (38.6 ± 0.2°C SEM), noon (38.6 ± 0.1°C SEM), and evening (38.7 ± 0.1° SEM) measurements within each period.

### Water Balance

Data for the water balance components are presented in Table 3. Rate of WTO was 2.65 and 3.29 times greater in periods 2 and 3, respectively, than

that in period 1, and MFWB was 1.8 and 2.4 times greater in periods 2 and 3, respectively, than that in period 1. Free water intake was threefold higher postpartum than that prepartum.

The calculated RCW loss may be overestimated if substantial water retention occurs, because RCW includes water retention. According to Woodford et al. (26), 1.3 kg/d of water retention should be expected during early lactation; that amount accounts for approximately 3.5% of the daily balance in the present experiment. Hence, the contribution of water retention to RCW loss did not impair the results, and a steady-state condition can be safely assumed within each balance period. Loss of RCW was three- to fourfold higher postpartum than that during the preparatum period.

Loss of RCW during lactation was related linearly and positively to DMI ( $n = 12$ ;  $r^2 = 0.78$ ;  $P < 0.004$ ) and WTO rate ( $n = 12$ ;  $r^2 = 0.97$ ;  $P < 0.0001$ ) and was related negatively to milk yield ( $n = 12$ ;  $r^2 = 0.75$ ;  $P < 0.006$ ).

Absolute water loss in feces was greatest in period 3 followed subsequently by loss in periods 1 and 2. However, as a fraction of MFWB, water loss in feces

TABLE 3. Water balance of six cows 2 wk before calving (period 1), 2 wk postpartum (period 2), and 7 wk postpartum (period 3).

Measure	Intake			Output			
	Drinking	Feed <sup>1</sup>	Total	Milk	Urine	Feces	RCW <sup>2</sup>
	Period 1						
Water balance, kg/d	36.2 <sup>a</sup>	4.8 <sup>a</sup>	41.0 <sup>a</sup>	. . .	11.7 <sup>a</sup>	18.7 <sup>a</sup>	10.6 <sup>a</sup>
Fraction of MFWB <sup>3</sup>					0.29 <sup>a</sup>	0.46 <sup>a</sup>	0.25 <sup>a</sup>
	Period 2						
Water balance, kg/d	87.3 <sup>b</sup>	21.4 <sup>b</sup>	108.7 <sup>b</sup>	34.9	11.8 <sup>a</sup>	25.3 <sup>b</sup>	36.9 <sup>b</sup>
Fraction of MFWB					0.17 <sup>b</sup>	0.35 <sup>b</sup>	0.48 <sup>b</sup>
	Period 3						
Water balance, kg/d	106.6 <sup>b</sup>	28.4 <sup>c</sup>	135.0 <sup>c</sup>	37.0	15.4 <sup>b</sup>	36.1 <sup>c</sup>	41.4 <sup>b</sup>
Fraction of MFWB					0.16 <sup>b</sup>	0.37 <sup>b</sup>	0.47 <sup>b</sup>
SEM <sup>4</sup>	6.0	1.0	2.9	2.0	0.9	1.7	4.1
SEM <sup>5</sup>					0.02	0.02	0.02

<sup>a,b,c</sup>Within columns, means with different superscripts differ ( $P < 0.05$ ).

<sup>1</sup>Moisture plus metabolic water. Metabolic water was calculated assuming 1 kg of water/kg of OM digested.

<sup>2</sup>Respiratory-cutaneous water output, calculated as total intake minus milk, urinary, and fecal losses.

<sup>3</sup>Milk-free water balance.

<sup>4</sup>For absolute values.

<sup>5</sup>For fraction of MFWB.

TABLE 4. The Na<sup>+</sup>, K<sup>+</sup>, and Cl<sup>-</sup> balance (milliequivalents per day) in six cows 2 wk before calving (period 1), 2 wk postpartum (period 2), and 7 wk postpartum (period 3).

Period	Intake			Output			Apparent retention
	Feed	Water	Total	Milk	Urine	Feces	
	Na <sup>+</sup>						
1	1866 <sup>a</sup>	109 <sup>a</sup>	1975 <sup>a</sup>	. . .	1834 <sup>a</sup>	377 <sup>a</sup>	-236
2	1786 <sup>a</sup>	262 <sup>b</sup>	2048 <sup>a</sup>	696	1015 <sup>b</sup>	458 <sup>b</sup>	-122
3	2579 <sup>b</sup>	320 <sup>b</sup>	2899 <sup>b</sup>	750	1357 <sup>ab</sup>	730 <sup>b</sup>	61
SEM	111	17	120	27	159	81	104
	K <sup>+</sup>						
1	2693 <sup>a</sup>	0.0	2693 <sup>a</sup>	. . .	2583 <sup>a</sup>	397 <sup>a</sup>	-288
2	3219 <sup>a</sup>	0.0	3219 <sup>a</sup>	1746	1796 <sup>b</sup>	611 <sup>a</sup>	-925 <sup>*</sup>
3	4763 <sup>b</sup>	0.0	4763 <sup>b</sup>	1847	2176 <sup>ab</sup>	1201 <sup>b</sup>	-461
SEM	176	0.0	176	114	170	85	179
	Cl <sup>-</sup>						
1	2880 <sup>ab</sup>	201 <sup>a</sup>	3081 <sup>a</sup>	. . .	2319 <sup>a</sup>	470 <sup>a</sup>	292 <sup>a*</sup>
2	2620 <sup>b</sup>	484 <sup>b</sup>	3104 <sup>a</sup>	1252	1056 <sup>b</sup>	625 <sup>a</sup>	171 <sup>a</sup>
3	3673 <sup>a</sup>	591 <sup>b</sup>	4264 <sup>b</sup>	1396	1112 <sup>ab</sup>	920 <sup>b</sup>	836 <sup>b*</sup>
SEM	278	33	299	98	234	76	111

<sup>a,b</sup>Within columns and ions, means with different superscripts differ ( $P < 0.05$ ).

<sup>\*</sup>Significantly different from 0 by Student's  $t$  test analysis.

was smaller in periods 2 and 3 than that in period 1. Fecal water excretion was related linearly to DMI ( $n = 18$ ;  $r^2 = 0.97$ ;  $P < 0.0001$ ), WTO rate, and FWI ( $n = 18$ ;  $r^2 = 0.93$ ;  $P < 0.0001$ ).

The water excreted in urine was greater in period 3 than in periods 1 and 2. However, as a fraction of MFWB, water excreted in urine was smaller in periods 2 and 3 than that in period 1. Urinary excretion of water was related linearly and positively to DMI ( $n = 18$ ;  $r = 0.55$ ;  $P < 0.01$ ); WTO rate ( $n = 18$ ;  $r^2 = 0.47$ ;  $P < 0.05$ ); Na<sup>+</sup>, K<sup>+</sup>, and Cl<sup>-</sup> intakes ( $n = 18$ ;  $r^2 = 0.68$  to  $0.70$ ;  $P < 0.001$  to  $0.002$ ); and urinary excretions of Na<sup>+</sup>, K<sup>+</sup>, and Cl<sup>-</sup> ( $n = 18$ ;  $r^2 = 0.48$  to  $0.54$ ;  $P < 0.05$  to  $0.01$ ).

### Na<sup>+</sup> Balance

The components of Na<sup>+</sup> balance are presented in Table 4. Because of the higher concentration of Na<sup>+</sup> in the prepartum diet (Table 1) and because of the relatively low DMI at the initiation of lactation (Table 2), total Na<sup>+</sup> intake was similar in periods 1 and 2. As a result of the increase in DMI in period 3, total Na<sup>+</sup> intake in this period was higher than that in periods 1 and 2.

The Na<sup>+</sup> excretion in urine decreased by 45% from period 1 to period 2 and then rose again in period 3, which was not different from excretion in periods 1 or 2. The Na<sup>+</sup> secreted in milk was similar in periods 2 and 3. Fecal excretion of Na<sup>+</sup> during lactation (peri-

ods 2 and 3) was higher than that prepartum (period 1).

No differences existed between periods in total Na<sup>+</sup> excretion or in Na<sup>+</sup> retention. Retention of Na<sup>+</sup> did not differ across periods and did not differ from zero.

### K<sup>+</sup> Balance

The components of K<sup>+</sup> balance are presented in Table 4. Because of the higher concentration of K<sup>+</sup> in the prepartum diet (Table 1) and because of the relatively low DMI at the onset of lactation (Table 2), total K<sup>+</sup> intake was similar in periods 1 and 2. As a result of the increase in DMI in period 3, total K<sup>+</sup> intake in this period was higher than that in periods 1 and 2.

Urinary excretion of K<sup>+</sup> decreased from period 1 to period 2 by 30% and then rose again in period 3, which was not different from the excretion in periods 1 or 2. The amount of K<sup>+</sup> secreted in milk was similar in periods 2 and 3. Fecal excretion of K<sup>+</sup> during lactation (periods 2 and 3) was higher than that excreted prepartum (period 1).

Retention of K<sup>+</sup> did not differ across periods but was ( $P < 0.05$ ) in period 2.

### Cl<sup>-</sup> Balance

The components of Cl<sup>-</sup> balance are presented in Table 4. Because of the higher concentration of Cl<sup>-</sup> in the prepartum diet and because of the relatively low

DMI at the initiation of lactation, total  $\text{Cl}^-$  intake was similar in periods 1 and 2. As a result of the increase in DMI in period 3, total  $\text{Cl}^-$  intake in this period was higher than that in periods 1 and 2.

Urinary excretion of  $\text{Cl}^-$  decreased by 54% from period 1 to period 2 and then rose again in period 3, which was not different from the excretion in periods 1 or 2. Milk excretion of  $\text{Cl}^-$  was similar in periods 2 and 3. Fecal  $\text{Cl}^-$  excretion did not differ between periods 1 and 2 but was highest in period 3. Retention of  $\text{Cl}^-$  was highest in period 3 and was positive in periods 1 and 2.

### Interrelationships Between Milk Yield and Experimental Variables

High linear correlations were found between DMI and FWI ( $n = 18$ ;  $r^2 = 0.95$ ;  $P < 0.0001$ ), DMI and WTO rate ( $n = 18$ ;  $r^2 = 0.96$ ;  $P < 0.0001$ ), milk yield and FWI ( $n = 12$ ;  $r^2 = 0.63$ ;  $P < 0.002$ ), and milk water and WTO rate ( $n = 12$ ;  $r^2 = 0.64$ ;  $P < 0.002$ ).

Milk yield was related linearly and positively to  $\text{Cl}^-$  retention ( $n = 12$ ;  $r^2 = 0.63$ ;  $P < 0.01$ ) and  $\text{K}^+$  retention ( $n = 12$ ;  $r^2 = 0.26$ ;  $P < 0.05$ ), but not to  $\text{Na}^+$  retention ( $n = 12$ ;  $r^2 = 0.17$ ;  $P < 0.19$ ). Milk yield was related negatively and linearly to  $\text{Cl}^-$  concentration in urine and to  $\text{Cl}^-$  excretion in urine ( $n = 12$ ;  $r^2 = 0.36$ ;  $P < 0.04$ ). No such relationships were found with the two other ions.

## DISCUSSION

### Water Metabolism

The WTO in the present study was similar to that measured by Shalit et al. (22) in summer. However, in summer, the proportion of RCW loss was higher than that in winter, reflecting the higher needs for thermoregulation. Nevertheless, the absolute amount of RCW loss and its contribution to MFWB suggested that high yielding cows activated thermoregulation mechanisms for cooling during winter as well. As reflected by the smaller contribution of urinary excretion to MFWB, the contribution of the kidney to fluid conservation was larger in summer than in winter. Nevertheless, despite an increase of more than double the WTO rate in the transition from late pregnancy to lactation, urine production at wk 2 postpartum was similar to urine production at wk 2 prepartum. Thus, the role of the kidney in fluid conservation in early lactation was also demonstrated during winter (13).

Absolute amounts of water excreted in feces were larger in the winter experiment than the summer

experiment during both the prepartum and postpartum periods. Part of these differences could be related to the higher DMI in winter, because DMI was linearly related to the fecal excretion of water, in agreement with results of previous studies (5, 19). However, DMI by the prepartum cows in summer was 1 kg higher than that by prepartum cows in winter (probably because the digestibility of the wheat silage used in summer was better than that of the wheat hay used in winter), indicating that DMI was not the only factor that influenced fecal excretion of water. Based on the contribution of fecal water to MFWB, the gastrointestinal contribution to water conservation appeared to be more pronounced in summer and relatively larger than the kidney contribution. However, as described for the kidney, the function of the gastrointestinal tract in water conservation in winter was also demonstrated by the reduction in the ratio between fecal excretion of water and MFWB in the transition from late pregnancy to lactation.

The main factors that influence FWI and WTO rate in dairy cows are DMI and milk yield (5, 10, 16, 17, 22, 26). According to results of Maltz et al. (14) and results of the present study, an additional factor that may increase FWI and WTO rate is RCW loss. Thus, mean WTO rate was predicted for lactating cows as is shown in the equations that follow; all values are kilograms per day [ $n = 12$ ,  $r^2 = 0.98$ ,  $P < 0.0001$ ; for the intercept, the  $P$  value was nonsignificant; for DMI,  $P < 0.0001$ ; for milk water (MW),  $P < 0.04$ ; and for RCW loss,  $P < 0.0006$ ].

$$\text{WTO} = 5.2 + \text{DMI} \times 2.86 + \text{MW} \times 0.70 + \text{RCW loss} \times 0.86. \quad [1]$$

Maltz et al. (14) have shown that MFWB could be predicted for both dry and lactating cows [ $n = 15$ ,  $R^2 = 0.97$ ,  $P < 0.0001$ ; for the intercept,  $P < 0.03$ ; for digestible energy intake (DEI),  $P < 0.002$ ; and for RCW loss,  $P < 0.0001$ ] by the following equation:

$$\text{MFWB} = 11.7 + \text{DEI} \times 0.56 + \text{RCW loss} \times 0.97. \quad [2]$$

Application of the same multiple linear regression on the present results yielded a similar equation ( $n = 18$ ,  $R^2 = 0.96$ ,  $P < 0.0001$ ; for the intercept,  $P < 0.0001$ ; for DEI,  $P < 0.02$ ; and for RCW loss,  $P < 0.0001$ ):

$$\text{MFWB} = 14.2 + \text{DEI} \times 0.54 + \text{RCW loss} \times 1.0. \quad [3]$$

Consequently, the results of both studies could be combined into the following equation ( $n = 33$ ,  $R^2 =$

0.96,  $P < 0.0001$ ; for the intercept,  $P < 0.0001$ ; for DEI,  $P < 0.0001$ ; and for RCW loss,  $P < 0.0001$ ):

$$\text{MFWB} = 12.7 + \text{DEI} \times 0.58 + \text{RCW loss} \times 0.97. \quad [4]$$

### Interpretation of RCW Loss

Loss of RCW can be separated into passive and thermoregulatory components. Passive water loss is respiratory loss plus cutaneous diffusion loss; the latter constitutes approximately two-thirds of passive water loss (15). Thermoregulatory water loss is activated by panting and sweating, and sweating constitutes the major component of total evaporation under heat load (15). Based on activation of panting, the upper critical temperature is 26°C (1). However, sweating and panting can be activated independently, and, for goats, sweat secretion is activated long before panting (4).

From the allometric formula of Chew (3), relating BW and insensible (passive) water loss (IW) of mammals [IW (milliliters per hour) =  $2.58 \times \text{BW}^{0.826}$  (kilograms)], a 600-kg cow would lose 12 L of water/d, which is very close to the RCW loss of 13 L/d for dry cows in the present experiment. Interestingly, the intercept of Equation [4], which represents the minimal loss from the body of a cow, is very close to the prediction of Chew (3) for passive water loss. Consequently, the passive water loss in dairy cows may be assumed to be approximately 12 L/d. For lactating cows in a cold environment, evaporative water loss is even lower (8 to 9 L/d) (15), indicating that insensible water loss is reduced in a cold environment. However, whether sweat was measured directly (15) or whether evaporation was estimated by balance [(4); present study], RCW losses of lactating cows were considerably higher than 12 L/d, suggesting that sweating was activated.

Silanikove (23) suggested that the linear relationship between feed intake and WTO rate (or FWI) was, in fact, a derivation of a more basic relationship between digestible energy intake (or metabolism) and WTO rate. This linear relationship means that any increased contribution to WTO of urine, fecal, and evaporative water losses within the thermoneutral zone in diets that does not impose osmotic loads can be predicted by changes in digestible energy intake. Furthermore, the slope of the relationship between digestible energy intake and WTO rate in lactating mammals is essentially similar to that of nonlactating mammals if the amount of water secreted in milk is subtracted from the WTO rate, which suggests that the effect of digestible energy

intake on WTO is similar for lactating and nonlactating ruminants. From our results and those of Maltz et al. (14), this conclusion seems valid for dairy cows. However, as a result of the high metabolism of lactating dairy cows, sweating apparently is activated at fairly low temperatures, most likely when ambient temperatures exceed 12 to 14°C. Each increase in RCW loss increases MFWB and, therefore, is likely to increase FWI and WTO rate by the same amount as suggested by Equation [4]. In agreement, water consumption per unit of DM ingested by cows was constant between -12 to 4°C and rose at an accelerated rate between 4 and 38°C (25). The RCW loss determined by Woodford et al. (26) was calculated according to Equation [4]. The MFWB could be calculated from the data provided, and the effect of digestible energy intake was predicted assuming a digestibility of 60% for the diet of dry cows and 75% for the diet of lactating cows. These calculations yielded the following predictions: 15.8 L/d for prepartum cows, 18.0 L/d for cows at 24 d postpartum (milk yield = 21.5 L/d), and 23.7 L/d for cows at 42 d postpartum (milk yield = 25.7 L/d). Accordingly, internal heat effects on RCW loss under mild environmental conditions are expected to be significant when milk yield exceeds 27 L/d. The stability of the rectal body temperature among and within periods indicated that the cows had no problem maintaining a normothermic state.

### Ion Metabolism

Although  $\text{Na}^+$ ,  $\text{K}^+$ , and  $\text{Cl}^-$  concentrations in feed were considerably higher in the study of Shalit et al. (22) than those in the present experiment, the intake of those ions in the present experiment was much higher than that in the summer experiment. This result supports the conclusion of Shalit et al. (22) that DMI is the main factor limiting needed ions in early lactation, particularly when an increase in DMI is limited by hot weather. Seasonal differences in ion excretion in milk were parallel to differences in milk yield (i.e., in wk 2, excretion was higher in winter than in summer; the differences increased during wk 7). In accordance with the lower intake of ions during lactation in summer, the excretion of  $\text{Na}^+$ ,  $\text{K}^+$ , and  $\text{Cl}^-$  in urine and feces was much lower.

In summer, the prepartum cows were able to attain a positive balance of  $\text{Na}^+$ ,  $\text{K}^+$ , and  $\text{Cl}^-$ . These cows exceeded their needs for mineral accretion in the fetus (6), and thus minerals were available for secretion in sweat. In contrast, the cows that were in late pregnancy in winter were in negative  $\text{Na}^+$  and  $\text{K}^+$  balance, despite a higher intake of these ions than in that summer, indicating that the heat load per se induced

homeostatic responses that increased ion retention. A similar response was recorded by Richards (20) when lactating cows were transferred from thermoneutral to hot conditions. Nevertheless, as with water balance, the functions of the kidney and gastrointestinal tract in the retention of  $\text{Na}^+$ ,  $\text{K}^+$ , and  $\text{Cl}^-$  during the transition from late pregnancy to lactation in this study were demonstrated by the reduction in their concentration in excreta (13) and by the reduction in the proportion between  $\text{Na}^+$ ,  $\text{K}^+$ , and  $\text{Cl}^-$  excretions in urine and feces and the respective MFWB of these ions. Excess of  $\text{Na}^+$  or  $\text{K}^+$  may cause an increased excretion of the counterpart ion in urine, even if the counterpart ion is needed (2). The lack of reciprocal relationships between  $\text{Na}^+$  and  $\text{K}^+$  in urine (13) strengthened the conclusion that these ions were deficient.

### Nutritional Implications

Generally, the higher DMI during wk 7 postpartum than during wk 2 postpartum was associated with greater apparent retention of  $\text{Na}^+$ ,  $\text{K}^+$ , and  $\text{Cl}^-$ . However, because of the high variability among cows, these differences in ion retention were not significant (except for  $\text{Cl}^-$  in period 3). The peaks of feed intake and milk yield, the timing of those peaks, and the patterns of their curves varied considerably among individual cows maintained under similar husbandry conditions (11, 24). A large percentage of the individual variation in apparent retention of  $\text{Na}^+$ ,  $\text{K}^+$ , and  $\text{Cl}^-$  can be explained by multiple linear regression. The effect of DMI (in particular ion intake) was positive, and the effects of milk yield and ion excretion in urine ( $n = 12$ ;  $r^2 = 0.86$  for  $\text{Na}^+$ ,  $0.75$  for  $\text{K}^+$ , and  $0.94$  for  $\text{Cl}^-$ ) were negative. In agreement with previous conclusions (12), the results of the present experiment stress the importance of analyzing the nutritional and physiological response of dairy cows during this critical period by a dynamic approach.

The kidneys of mammals can easily eliminate a moderate excess of ions by increasing output through increased urine volume. No such response was encountered in the present experiment, which suggested that the demand for these ions was far from saturation. Furthermore, the linear relationship between  $\text{Cl}^-$  or  $\text{K}^+$  retention and milk yield suggested that these two ions might be rate-limiting factors in the ability of the cows to express their genetic yield potential in early lactation. Among the cows used in the present experiment, the most efficient increased DMI (hence, ion intake) faster and retained  $\text{Cl}^-$  in urine most efficiently.

Potassium and  $\text{Cl}^-$  are major constituents of sweat (7, 8). Thus, cows that had a higher apparent retention of these two ions had more of them available for sweating, which might explain the positive relationship between milk yield and retention of  $\text{Cl}^-$  and  $\text{K}^+$ . A deficiency of these ions might reduce milk yield, and milk yield might be adjusted relative to ion availability. Hence, higher supplementation of  $\text{Na}^+$ ,  $\text{K}^+$ , and  $\text{Cl}^-$  between wk 1 and 8 in lactating dairy cows should increase retention of these ions and thus potentially improve feed intake and milk yield.

The cows in the present experiment were in negative  $\text{K}^+$  balance for 8 wk without a reduction in plasma  $\text{K}^+$  concentration (13). Whole body depletion of  $\text{K}^+$  can reduce  $\text{K}^+$  concentrations in erythrocyte and muscles without reducing them in plasma (9). A reduction of  $\text{K}^+$  in plasma is undesirable and can lead to weakness and paralysis, impairment of renal concentration capacity, altered intestinal motility, hypertension, laminitis, and acid-base disturbances (9). Some of these complications are quite common in early lactation; therefore, the involvement of  $\text{K}^+$  deficiency should be considered.

In the present study, concentrations of  $\text{K}^+$  in the diet needed the most adjustment between meeting the requirements of the cow. Assuming a sweating rate (calculated as RCW loss - 12) of approximately 20 and 30 L/d in wk 2 and 7, respectively, the requirements for  $\text{K}^+$  for sweating [because  $\text{K}^+$  concentration in sweat can range between 20 and 80 meq/L; (7,8)] are 600 to 2400 meq/d. If this amount is added to the negative balance, the extra  $\text{K}^+$  requirements are 1500 to 3000 meq/d; the maximal estimation can be supplied in a diet that contains 1.5 to 1.6% total dietary  $\text{K}^+$ . Optimal concentrations of  $\text{Na}^+$  and  $\text{Cl}^-$  are probably higher than those used in the present study by 0.1 to 0.2% of total dietary content.

### CONCLUSIONS

The present study confirmed that DMI and milk yield are closely related to FWI and WTO rate. In addition, RCW loss was also found to be linearly related to WTO, suggesting that RCW loss is an additional factor that determines FWI and WTO in cows yielding 40 L/d, even under temperate environmental conditions. The increased loss of RCW after calving was most likely a result of activation of sweating in response to the large increment in internal heat production. The positive relationship between DMI and the apparent retention of  $\text{Na}^+$ ,  $\text{K}^+$ , and  $\text{Cl}^-$  in early lactation, as well as the negative balance of  $\text{K}^+$  and  $\text{Cl}^-$ , suggested that increased ion supply at

initiation of lactation might have a positive effect on DMI and milk yield of cows.

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