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Effect of cereal grain type and corn grain harvesting and processing methods on intake, digestion, and milk production by dairy cows through a meta-analysis

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ABSTRACT

A meta-analysis was performed to determine the influence of cereal grain type and corn grain harvesting and processing methods, dietary starch, rumen-digestible starch, and forage NDF concentrations on intake, digestion, and lactation performance by dairy cows using a data set comprising 414 treatment means from 102 peer-reviewed journal reports from 2000 to 2011. Categories for corn processing were dry ground, cracked or rolled corn (DRY), high-moisture shelled or ear corn (ENS), and steam-flaked or -rolled corn (STM); categories for kernel mean particle size were 500 to 1,000, 1,000 to 1,500, 1,500 to 2,000, 3,000 to 3,500, and 3,500 to 4,000 μm for dry corn and <2,000 and ≥2,000 μm for ensiled corn. Dietary starch and forage NDF concentrations were used as continuous variables. Data were analyzed using PROC MIXED in SAS (SAS Institute Inc., Cary, NC), with treatment as fixed and trial as random effects. Total-tract starch digestibility was reduced and milk fat content was greater for DRY compared with ENS or STM. Total-tract digestibility of dietary starch was reduced for both DRY and ENS as particle size increased. Increased dietary starch concentrations increased milk yield and protein content, but decreased ruminal and total-tract NDF digestibilities and milk fat content. Dry matter intake, total-tract starch digestibility, and milk protein concentration decreased as forage NDF in the diet increased. Total-tract starch digestibility was positively related to ruminal (percentage of starch intake) and postruminal (percentage of duodenal flow) starch digestibilities.
Key words: corn, digestion, milk production, starch

INTRODUCTION

Corn grain is the predominant feed energy source in the US ruminant livestock industry (USDA, 2011). Approximately 75% of the corn grain energy value is derived from starch (calculated from NRC, 2001) and, thus, improving starch utilization may improve lactation performance and reduce feed costs, especially during periods of high grain prices.

The corn kernel consists of 3 basic morphological parts; pericarp, germ, and endosperm (Huntington, 1997; Correa et al., 2002). Germ and endosperm are surrounded by the pericarp, which is largely resistant to microbial attachment (McAllister et al., 1994). Starch granules from corn grain are surrounded by a protein matrix in the endosperm (Kotarski et al., 1992), which influences digestion by microorganisms (McAllister et al., 1993). Several factors may affect the pericarp and starch-protein matrix and, therefore, starch digestibility, including harvest maturity, moisture content, and endosperm type (Correa et al., 2002; Lopes et al., 2009; Ngonyamo-Majee et al., 2009). Furthermore, ensiling high-moisture corn (Hoffman et al., 2011) or steam treatment of dry corn (Rooney and Pflugfelder, 1986) results in the break-down of the hydrophobic starch-protein matrix, allowing for a corresponding increase in starch digestibility over dry rolled corn (Owens et al., 1986; Theurer et al., 1999; Firkins et al., 2001) and, thus, greater NE_L (Wilkerson et al., 1997; Theurer et al., 1999). Likewise, reducing the mean particle size (**MPS**) of corn grain increases starch digestibility and NE_L (Moe and Tyrrell, 1977; Firkins et al., 2001) by increasing the surface area for bacterial attachment or enzymatic degradation (Huntington, 1997).

Dietary factors, such as starch and forage NDF (**FNDF**) concentrations, influence DMI by dairy cows (Mertens, 1987; Allen et al., 2009). Greater DMI increases passage rate through the gastrointestinal tract, thereby reducing the time for starch hydrolysis, which limits starch digestibility (Owens et al., 1986; Firkins et al., 2001). High corn prices have heightened the interest in feeding reduced-starch and high-forage diets.

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Table 1. Descriptive statistics for continuous variables used in the meta-analysis, and selected diet nutrient composition from corn grain-based diets experiments used in the meta-analysis

Item[1]	Average	SD	Minimum	Maximum
Total diet DMI (kg/d)	23.6	2.5	12.5	30.1
CP (% of diet DM)	17.0	1.7	12.9	21.7
NDF (% of diet DM)	31.2	4.8	18.7	48.2
Forage NDF (% of diet DM)	19.8	3.5	12.6	34.1
Starch (% of diet DM)	27.0	6.1	5.2	43.7
Forage (% of diet DM)	47.7	8.1	19.7	72.7
DRY mean particle size (μm)	1,681	1,085	540	4,000
ENS mean particle size (μm)	2,607	1,249	1,020	4,430

[1]DRY = dry ground or rolled corn; ENS = high-moisture shelled or ear corn.

Partially replacing corn grain with nonforage fibrous byproducts increased total-tract starch digestibility (**TTSD**) in some (Pereira and Armentano, 2000; Gencoglu et al., 2010; Ferraretto et al., 2012), but not all, trials (Voelker and Allen, 2003b). Similarly, increasing dietary FNDF content either increased (Bal et al., 2000a), decreased (Agle et al., 2010b), or did not affect TTSD (Pereira and Armentano, 2000; Lechartier and Peyraud, 2010; Weiss et al., 2011b).

Although numerous reports on feeding trials with lactating dairy cows assessing one or more of these corn or dietary factors can be found in the literature, attempts to quantify observed responses for lactating dairy cows across reports over the last 10 yr were not found. Therefore, the objective of this study was to perform a meta-analysis using literature data on the effects of cereal grain type, harvesting and processing methods of corn grain, and dietary starch and FNDF concentrations on intake, digestion, and lactation performance by dairy cows. Sites of starch digestion were also evaluated.

MATERIALS AND METHODS

A data set comprising 414 treatment means from 102 trials reported in 102 papers published January 2000 through June 2011 in the *Journal of Dairy Science*, *Journal of Animal Science*, or *Animal Feed Science and Technology* was used for the meta-analysis (Appendix Table A1). The reports included in this data set were with lactating dairy cows fed TMR, and contained data for TTSD and ruminal starch digestibility (**RSD**). Reports that did not include a description of grain processing were not included in the data set. Comparative analysis of cereal grain type contained 3 categories: barley, corn, and wheat. The corn grain harvesting and processing methods were in 3 categories: dry ground, cracked or rolled corn (**DRY**), high-moisture shelled or ear corn (**ENS**), and steam-flaked or steam-rolled corn (**STM**). The MPS treatments for DRY were in 5 categories: 500 to 1,000, 1,000 to 1,500, 1,500 to 2,000, 3,000 to 3,500, and 3,500 to 4,000 μm. The MPS treatments for ENS were in 2 categories: <2,000 and ≥2,000 μm. The STM treatments were in 2 categories: flaked or rolled. The dietary starch, rumen-digestible starch, and FNDF concentrations (DM basis); DMI; and comparisons among sites of starch digestion were evaluated as continuous variables. The MPS was not evaluated as a continuous variable because of the high standard deviations reported within trials. Except for a comparison between various cereal grains, the analyses were performed only for corn grain-based diets. Descriptive statistics for variables included in the analysis and selected diet nutrient composition from the corn-grain based experiments are presented in Table 1.

The dependent variables evaluated were actual-milk and FCM yields; milk fat, protein, and MUN concentrations; DMI; actual-milk and FCM feed conversions; ruminal digestibilities of dietary NDF (**RNDFD**) and starch; and total-tract digestibilities of diet DM (**DMD**), OM (**OMD**), NDF (**TTNDFD**), and starch. Ruminal NDF and starch digestibility data were from experiments with ruminally and intestinally cannulated lactating dairy cows. Data were analyzed using PROC MIXED of SAS (SAS Institute, 2004). For either categorical or continuous independent variables, the model included the fixed effects of treatment and the random effect of trial; treatments were weighted according to the number of experimental units reported in each article (St-Pierre, 2001). Statistical significance and trends were declared at $P \leq 0.05$ and $P \geq 0.06$ to $P < 0.10$, respectively. Root mean square error was calculated based on the adjusted observation plotted against the actual treatment observations (St. Pierre, 2001).

RESULTS AND DISCUSSION

Effects of cereal grain type on covariate-adjusted least squares means for apparent ruminal and total-tract nutrient digestibilities are presented in Table 2. The RSD was affected by cereal grain source ($P =$

Table 2. Effect of cereal grain type on adjusted least squares means for ruminal and total-tract digestibility of dietary nutrients

Item	Barley	Corn	Wheat	SEM	P-value
Ruminal digestibility[1] (% of intake)					
NDF	39.4	39.3	44.8	6.0	0.89
Starch	70.6[a]	54.1[b]	78.9[a]	5.3	0.001
Total-tract digestibility[2] (% of intake)					
DM	64.6	66.6	63.2	1.3	0.07
OM	66.9	68.4	65.4	1.2	0.15
NDF	47.2	45.6	40.4	2.8	0.29
Starch	92.8	92.6	93.9	1.5	0.80

[a,b]Means in the same column with different superscripts differ ($P \leq 0.05$), according to Saxton (1998).

[1]Number of treatment means were 30, 82, and 6 for barley, corn, and wheat, respectively.

[2]Number of treatment means were 62, 335, and 11 for barley, corn, and wheat, respectively.

0.001), with barley and wheat 17 percentage units and 25 percentage units, respectively, greater than corn. Similar results were reported in previous reviews by Theurer (1986), Huntington (1997), and Firkins et al. (2001), and thought to be related to differences in the starch-protein matrix among cereal grains (Theurer, 1986; Kotarski et al., 1992). The TTSD did not differ among treatments ($P = 0.80$). Greater TTSD for barley and wheat compared with corn was reported previously (Theurer, 1986; Huntington, 1997; Firkins et al., 2001), although the magnitude of the difference was 15percentage units less, on average, for TTSD than observed for RSD. The RNDFD and TTNDFD were similar among treatments ($P = 0.89$ and 0.29, respectively). Firkins et al. (2001) reported reduced TTNDFD for barley- compared with corn-grain based diets. Apparently, any negative effect on fiber digestibility of greater ruminal starch digestion (Russell and Wilson, 1996) was attenuated by the lack of rumen pH changes for barley compared with corn for studies evaluated in the present meta-analysis (Tothi et al., 2003; Foley et al., 2006; Gozho and Mutsvangwa, 2008). The DMD tended to be greater ($P = 0.07$) for corn- than barley- or wheat-grain-based diets.

Effects of cereal grain type on covariate-adjusted least squares means for DMI and lactation performance are presented in Table 3. Cows fed corn-grain based diets consumed 2.6 kg/d more ($P = 0.001$) DM, on average, than cows fed barley- or wheat-grain-based diets. Greater DMI for corn- compared with barley- and wheat-grain-based diets was previously reported by Firkins et al. (2001). Milk and FCM yield were 3.6 and 4.1 kg/d, respectively, greater ($P = 0.01$), on average, for corn- than barley- and wheat-grain-based diets. However, actual-milk and FCM feed conversion were unaffected ($P = 0.78$ and 0.69, respectively) by treatment. Likewise, milk fat, protein, and urea nitrogen concentrations were unaffected by treatment ($P = 0.40$, 0.78, and 0.82, respectively) and averaged 3.51, 3.13, and 13.7 mg/dL, respectively.

Effects of corn grain harvesting and processing methods on covariate-adjusted least squares means for apparent ruminal and total-tract nutrient digestibilities are presented in Table 4. The RSD approached a trend to be greater ($P = 0.12$) and TTSD was greater ($P = 0.001$) for ENS and STM than DRY, in agreement with previous reviews (Huntington, 1997; Theurer et al., 1999; Firkins et al., 2001). These results are likely related to disruption of the protein matrix surrounding starch by heat and moisture during steam treatment (Rooney and Pflugfelder, 1986) or proteolysis during ensiling (Philippeau and Michalet-Doreau, 1998; Hoff-

Table 3. Effect of cereal grain type on adjusted least squares means for lactation performance by dairy cows[1]

Item	Barley	Corn	Wheat	SEM	P-value
DMI (kg/d)	21.3[b]	23.4[a]	19.8[b]	0.6	0.001
Milk (kg/d)	33.0[b]	35.5[a]	30.7[b]	0.9	0.01
4% FCM (kg/d)	30.2[b]	32.9[a]	27.3[b]	1.0	0.01
Milk fat (%)	3.45	3.56	3.54	0.11	0.40
Milk protein (%)	3.14	3.12	3.15	0.05	0.78
MUN (mg/dL)	13.6	13.8	NA[2]	0.5	0.82
kg of milk/kg of DMI	1.52	1.50	1.47	0.04	0.78
kg of FCM/kg of DMI	1.39	1.39	1.33	0.04	0.69

[a,b]Means within a column with different superscripts differ ($P \leq 0.05$), according to Saxton (1998).

[1]Number of treatment means were 37, 320, and 5 for barley, corn, and wheat, respectively.

[2]Data not available (NA).

Table 4. Effect of corn grain harvesting and processing methods on adjusted least squares means for ruminal and total-tract digestibility of dietary nutrients[1]

Item	DRY	ENS	STM	SEM	*P*-value
Ruminal digestibility[2] (% of intake)					
NDF	37.6	35.7	51.3	4.5	0.17
Starch	53.5	64.1	58.5	6.4	0.12
Total-tract digestibility[3] (% of intake)					
DM	66.2	67.7	65.8	0.8	0.11
OM	68.0	69.4	67.6	0.8	0.11
NDF	45.8	42.2	44.6	1.4	0.02
Starch	92.0[b]	94.2[a]	93.9[a]	0.8	0.001

[a,b]Means within a column with different superscripts differ ($P \leq 0.05$), according to Saxton (1998).

[1]DRY = dry ground or rolled corn; ENS = high-moisture shelled and ear corn; STM = steam-flaked and rolled corn.

[2]Number of treatment means were 65, 6, and 10 for DRY, ENS, and STM, respectively.

[3]Number of treatment means were 274, 25, and 36 for DRY, ENS, and STM, respectively.

man et al., 2011). Although RNDFD was similar among treatments ($P = 0.17$), TTNDFD was greater ($P = 0.02$) for DRY compared with ENS, in agreement with Firkins et al. (2001). The DMD and OMD approached a trend to be greater for ENS compared with DRY and STM ($P = 0.11$). Firkins et al. (2001) reported greater OMD for high-moisture corn than dry corn or steam-treated corn-based diets.

Effects of corn grain harvesting and processing methods on covariate-adjusted least squares means for DMI and lactation performance are presented in Table 5. The DMI was 1.2 kg/d lower ($P = 0.01$) for ENS compared with DRY. Milk yield was unaffected by treatment ($P = 0.75$) and averaged 35.9 kg/d. Consequently, feed conversion (milk/DMI) was greater ($P = 0.001$) for ENS than DRY and may be related to greater NE_L for diets containing ENS (Wilkerson et al., 1997). The FCM yield was greater ($P = 0.05$) for DRY compared with ENS, which may be related to greater ($P = 0.01$) milk fat concentration for DRY than ENS (3.59 vs. 3.41%). However, FCM feed conversion (FCM/DMI) did not differ ($P = 0.32$). Milk protein concentration tended to be greater ($P = 0.05$) for STM than the other treatments and MUN concentration tended ($P = 0.08$) to be greater for DRY than STM, suggesting better ruminal nitrogen utilization (NRC, 2001) for cows fed STM than DRY. Similar results were reported by others (Theurer et al., 1999; Firkins et al., 2001) with greater microbial nitrogen flow to duodenum for cows that were fed STM.

Effects of MPS in DRY and ENS and different STM treatments on covariate-adjusted least squares means for apparent ruminal and total-tract nutrient digestibilities are presented in Table 6. The DMD and OMD were affected by MPS for both DRY ($P = 0.001$) and ENS ($P = 0.06$), but not by STM ($P = 0.73$). The OMD was not affected by STM treatment in the review of Firkins et al. (2001). Similar ($P = 0.48$ and 0.74, respectively) TTNDFD across MPS was observed for DRY and ENS. Likely, TTNDFD did not ($P = 0.70$) differ between STM treatments. Firkins et al. (2001) reported similar TTNDFD for coarse and finely ground DRY and ENS corn or different STM treatments. Increased MPS reduced ($P = 0.001$) TTSD for both DRY (77.7 to 93.3%)

Table 5. Effect of corn grain harvesting and processing methods on adjusted least squares means for lactation performance by dairy cows[1,2]

Item	DRY	ENS	STM	SEM	*P*-value
DMI (kg/d)	23.6[a]	22.4[b]	23.4[ab]	0.4	0.01
Milk (kg/d)	35.7	35.7	36.2	0.6	0.75
4% FCM (kg/d)	33.4[a]	32.1[b]	32.7[ab]	0.5	0.05
Milk fat (%)	3.59[a]	3.41[b]	3.48[ab]	0.06	0.01
Milk protein (%)	3.10	3.10	3.16	0.03	0.07
MUN (mg/dL)	13.9	NA[3]	13.2	0.5	0.11
kg of milk/kg of DMI	1.50[a]	1.58[a]	1.52[ab]	0.03	0.001
kg of FCM/kg of DMI	1.40	1.42	1.38	0.04	0.32

[a,b]Means within a column with different superscripts differ ($P \leq 0.05$), according to Saxton (1998).

[1]DRY = dry ground or rolled corn; ENS = high-moisture shelled and ear corn; STM = steam-flaked and rolled corn.

[2]Number of treatment means were 260, 25, and 35 for DRY, ENS, and STM, respectively.

[3]Data not available (NA).

Table 6. Effect of corn grain mean particle size and steam treatments on adjusted least squares means for total-tract digestibility of dietary nutrients[1]

	DRY[2]							ENS[3]				STM[4]			
Item	500 to 1,000 µm	1,000 to 1,500 µm	1,500 to 2,000 µm	3,000 to 3,500 µm	3,500 to 4,000 µm	SEM	*P*-value	<2,000 µm	>2,000 µm	SEM	*P*-value	Flaked	Rolled	SEM	*P*-value
DM	69.5[a]	69.3[a]	67.8[ab]	66.1[b]	59.2[c]	1.5	0.001	71.9	69.4	1.5	0.04	67.4	65.6	3.5	0.73
OM	70.9[a]	70.7[a]	69.3[a]	69.0[a]	61.4[b]	1.6	0.001	73.1	70.9	1.4	0.06	70.8	68.9	3.3	0.69
NDF	46.0	48.2	49.2	48.8	41.5	2.6	0.48	44.4	44.0	1.9	0.74	46.6	49.7	5.3	0.70
Starch	93.3[a]	93.2[a]	89.8[b]	89.6[b]	77.7[c]	1.4	0.001	95.2	89.5	1.3	0.001	94.6	91.9	2.9	0.51

[a–c]Means within a column with different superscripts differ ($P \leq 0.05$), according to Saxton (1998).

[1]DRY = dry ground or rolled corn; ENS = high-moisture shelled and ear corn; STM = steam-flaked and rolled corn.

[2]Number of treatment means were 19, 20, 10, 7, and 7 for 500 to 1,000, 1,000 to 1,500, 1,500 to 2,000, 3,000 to 3,500, and 3,500 to 4,000 µm, respectively.

[3]Number of treatment means were 9 and 8 for <2,000 and >2,000 µm, respectively.

[4]Number of treatment means were 11 and 13 for flaked and rolled, respectively.

Table 7. Effect of corn grain mean particle size and steam treatments on covariate-adjusted least squares means for lactation performance by dairy cows[1]

	DRY[2]							ENS[3]				STM[4]			
Item	500 to 1,000 µm	1,000 to 1,500 µm	1,500 to 2,000 µm	3,000 to 3,500 µm	3,500 to 4,000 µm	SEM	*P*-value	<2,000 µm	>2,000 µm	SEM	*P*-value	Flaked	Rolled	SEM	*P* -value
DMI (kg/d)	23.9	23.4	24.0	23.5	23.1	1.1	0.93	21.8	21.8	0.9	0.95	23.1	23.2	0.9	0.98
Milk (kg/d)	37.2	36.6	36.9	36.3	36.3	1.7	0.60	36.3	35.9	1.6	0.75	35.0	34.0	2.0	0.74
4% FCM (kg/d)	34.4	33.3	33.2	33.5	34.6	1.5	0.67	32.2	32.7	0.9	0.70	31.3	32.2	2.0	0.76
Milk fat (%)	3.50	3.49	3.60	3.57	3.77	0.10	0.30	3.25	3.38	0.15	0.36	3.30	3.70	0.15	0.08
Milk protein (%)	3.06	3.07	3.03	3.05	2.96	0.05	0.36	3.14	3.14	0.11	0.99	3.09	3.21	0.06	0.20
MUN (mg/dL)	13.9	14.1	14.7	NA[5]	NA	0.8	0.07	NA	NA	NA	NA	12.8	13.1	0.9	0.81
kg of milk/kg of DMI	1.55	1.56	1.50	1.53	1.41	0.08	0.32	1.67	1.65	0.10	0.62	1.52	1.36	0.08	0.20
kg of FCM/kg of DMI	1.44	1.42	1.39	1.42	1.37	0.07	0.86	1.48	1.50	0.04	0.60	1.36	1.30	0.09	0.64

[1]DRY = dry ground or rolled corn; ENS = high-moisture shelled and ear corn; STM = steam-flaked and rolled corn.

[2]Number of treatment means were 19, 20, 10, 7, and 7 for 500 to 1,000, 1,000 to 1,500, 1,500 to 2,000, 3,000 to 3,500, and 3,500 to 4,000 µm, respectively.

[3]Number of treatment means were 9 and 8 for <2,000 and >2,000 µm, respectively.

[4]Number of treatment means were 11 and 13 for flaked and rolled, respectively.

[5]Data not available (NA).

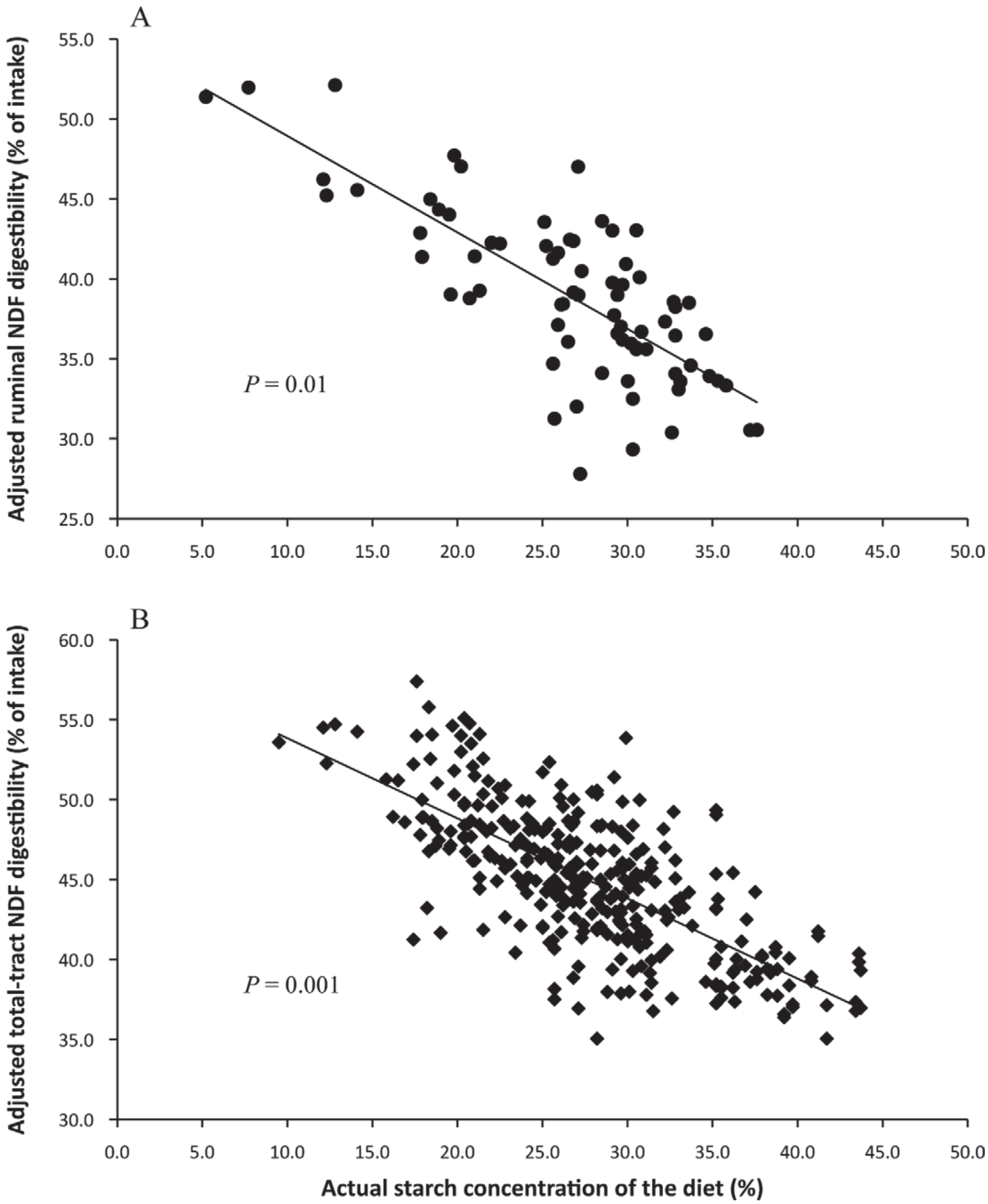

Figure 1. Effect of starch concentration of the diet on ruminal and total-tract digestibility of diet NDF adjusted for the random effect of trial. Ruminal digestibility data (panel A) were predicted from the following equation: y = 54.9746 + (−0.605 × starch concentration) + (0.063 ± 3.524); n = 70, root mean square error (RMSE) = 3.55. Total-tract digestibility diet (panel B) was predicted from the following equation: y = 58.2843 + (−0.4817 × starch concentration) + (0.059 ± 3.191); n = 320, RMSE = 3.20.

and ENS (89.5 to 95.2%). Increased surface area for bacterial and enzymatic digestion (Huntington, 1997) of finer particles and increased passage rate of coarser and denser particles through the gastrointestinal tract (Nocek and Tamminga, 1991) may explain the effect of MPS on TTSD. Similar results were reported by Firkins et al. (2001), although the magnitude of the difference was less (85 to 92% TTSD). Steam-flaked had numerically higher (P = 0.51) TTSD compared with steam-rolled corn. Greater starch digestibility was previously reported for steam-flaked than steam-rolled corn and thought to be related to greater extent moisture and heat applied during flaking (Theurer et al., 1999; Firkins et al., 2001).

Table 8. Equations for linear regression of effects of dietary starch concentration (DM basis) on lactation performance by dairy cows[1]

Item	n[2]	Intercept	SE	Slope	SE	*P*-value	RMSE[3]
Milk (kg/d)	320	33.5	1.3	0.085	0.043	0.06	1.30
Milk fat (%)	317	4.08	0.12	−0.019	0.004	0.001	0.16
Milk protein (%)	315	2.94	0.05	0.006	0.002	0.001	0.07
MUN (mg/dL)	208	16.0	0.5	−0.087	0.020	0.001	0.90
kg of FCM/kg of DMI	320	1.56	0.05	−0.006	0.002	0.001	0.06

[1]Adjusted for the random effect of experiment.

[2]Number of treatment means.

[3]Root mean square error.

Effects of MPS in DRY and ENS and different STM treatments on covariate-adjusted least squares means for DMI and lactation performance are presented in Table 7. The MPS did not affect DMI ($P = 0.93$ and 0.95, respectively) or milk yield ($P = 0.60$ and 0.75, respectively) for either DRY or ENS. Similar DMI with a 1.0 kg/d, on average, increase in milk yield for dry ground and finely ground corn over dry-rolled corn was reported by Firkins et al. (2001). Likewise, STM treatments did not affect DMI or milk yield ($P = 0.98$ and 0.74, respectively) in the present study. Similar response was observed by Firkins et al. (2001), but not Theurer et al. (1999), who reported greater milk yield for steam-flaked corn. Milk fat content did not differ ($P = 0.30$ and 0.36, respectively) among MPS treatments for either DRY or ENS. Milk fat content was greater for coarsely ground DRY and ENS in the review of Firkins et al. (2001). Steam-flaked corn tended ($P = 0.07$) to decrease milk fat concentration compared with steam-rolled corn, in agreement with previous reviews (Theurer et al., 1999; Firkins et al., 2001). The FCM yield and feed conversion were similar among MPS treatments for both DRY ($P = 0.67$ and 0.86, respectively) and ENS ($P = 0.70$ and 0.60, respectively) or STM treatments ($P = 0.76$ and 0.64, respectively). Milk protein was unaffected by MPS ($P = 0.36$ and 0.99, respectively) or STM treatment ($P = 0.20$). Firkins et al. (2001) reported decreased milk protein concentration for cows fed finely ground DRY- but not ENS-based diets. Similar milk protein concentrations between STM treatments were observed by Theurer et al. (1999) and Firkins et al. (2001). The MUN concentrations tended to increase with increasing MPS for DRY ($P = 0.07$) but not STM treatment ($P = 0.81$).

Presented in Figure 1 is the effect of dietary starch concentration on fiber digestibility. Increased dietary starch concentration reduced both RNDFD ($P = 0.01$) and TTNDFD ($P = 0.001$). The digestibility of dietary NDF decreased 0.61 percentage units ruminally and 0.48 percentage units total tract per percentage unit increase in dietary starch content. Decreased fiber digestibility may be partially explained by a decrease in rumen pH (Krause and Oetzel, 2006) as a consequence of greater amounts of starch (kg/d) being digested in the rumen as starch intake increases (Nocek and Tamminga, 1991). Low rumen pH is known to affect microbial growth and bacterial adherence and, thereby, fiber digestion (Hoover, 1986; Mouriño et al., 2001). Also, the inherently high fiber digestibility of nonforage fibrous byproducts (Firkins, 1997) used to partially replace corn grain in reduced-starch diets may be partly responsible. The RSD, TTSD, DMD, and OMD were unaffected ($P > 0.10$) by treatment (data not provided in table or figure). Nocek and Tamminga (1991) report-

Table 9. Equations for linear regression of effects of dietary forage NDF concentration (DM basis) on digestibility of dietary nutrients and lactation performance by dairy cows[1]

Item	n[2]	Intercept	SE	Slope	SE	*P*-value	RMSE[3]
Digestibility[4] (% of intake)							
DMD	259	71.7	2.7	−0.266	0.126	0.05	1.75
OMD	259	73.1	2.4	−0.245	0.114	0.04	1.75
TTSD	267	95.3	1.7	−0.170	0.082	0.05	1.85
Lactation performance							
DMI (kg/d)	273	27.1	1.5	−0.167	0.075	0.04	0.90
Milk fat (%)	253	3.24	0.17	0.014	0.007	0.06	0.18
Milk protein (%)	251	3.26	0.08	−0.008	0.004	0.03	0.07

[1]Adjusted for the random effect of experiment.

[2]Number of treatment means.

[3]Root mean square error.

[4]DMD = total-tract DM digestibility; OMD = total-tract OM digestibility; TTSD = total-tract starch digestibility.

Table 10. Equations for linear regression of effects of DMI (kg/d) on digestion and lactation performance by dairy cows[1]

Item	n[2]	Intercept	SE	Slope	SE	*P*-value	RMSE[3]
Digestibility (% of intake)[4]							
RSD	80	86.5	12.5	−1.433	0.590	0.03	6.22
OMD	327	73.0	2.9	−0.211	0.119	0.08	1.70
TTSD	335	98.1	2.8	−0.243	0.120	0.05	1.95
Lactation performance							
Milk (kg/d)	320	15.5	3.0	0.866	0.119	0.001	1.15
4% FCM (kg/d)	320	10.2	2.7	0.975	0.110	0.001	1.39

[1]Adjusted for the random effect of experiment.
[2]Number of treatment means.
[3]Root mean square error.
[4]RSD = ruminal starch digestibility; OMD = total-tract OM digestibility; TTSD = total-tract starch digestibility.

ed similar RSD and TTSD as starch intake increased in a previous review.

Effects of dietary starch concentration on lactation performance adjusted for the random effect of trial are presented in Table 8. The DMI was not affected ($P = 0.31$; data not provided in table) by starch concentration in the diet. These results are possibly related to rumen fill limitation (Mertens, 1987) and increased ruminal propionate concentrations with corresponding decreased meal size (Allen et al., 2009) when corn grain was partially replaced by forage and nonforage fiber sources, respectively. These opposing effects could explain the lack of effect in the present study. Milk yield tended to increase ($P = 0.06$) 0.08 kg/d per percentage unit increase in dietary starch content, although it did not result in greater feed conversion (milk/DMI; $P = 0.76$; data not provided in table). Conversely, milk fat content decreased ($P = 0.001$) as dietary starch content increased, with a similar pattern of response observed for FCM feed conversion ($P = 0.001$) but not FCM yield ($P = 0.32$; data not provided in table). Firkins et al. (2001) reported decreased milk fat content with greater grain intakes. Milk fat depression in high-starch diets is likely related to greater starch and lower NDF intakes (Jenkins and McGuire, 2006). Increased dietary starch concentration resulted in greater milk protein concentration ($P = 0.001$). Increased grain intake increased milk protein content in the review of Firkins et al. (2001). Although starch digestibility is not improved by dietary starch concentration, a greater amount of starch (kg/d) is digested in the rumen as starch intake increases (Nocek and Tamminga, 1991), resulting in greater propionate concentrations and increased microbial protein production when RDP is adequate (Firkins et al., 2006). Alternatively, greater starch intake leads to greater amounts of starch (kg/d) escaping the rumen (Nocek and Tamminga, 1991) and thereby increases milk protein concentration through changes in arterial insulin concentration (Rius et al., 2010). The MUN concentration was reduced ($P = 0.001$) by increasing dietary starch concentrations, which is in agreement with recent studies from our laboratory (Gencoglu et al., 2010; Ferraretto et al., 2011, 2012). Intraruminal dosing with starch decreased ruminal ammonia concentration and MUN more than dosing with NDF or a mixture of carbohydrates (Hristov et al., 2005), suggesting better ruminal nitrogen utilization (NRC, 2001) as starch in the diet increases.

Effects of dietary FNDF concentration on nutrient digestibilities and lactation performance adjusted for the random effect of trial are presented in Table 9. Fiber digestibility was unaffected by FNDF concentration in the diet either ruminally or total tract ($P = 0.11$ and $P = 0.61$, respectively; data not provided in table). Similar results were reported by Zebeli et al. (2006). Starch digestibility decreased 0.17 percentage units per percentage unit increase in dietary FNDF total tract ($P = 0.05$), but not ruminally ($P = 0.12$; data not provided in table). Likewise, total-tract digestibilities of dietary DM and OM decreased ($P = 0.05$ and 0.04, respectively) as concentration of dietary FNDF increased.

The DMI was reduced ($P = 0.05$) by 0.27 kg/d for each percentage unit increase in dietary FNDF content. The negative effect of FNDF content on DMI was also reported in previous reviews (Allen, 2000; Firkins et al., 2001; Zebeli et al., 2006). Increased dietary FNDF content may reduce DMI through rumen fill limitations (Mertens, 1987). Surprisingly, milk yield was unaffected ($P = 0.36$; data not provided in table) by dietary FNDF concentration in the present study. Firkins et al. (2001) and Zebeli et al. (2006) observed reduced milk yield with greater dietary FNDF concentration, presumably in relation to greater ruminal propionate concentrations coupled with increased microbial protein production for reduced-FNDF diets (Jenkins and McGuire, 2006). Actual-milk feed conversion (milk/DMI) did not differ ($P = 0.99$; data not provided in table) with increased FNDF concentration. Milk fat concentration tended ($P = 0.06$) to be 0.01 percentage units greater per percentage unit increase in dietary FNDF concentration.

Similar responses were reported in reviews by Firkins et al. (2001) and Zebeli et al. (2006). Increased milk fat content for cows fed higher concentrations of FNDF was likely related to greater ruminal acetate:propionate ratio and ruminal pH (Firkins et al., 2001; Zebeli et al., 2006). A positive relationship between ruminal acetate:propionate ratio or pH and milk fat content was reported by Erdman (1988) and Allen (1997). Despite the increase in milk fat concentration, the FCM yield and feed conversion were unaffected ($P = 0.69$ and 0.47, respectively; data not provided in table) by treatment. Conversely, milk protein was decreased ($P = 0.03$) by 0.01 percentage units for each percentage unit increase in dietary FNDF concentration. Lower milk protein content was likely related to deficit in energy supply caused by either reduced DMI or lower starch digestibility, which thereby reduced propionate concentrations and microbial protein production (Firkins et

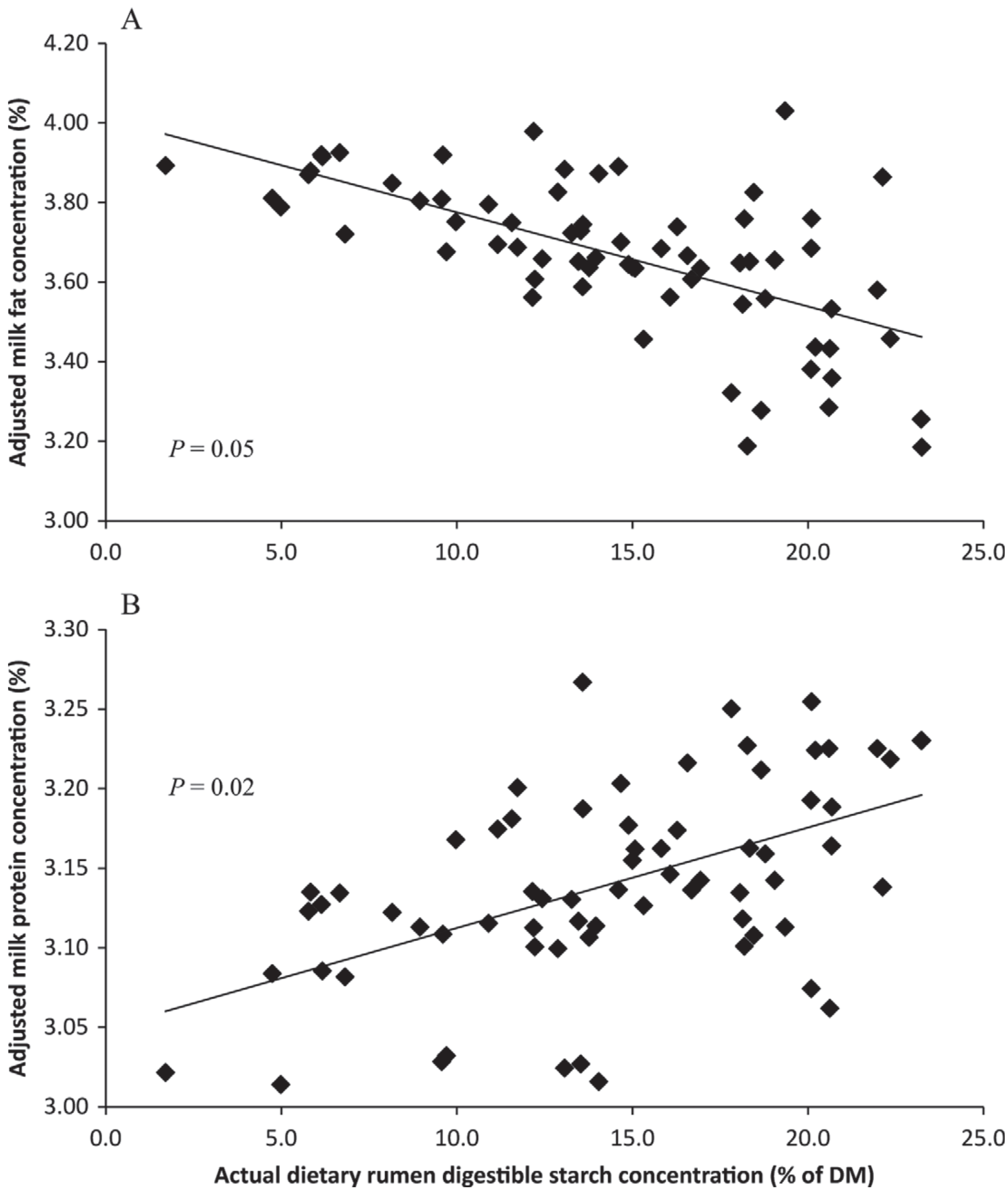

Figure 2. Effect of rumen digestible starch concentration of the diet on milk fat and protein concentrations adjusted for the random effect of trial. Milk fat data (panel A) best-fit linear regression: y = 4.016 + (−0.024 × rumen digestible starch concentration) + (0.002 ± 0.150); n = 69, root mean square error (RMSE) = 0.151. Milk protein data (panel B) best-fit linear regression: y = 3.056 + (0.025 × rumen digestible starch concentration) + (0.001 ± 0.052); n = 69, RMSE = 0.072.

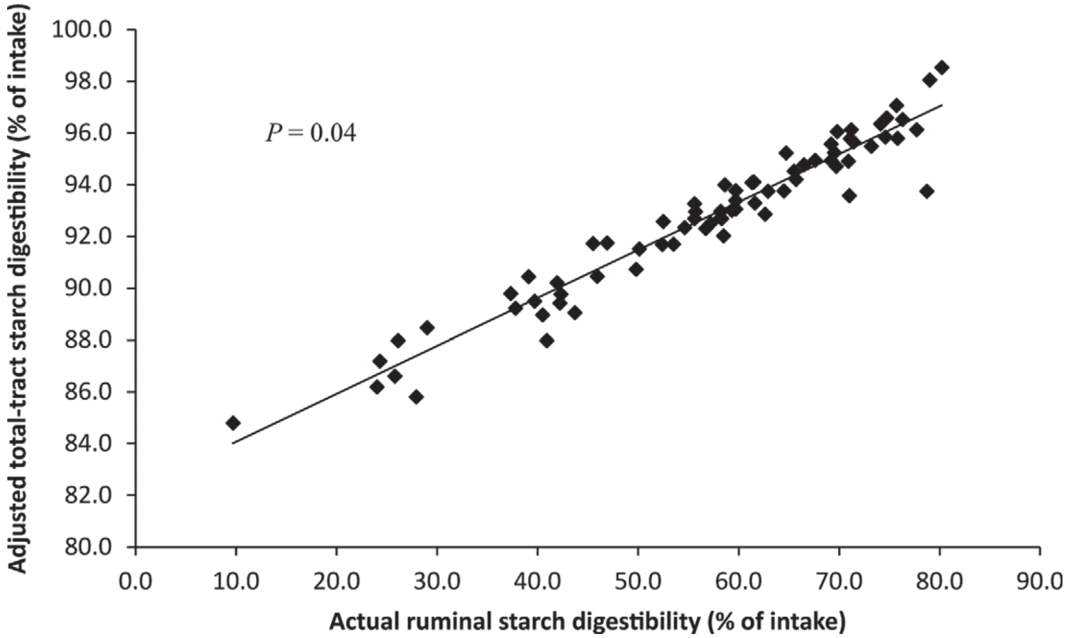

Figure 3. Relationship between ruminal and total-tract starch digestibility adjusted for the random effect of trial. Prediction equation: y = 82.224 + (0.185 × ruminal) + (−0.002 ± 0.772); n = 72, root mean square error (RMSE) = 0.78.

al., 2006; Jenkins and McGuire, 2006). Firkins et al. (2001) reported decreased milk protein content with increased dietary FNDF. The MUN concentration did not differ ($P = 0.46$; data not provided in table).

Effects of DMI (kg/d) on nutrient digestibilities and lactation performance adjusted for the random effect of trial are presented in Table 10. Greater DMI tended to decrease ($P = 0.08$) OMD. A similar response was reported by Huhtanen et al. (2009) and explained by increased passage rates. Ruminal and total-tract NDF digestibility were unaffected ($P = 0.91$ and 0.72, respectively; data not provided in table) by DMI. The literature is equivocal with reports of similar RNDFD (Firkins et al., 2001) or decreased TTNDFD (Huhtanen

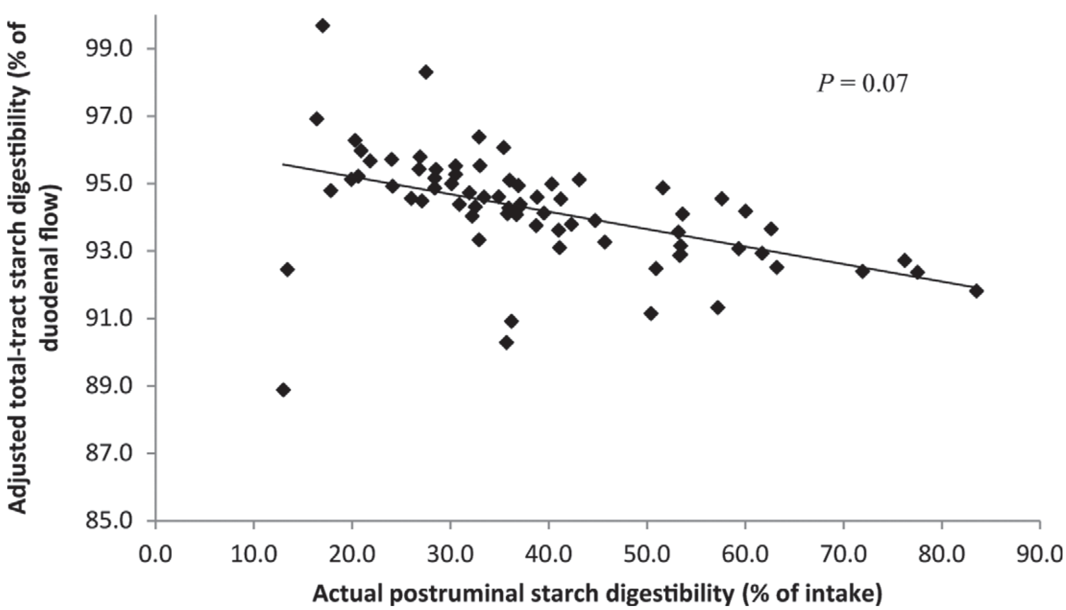

Figure 4. Relationship between postruminal and total-tract starch digestibility adjusted for the random effect of trial. Prediction equation: y = 96.4026 + (−1.313 × postruminal percentage intake) + (−0.006 ± 1.477); n = 72, root mean square error (RMSE) = 1.49.

et al., 2009). Increasing DMI by1 kg/d resulted in reduced ruminal (1.4 percentage units; $P = 0.03$) and total-tract (0.2 percentage units; $P = 0.05$) starch digestibilities. Firkins et al. (2001) observed a 1.2 percentage unit decrease in RSD per kilogram of change in DMI. Decreased starch digestibility may be related to increased passage rates and, thus, reduced time for starch hydrolysis (Owens et al., 1986).

Milk yield was increased ($P = 0.001$) 0.9 kg/d when DMI increased by 1 kg/d. A similar response was observed by Hristov et al. (2004). Greater milk production with increased DMI is likely related to greater energy intake (Jenkins and McGuire, 2006). Likewise, FCM yield increased ($P = 0.001$) with greater DMI, although milk fat concentrations were similar ($P = 0.55$; data not provided in table). A negative effect of DMI on milk fat concentration was reported by Firkins et al. (2001). Milk protein concentrations were also unaffected ($P = 0.26$; data not provided in table) by DMI. Hristov et al. (2004) observed an increase in milk protein yield with greater DMI.

Presented in Figure 2 are the effects of dietary rumen digestible starch concentration on milk component concentrations. Milk fat content was reduced ($P = 0.05$) by 0.02 percentage units for each percentage unit decrease in rumen-digestible starch concentration. Reduced milk fat content for cows fed higher concentrations of rumen-digestible starch was likely related to lower ruminal acetate:propionate ratio and ruminal pH (Firkins et al., 2001). Milk fat content is positively related to ruminal acetate:propionate ratio and pH (Erdman, 1988; Allen, 1997). Conversely, each percentage unit increase in rumen-digestible starch concentration resulted in a 0.02 percentage unit increase ($P = 0.02$) in milk protein content. Increased dietary rumen-digestible starch increases propionate concentrations and microbial protein production when RDP is adequate (Firkins et al., 2006). Alternatively, greater amounts of starch being digested in the rumen reduces starch flow to the duodenum (kg/d; Nocek and Tamminga, 1991) and optimizes starch hydrolysis in the small intestine (Owens et al., 1986; Theurer et al., 1999), thereby possibly increasing milk protein concentration through changes in arterial insulin concentration (Rius et al., 2010). Despite the effects on milk fat and protein concentration, dietary rumen-digestible starch concentration did not affect ($P > 0.10$) other lactation performance parameters (data not provided in table or figure).

Relationships between ruminal, postruminal, and total-tract starch digestibilities are presented in Figures 3 to 6. The RSD and TTSD were related positively ($P = 0.04$; Figure 3), with an increase of 0.19 percentage units total tract per percentage unit increase ruminally. These results are in agreement with previous reviews (Owens et al., 1986; Nocek and Tamminga 1991; Theurer et al., 1999). Conversely, postruminal starch digestibility measured as percentage of intake and TTSD tended ($P = 0.07$; Figure 4) to be inversely related

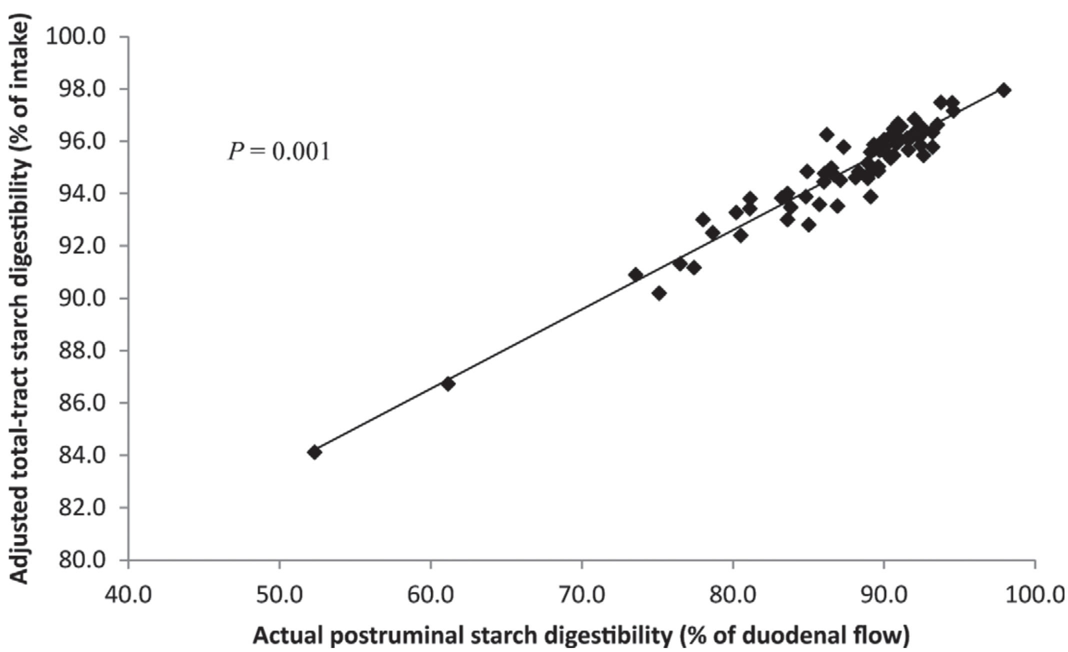

Figure 5. Relationship between postruminal starch digestibility as a percentage of duodenal flow and total-tract starch digestibility adjusted for the random effect of trial. Prediction equation: y = 68.287 + (0.304 × postruminal percentage of flow) + (0.013 ± 0.574); n = 72, root mean square error (RMSE) = 0.58.

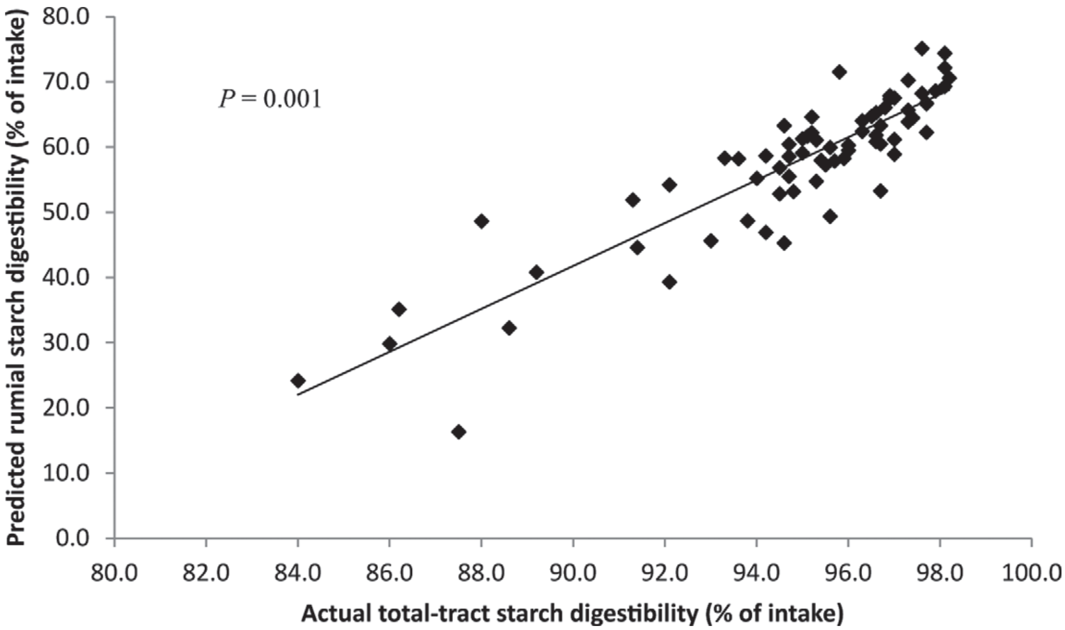

Figure 6. Relationship between total-tract and ruminal starch digestibility adjusted for the random effect of trial. Prediction equation: y = −260.68 + (3.357 × total tract) + (0.027 ± 5.195); n = 72, root mean square error (RMSE) = 5.23.

to a decrease of 1.3 percentage units total tract per percentage unit increase postruminally, suggesting that postruminal starch digestion does not fully compensate for starch that escapes ruminal degradation. Postruminal starch digestibility measured as percentage of flow to the duodenum (**PSDF**) was positively related to TTSD (P = 0.001; Figure 5). Reduced RSD has been related to reduced PSDF (Nocek and Tamminga, 1991; Theurer et al., 1999; Huntington et al., 2006) and may explain the positive relationship between RSD and TTSD, although our observed relationship between RSD or postruminal starch digestibility measured as percentage of intake and PSDF ($P > 0.10$) does not support this premise. Reduced PSDF due to increased starch flow to the duodenum (kg/d) may be related to the higher passage rate through the intestines and, thus, insufficient time for complete starch hydrolysis (Owens et al., 1986) or insufficient pancreatic amylase activity (Huntington, 1997). Alternatively, factors that reduce RSD (i.e., grain particle size or endosperm type) may also reduce PSDF (Owens et al., 1986). Presented in Figure 6 is the relationship between TTSD and RSD, with an increase of 3.4 percentage units ruminally per percentage unit increase total tract.

CONCLUSIONS

Starch digestibility was improved for dairy cows fed diets containing corn grain that was ensiled or steam processed, or dry corn with reduced MPS. However, increased starch digestibility coincided with reduced milk fat content. Increased dietary starch concentration increased milk yield and protein content, and decreased fiber digestibility and milk fat and urea-nitrogen concentrations. Feeding diets that contained high starch also decreased FCM feed conversion. Dairy cows fed diets that contained high forage NDF had reduced DMI and milk protein concentration, but greater milk fat content. Comparisons among sites of starch digestion indicate that increased RSD results in increased starch digestibility in the total tract, and that postruminal starch digestion does not fully compensate for starch that escapes ruminal degradation.

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APPENDIX

Table A1. Summary of the 102 references used for the meta-analysis

Article	n[1]	Cereal type[2]	Grain MPS[3]	Forage NDF[4]	Sites of starch digestion[5]
Agle et al. (2010a)	6	CRN	—	*	—
Agle et al. (2010b)	6	CRN	—	*	—
Akay and Jackson (2001)	6	CRN	—	*	—
Avila et al. (2000)	4	CRN	—	*	*
Bal et al. (2000a)	24/24	CRN	—	*	—
Bal et al. (2000b)	24	CRN	—	*	—
Beckman and Weiss (2005)	6	CRN	—	*	—
Benchaar et al. (2006)	4	CRN	—	—	—
Benchaar et al. (2007)	4	CRN	—	—	—
Benefield et al. (2006)	20	CRN	—	*	—
Chow et al. (2008)	30	BAR	—	—	—
Cooke and Bernard (2005)	8	CRN	—	*	—
Dann et al. (2006)	40	CRN	—	—	—
Dann et al. (2008)	12	CRN	—	*	—
Dhiman et al. (2000)	21	CRN	—	*	—
Dhiman et al. (2002)	20	CRN	*	*	—
Eastridge et al. (2011)	5	CRN	*	—	—
Ebling and Kung (2004)	8	CRN	—	—	—
Eun and Beauchemin (2005)	8	BAR	—	—	—
Eun et al. (2004)	12	CRN	—	*	—
Ferraretto et al. (2012)	8	CRN	*	*	—
Foley et al. (2006)	6	BAR, CRN	—	*	—
Gabel et al. (2003)	8	CRN	*	—	—
Gencoglu et al. (2010)	12	CRN	*	*	—
Gozho and Mutsvangwa (2008)	8	BAR, CRN, WHT	—	—	—
Gozho et al. (2008)	4	BAR	—	—	—
Greenfield et al. (2001)	5	CRN	—	*	*
Gressley and Armentano (2005)	3/6	CRN	—	*	—
Gressley and Armentano (2007)	8	CRN	—	*	—
Harvatine and Allen (2006a,b,c)	8	CRN	—	*	*
Hristov et al. (2009)	6	CRN	—	*	—
Hristov et al. (2011)	6	CRN	—	*	—
Ipharraguerre and Clark (2005); Ipharraguerre et al. (2005b)	6	CRN	—	*	*
Ipharraguerre et al. (2005a)	4	CRN	—	*	*
Ivan et al. (2005)	40/40	CRN	—	*	—
Johnson et al. (2002)	6/6	CRN	—	*	*
Johnson et al. (2003)	6/4	CRN	—	*	*
Klingerman et al. (2009)	28	CRN	—	*	—
Krause and Combs (2003)	8	CRN	*	*	—
Krause et al. (2002)	8	CRN	*	*	—
Krause et al. (2003)	12	CRN	*	*	—
Krizsan et al. (2007)	30	CRN	*	*	—
Larsen et al. (2009)	3	BAR, CRN, WHT	—	—	—
Lechartier and Peyraud (2010)	6	CRN, WHT	—	*	—
Lopes et al. (2009)	6	CRN	*	*	—
Martin et al. (2008)	8	WHT	—	—	—
Mathew et al. (2011)	6	CRN	—	—	—
Maulfair et al. (2011)	4	CRN	—	*	—
Nennich et al. (2003)	20	CRN	—	*	—
Neylon and Kung (2003)	10	CRN	—	*	—
Oba and Allen (2000a,b)	8	CRN	—	—	—
Oba and Allen (2003a)	5	CRN	—	*	—
Oba and Allen (2003b,c)	8	CRN	*	*	*
Oba et al. (2010)	12	CRN	—	*	—
Oliver et al. (2004)	16	CRN	—	*	—
Ouellet et al. (2003)	8	CRN	—	*	—
Penner and Oba (2009)	25	CRN	—	—	—
Penner et al. (2009)	8	CRN	—	—	—
Pereira and Armentano (2000)	12	CRN	—	*	—
Prestløkken and Harstad (2001)	3	BAR	—	—	—
Qiu et al. (2003)	4	CRN	—	—	*

Continued

Table A1 (Continued). Summary of the 102 references used for the meta-analysis

Article	n[1]	Cereal type[2]	Grain MPS[3]	Forage NDF[4]	Sites of starch digestion[5]
Raeth-Knight et al. (2007)	19	CRN	—	—	—
Reis et al. (2001)	9/9	CRN	*	*	—
Rémond et al. (2004)	6/4	CRN	*	—	*
Ruppert et al. (2003)	6	CRN	—	*	—
San Emeterio et al. (2000)	8	CRN	*	*	—
Schwab et al. (2002)	24	CRN	—	*	—
Schwab et al. (2006)	8	CRN	—	*	—
Silveira et al. (2007a)	31	BAR, CRN	—	*	—
Silveira et al. (2007b)	4	BAR	—	—	—
Sniffen et al. (2006)	20	CRN	—	—	—
Tager and Krause (2011)	8	CRN	—	*	—
Taylor and Allen (2005a,b)	8	CRN	*	*	*
Tothi et al. (2003)	4	BAR, CRN	—	*	*
Uchida et al. (2001)	22	CRN	*	—	—
Ueda et al. (2003)	4	WHT	—	—	—
Vander Pol et al. (2008)	12	CRN	—	*	—
Vander Pol et al. (2009)	6	CRN	—	*	—
Voelker and Allen (2003a,b)	8	CRN	—	*	*
Voelker et al. (2002)	32	CRN	—	*	—
Voelker Linton and Allen (2007)	14	CRN	—	*	—
Weiss et al. (2009)	18	CRN	—	*	—
Weiss et al. (2011a)	8	CRN	—	—	—
Weiss et al. (2011b)	8	CRN	*	*	—
Weiss and Wyatt (2002)	8	CRN	—	—	—
Weiss and Wyatt (2004)	5	CRN	—	—	—
Weiss and Wyatt (2006)	8	CRN	—	—	—
Yang and Beauchemin (2005)	6	BAR	—	—	—
Yang and Beauchemin (2006a)	6	BAR	—	—	—
Yang and Beauchemin (2006b)	6	CRN	—	*	—
Yang and Beauchemin (2007)	12	BAR	—	—	—
Yang et al. (2000)	4	BAR	—	—	—
Yang et al. (2002)	4	BAR	—	—	—
Zhang et al. (2010)	6	BAR	—	—	—
Zhong et al. (2008)	12	CRN	*	—	—

[1]Number of experimental units used in trial.

[2]BAR = barley; CRN = corn; WHT = wheat.

[3]Grain mean particle size (MPS) reported (*) or not reported (—).

[4]Forage NDF reported or calculated (*); not reported or wheat- and barley-based diets (—).

[5]Ruminal digestibility reported (*); not measured or wheat- and barley-based diets (—).