Soyhulls as an Alternative Feed for Lactating Dairy Cows: A Review

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ABSTRACT

Dairy producers use soyhulls, a byproduct of soybean processing, to replace either grain or forage in diets of lactating dairy cows. In view of the nutritional and economical value of soyhulls it is anticipated that this practice will continue to increase in popularity among nutritionists and producers of ruminant animals. This paper reviews information regarding the nutritional value of soyhulls and the effects of feeding this alternative feed on ruminal fermentation, nutrient digestion and utilization, and performance of dairy cows. Soyhulls can replace corn grain to supply about 30% of the dry matter (DM) in high-grain diets without negatively affecting either the fermentation or digestion of nutrients in the gastrointestinal tract or the performance of dairy cows. Additionally, data suggest that soyhulls might successfully replace forage to supply $\leq 25\%$ of the DM in diets of dairy cows when the supply of effective fiber, which includes a chemical and a physical component, remains adequate after including the hulls. However, caution should be exercised when data from different studies are extrapolated to practical situations because the response to feeding soyhulls appears to be largely affected by the type of carbohydrate being replaced by soyhulls; the amount, type, and physical form of the dietary forage; and the incidence of either negative or positive associative effects before and after the addition of soyhulls to the original diet. Unfortunately, the paucity of data from experiments in which soyhulls constituted more than 25 to 30% of the dietary DM restricts the ability to identify the maximum amount of soyhulls that can be used in diets of dairy cows. Information from studies in which ≥ 25 to 30% of dietary DM supplied as either cereal grains or forages are replaced with soyhulls is needed to better understand and predict the production of dairy cows fed diets containing the hulls. This knowledge is essential for maximizing the use of soyhulls in diets for dairy cows.

(Key words: soyhulls for dairy cows, nutrient passage to duodenum, rumen fermentation and nutrient digestion)

Abbreviation key: NFC = nonfibrous carbohydrates, SB = soybeans, SBM = defatted-high-protein soybean meal, SH = soyhulls.

INTRODUCTION

The American Soybean Association (2001) describes the current processing or crushing of soybeans (SB) as a biphasic operation that begins with the preparation of the raw SB and culminates with the extraction of oil and many other soy-products such as lecithin and defatted-high-protein meal (SBM). After being graded and cleaned, whole-raw SB are dried to about 10% moisture, cracked, and separated into meat and hulls (Rhee, 2000). The primary goal of this initial step is to facilitate the subsequent flaking by removing the seed coats (i.e., hulls) and cracking the whole SB into smaller pieces. After being removed, the whole hulls, which have very low bulk density (170 kg/m^3 [Anderson et al., 1988]), are normally ground and/or pelleted to reduce transportation costs. Ground or pelleted hulls, known on the market as soybean hulls or soyhulls (SH), consist largely of the outer covering of the SB (AAFCO, 1996). For this reason, well-cleaned SH are mainly composed of fiber that has little value either for edible human food or for industrial uses. In contrast, these physico-chemical characteristics are a factor, among others, that make SH a suitable feed for dairy cattle.

Over the last five years, total SB production in the US has increased at an average rate of about 5.6 million tons per year (USDA, 2001b). This remarkable rate of growth resulted from the combined increase in the planted area with SB ($\sim 19\%$) and in the yield of SB per unit of area ($\sim 8\%$ [USDA, 2001b]). The USDA (2001a) projects that both variables will continue to increase during the next 10 years, raising total SB production in the US to about 87 million tons by 2010. This increase in SB supply is expected to enhance domestic crushing by about 11.5 million tons over the same period (USDA, 2001a). Based on these projections, and assuming a yield of SH of 5% of the original raw SB weight (Blasi et al., 2000), it is estimated that production of SH will increase by about 27% (i.e., 0.5 million tons) by 2010.

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Consequently, one could anticipate that the increasing availability of SH in the US will promote their utilization in diets for ruminant animals.

Feed costs account for 35 to 50% of the total costs to produce milk (Hutjens, 2001). Thus, dairy producers attempt to minimize the costs of feeding their herds, particularly when milk prices are low, in order to maximize the efficiency of production. In several areas of the US, SH are readily available and usually at competitive prices; hence, feeding this byproduct to dairy cows may represent an excellent opportunity to reduce feed costs.

In addition to the potential of providing an economical alternative, replacing cereal grains with SH in diets for dairy cows may contribute to elevated intakes of energy while preventing a disruption of rumen functionality. Alternatively, SH can be successfully used as a source of fiber in rations for dairy cattle when forages either are of poor quality or are in short supply.

In view of the aforementioned reasons and others, it appears that feeding SH to dairy cows, and to other ruminants, is a practice that will continue to increase in popularity among nutritionists and producers of ruminant animals.

The objectives of this paper are to review the current knowledge regarding the potential nutritional value of SH for lactating dairy cattle and the effects of replacing cereal grains or forages with SH on ruminal fermentation, nutrient digestion and utilization, and production by dairy cows. This review will also point out areas where additional research is needed to enhance SH utilization by lactating dairy cows.

NUTRITIONAL VALUE OF SH

Chemical Composition

In part, the nutritional value of SH for ruminants is determined by the chemical nature of the hulls. As for many other byproduct feeds, the chemical composition of SH usually varies widely among processor plants (Belyea et al., 1989; Arosemena et al., 1995; DePeters et al., 1997). In some cases, part of this variation can be explained by the misclassification of SB mill run and SB mill feed as SH (Titgemeyer, 2000). Whereas SB mill run and SB mill feed contain a portion of meat and hulls, SH are composed mainly of pericarp (i.e., seed coat). Other factors presumably associated with the variable chemical composition of SH include the following: differences between and within processing methods (DePeters et al., 1997), lack of rigorous quality-control programs during the production and handling of byproduct feeds (Belyea et al., 1989), genetic differences among plant materials (Westgate et al., 2000), and differences in cultural (e.g., planting date and nitrogen fertilization) and environmental (e.g., temperature and

Table 1. Chemical composition of soyhulls.¹

Item	Minimum	Maximum	Mean	SD	n
	(%)				
CP	9.4	19.2	11.8	2.3	27
ADF	39.6	52.8	47.7	3.9	27
NDF	53.4	73.7	65.6	5.0	27
Cellulose	29.0	51.2	43.0	8.4	5
Hemicellulose	15.1	19.7	17.8	2.7	3
Uronic acids ²	11.1	14.8	13.0	2.6	2
ADL ³	1.4	3.9	2.1	0.8	13
NSC	5.3	12.8	7.9	3.4	4
Starch	0.0	9.4	2.9	3.2	8
EE	0.8	4.4	2.7	1.6	9

¹Data from: Quicke et al., 1959; Nocek and Hall, 1984; Hsu et al., 1987; Anderson et al., 1988; Garleb et al., 1988; Belyea et al., 1989; Nakamura and Owen, 1989; Cunningham et al., 1993; Shain et al., 1993; Faulkner et al., 1994; Mansfield and Stern, 1994; Arosemena et al., 1995; Bhatti and Firkins, 1995; Piwonka and Firkins, 1996; Stone, 1996; DePeters et al., 1997; Garcés-Yepéz et al., 1997; Batajoo and Shaver, 1998; Miller and Hoover, 1998; Mowrey et al., 1998; Bach et al., 1999; Mulligan et al., 1999; van Laar et al., 1999; Shiver et al., 2000; Miron et al., 2001; Ipharraguerre et al., 2002a, 2002b.

²Determined by colorimetric assay (Blumenkrantz and Asboe-Hansen, 1973).

³Acid detergent lignin.

water supply) conditions during SB growth (Westgate et al., 2000).

The chemical composition of SH reported in several research publications is summarized in Table 1. Miron et al. (2001) found that carbohydrates, predominantly polymers of glucose, make up approximately 80% of the DM in SH and that most of these carbohydrates (~75%) derive from polysaccharides recovered in the NDF fraction. This is because the hulls, whose primary function is to protect the endosperm of the SB, consist mainly of thick cell walls (~62% of SH DM [van Laar et al., 1999]). According to the NRC (2001), SH contain 60.3% NDF and 44.6% ADF on a DM basis. Nevertheless, the fiber content of SH has been shown to be variable (Table 1), and this variation seems to be directly related to the meat content of the products classified as SH (Titgemeyer, 2000). For instance, Anderson et al. (1988) found that well-cleaned SH contained 73.7% NDF and 50.8% ADF, whereas DePeters et al. (1997) reported that SH, which apparently contained some meat, had 57.5 and 45.4% NDF and ADF, respectively. The fiber fraction of SH, which contains relatively large quantities of both cellulose (~43% of SH DM) and hemicellulose (~18% of SH DM), is poorly lignified (Table 1). The lignin content of SH ranged from 1.4% (Mulligan et al., 1999) to 3.9% (Anderson et al., 1988) when measured as acid detergent lignin and averaged 4.3% (Hsu et al., 1987) when measured as permanganate lignin. In addition, SH have low concentrations of ferulic and *p*-cumaric acids, which are the primary phenolic mono-

mers involved in the cross-linking between lignin and hemicelluloses (Garleb et al., 1988).

There are few studies in which the NSC or starch content of SH has been measured (Table 1). Although very low or even negligible amounts of these carbohydrates might be expected in SH, the starch content of SH has been shown to range from 0 (Hsu et al., 1987) to 9.4% (Batajoo and Shaver, 1998) and averaged 2.9% (Table 1). DePeters et al. (1997) calculated an average content of about 20% nonfibrous carbohydrates (NFC) for three different batches of SH, which increased to about 24% when corrections for fiber-bound protein were made. When determined by an enzymatic method, however, the NSC content of SH seems to be considerably lower (~8%; Table 1). This apparent discrepancy is largely caused by the considerable concentration of uronic acids or pectin substances in the cell walls of SH (Table 1), which are only accounted for by the NFC fraction. In fact, pectin represents the largest proportion (62%) of NFC in SH, whereas starch (19%) and simple sugars (19%) are only minor components (NRC, 2001).

The CP content of SH averaged 11.8% (Table 1), which is within the range ($13.9\% \pm 4.6$) reported by the NRC (2001). In studies where SH were thoroughly cleaned, the CP percentage ranged from 9.4 (Anderson et al., 1988) to 9.6 (Shiver et al., 2000). On the other hand, Batajoo and Shaver (1998) found that SH can contain up to 19.2% CP, but they suggested that some meat must have been present in the hulls because of their high concentration of starch (9.4%).

Similar to SBM, SH are a rich source of Lys (0.71 to 0.72% of DM), but not of Met and Cys, which are even more deficient in SH (0.30 to 0.33% of DM [Cunningham et al., 1993; Degussa, 1996]). In comparison to protein from SBM, CP from SH is lower in Arg (~35%), Ile (~27%), Leu (~25%), Val (~16%), Phe (~28%), Thr (~16%), and Trp (~18%), but higher in Tyr (~30% [Degussa, 1996; Rackis et al., 1961]). On average, protein from SH contains about 3.5% less nonessential AA than SBM protein, but protein from SH has an uncommonly high Gly content, which is about 48% higher than that of the SBM fractions (Rackis et al., 1961; Degussa, 1996).

The fat content of SH, measured as ether extract, has been shown to be highly variable (Table 1). There is not a clear relationship between the content of fat in SH and either their CP or NDF concentration (Titgemeyer, 2000). Belyea et al. (1989), for instance, observed that SH from three different sources averaged 4.3% ether extract, 72.5% NDF, and 11.8% CP, whereas DePeters et al. (1997) reported similar ether extract values (4.4%) in SH with significantly lower NDF (57.5%) and higher CP (13%) concentrations.

Ruminal Digestion Kinetics

The nutritional value of SH is affected by the rate at which they are digested in the rumen and by the rate at which they pass from the rumen to the lower gastrointestinal tract (Firkins, 1997; Grant, 1997; Titgemeyer, 2000). Data from in situ and in vitro experiments have shown that ruminal microorganisms are capable of extensively fermenting SH at high rates (Table 2). For example, in seven in situ studies (Table 2), the NDF fraction of SH was fermented at an average rate of about 5.6%/h, and, in four studies, total NDF disappearance averaged about 90% after 96 h of incubation. Apparently, the low content of lignin and phenolic monomers in SH (Garleb et al., 1988), as well as the relatively large thickness and particle size of SH cell walls (van Laar et al., 1999), allow the rapid and extensive fermentation of the fiber fraction. However, when diets containing SH and concentrates are used, the in vitro and in situ digestion kinetics parameters (i.e., lag time, digestion rate, and extent) of SH do not remain constant (Firkins, 1997). Piwonka and Firkins (1996) found that the in vitro rate of digestion of SH was reduced when 2 ml of a glucose solution (0.0721 g/ml) were added to the incubation medium that contained 30 ml of inoculum and 0.5 g of SH. Sarwar et al. (1992) reported that, after 96 h of in situ incubation, the extent of digestion of NDF in SH decreased about 23% when the percentage of concentrate (50% of ground corn) in the diet increased from 61 to 73%. In addition, for a given source and amount of dietary concentrate, the digestion kinetics can vary markedly among sources of SH because of differences in their chemical or physical characteristics or both.

Although fermentation of SH by ruminal microbes is relatively rapid and almost complete, in vivo digestion of the SH is much lower than fermentation in vitro and in situ (Quicke et al., 1959; Johnson et al., 1962; Hintz et al., 1964; Hsu et al., 1987; Anderson et al., 1988). These differences were even greater when SH were fed alone or constituted the major ingredient of the diet. For example, Quicke et al. (1959) measured the in vitro digestibility of cellulose and crude fiber in SH after 48 h as 96 and 97%, respectively. In contrast, when SH were fed ad libitum as the sole feed to sheep, in vivo digestibility coefficients for cellulose and crude fiber were 54 and 57%, respectively. In another early study (Johnson et al., 1959), the in vitro digestibility of cellulose present in feces from sheep fed soybran flakes (i.e., steam-treated SH flaked by rolling) was considerably higher than the digestibility of fecal cellulose of sheep fed other roughages (60 to 80% vs. 0 to 20%). These findings suggest that the rate at which SH pass from the rumen to the lower tract may be too rapid to max-

Table 2. Characterization of digestion of soyhulls in situ and in vitro.

Study	Diet	Digestion parameters		
		Extent, %/time, h	Rate, h ⁻¹	Lag time, h
In situ DM disappearance				
Nocek and Hall (1984)	25% Hay crop silage,25% corn silage, 50% concentrate	50.6/24	0.025	NR ¹
Hsu et al. (1987)	Alfalfa hay	104.0/36	0.077	NR
Kerley et al. (1992)	39 to 93% brome hay, 0 to 58% soyhulls	95.5/96	0.044	NR
DePeters et al. (1997)	70% forage, 30% concentrate	87.2/72	0.047	NR
Batajoo and Shaver (1998)	55% alfalfa silage, 45% concentrate	97.7/72 ²	0.039	NR
Mulligan et al. (1999)	15% forage, 85% concentrate	100.0/72	0.042	NR
In situ NDF disappearance				
Nocek and Hall (1984)	25% hay crop silage, 25% corn silage, 50% concentrate	53.5/24	0.030	NR
Highfill et al. (1987)	73% fescue hay, 27% soyhulls	95.6/96	NR	NR
Anderson et al. (1988)	Alfalfa hay	95.0/96	0.074	NR
Sarwar et al. (1991)	27% forage, 73% concentrate	65.9/96	0.036	NR
	39% forage, 61% concentrate	88.7/96	0.033	NR
Pantoja et al. (1994)	40% forage, 60% concentrate	95.7/96	0.046	4.9
	40% forage, 55% concentrate, 5% fat	95.8/96	0.054	6.0
DePeters et al. (1997)	70% forage, 30% concentrate	95.8/72	0.038	NR
Abel-Caines et al. (1998)	50% forage, 48% concentrate, 2% fat	95.3/72	0.092	8.6
	40% forage, 60% concentrate	95.8/72	0.103	8.3
In vitro NDF disappearance				
Anderson et al. (1988)	Alfalfa hay	93.0/96	0.060	NR
Belyea et al. (1989)	Alfalfa hay	87.0/36	0.113	NR
Bhatti and Firkins (1995)	Grass and legume hay	82.8/96	0.033	5.7
Piwonka and Firkins (1996)	Alfalfa hay, 1 kg corn grain	94.6/96	0.031	11.3
Trater et al. (2001)	40% forage, 30% sorghum grain, 30% corn grain	80.7/48	NR	NR

¹Data not reported or determined.²Predicted by nonlinear regression.

imize fiber digestion by ruminal microbes. Nakamura and Owen (1989) determined the fractional rate of passage of SH in lactating dairy cows consuming diets in which SH replaced corn to supply either 25 or 48% of the dietary DM. They reported that the rate of passage of SH was 8% faster when SH constituted 48% of the dietary DM; moreover, the rate at which SH exited the rumen for diets that contained 25 and 48% SH (0.093/h and 0.10/h, respectively) almost doubled that of the forage (0.054/h and 0.055/h). Even though differences among treatments were not significant, Nakamura and Owen (1989) suggested that an 8% increase in the passage rate could be enough to account for the lower digestibility of NDF and ADF observed for the diet that contained 48% SH.

The relatively rapid passage rate of SH can be explained by their small particle size and high specific gravity when hydrated (Titgemeyer, 2000). Based on the small particle size of most nonforage fiber sources, Grant (1997) postulated that the functional specific gravity of those feeds, and not their particle size, is the most likely determinant of their ruminal rate of passage. Data from experiments with cattle suggest that particles with specific gravity ranging from 1.2 to 1.5 have the highest rate of passage (Murphy et al., 1989). For SH, Bhatti and Firkins (1995) reported that

their functional specific gravity remained between 1.48 and 1.35 during 27 h of in vitro incubation. Weidner and Grant (1994a) found that the initial specific gravity of 60% of SH particles ranged from 1.2 to 1.4 and, after 3 h of ruminal incubation, the specific gravity of most of them increased above 1.4.

Nevertheless, rate of passage reflects other factors that might affect intake and rumen characteristics, such as restricted feed intake and diet composition (Offer and Dixon, 2000; Poppi et al., 2000). Woods et al. (1998) observed an average decline of 14% in the digestibility of OM from SH as the feeding of a mixture of 85% SH and 15% hay (DM basis) increased from maintenance to two times maintenance for cattle and sheep. Mulligan et al. (1999) hypothesized that the depression in digestibility was the result of an increase in the ruminal passage rate of SH as DMI was doubled. To test this hypothesis, fistulated steers were fed a diet that contained 83% SH, 15% hay, and 2% SBM (DM basis) at two DMI, maintenance and twice maintenance. Digestion of SH was depressed only 8% at the highest DMI, and the rumen outflow rate of SH was increased by about 12%. As expected, when DMI increased, the passage rate of SH increased; however, the magnitude of the increased passage rate, as well as the resulting effects on ruminal fiber digestibility, are

apparently dependent upon some other factors. For example, lactating dairy cows were fed three diets, a control diet in which alfalfa silage and corn silage (1:1, wt/wt, DM basis) supplied 60% of the DMI or diets in which a portion of the DM from the silage mixture was replaced with 25% SH or with 25% SH plus 20% long alfalfa hay (Weidner and Grant, 1994a). Although not significant but biologically important, the rate of passage of SH decreased by 16% when SH and long hay replaced part of the silage mixture, as opposed to when only SH were substituted for part of the silage mixture. Inclusion of long alfalfa hay in the diet that contained 25% SH increased the ruminal mat consistency, which in turn may have retained potentially escapable particles of SH through filtration and mechanical entanglement (Weidner and Grant, 1994a). In contrast, Trater et al. (2001) reported that replacing SH in SH-based diets (~96% of dietary DM) with alfalfa hay to supply 0, 10, 20, and 30% of the dietary DM fed in limited amounts to steers (1.75% of BW) increased the exit rate from the rumen of the liquid and solid fractions. In spite of the accelerated passage rates, the addition of alfalfa hay to the diet decreased DMI and had positive associative effects on the apparent total-tract digestibility of DM, OM, and NDF. The authors suggested that replacing SH with alfalfa hay may have stimulated rumination and the flow of saliva to the rumen, resulting in higher ruminal pH, fiber digestion rates, and dilution rates. These observations suggest that the outflow rate of SH from the rumen does not restrict the apparent total-tract digestibility of the diet when ruminants are fed limited amounts of feed.

Data indicate that the addition of coarse forage to diets that contained SH and were fed *ad libitum* resulted in large positive associative effects by increasing the time that SH were retained in the rumen and, hence, the time allowed for ruminal fermentation. Under these conditions, diet composition seems to affect the feeding value of SH by altering the consistency of the ruminal forage mat, which in turn influences their ruminal retention time. On the other hand, when ruminants are limited-fed diets containing SH the relatively low DMI negates any increase in the ruminal rate of passage that may be expected from the addition of SH to their diets.

Physical Form

The physical form of SH is another factor that may affect their nutritional value for ruminants. Prior to feeding, SH are normally ground, pelleted, or ground and pelleted to increase bulk density and reduce shipping cost. Anderson et al. (1988) evaluated the effect of physical processing methods on digestion and nutri-

tional value of SH for lambs and cattle. They fed diets that contained 38% corn stalkage, 3% molasses, 8% protein concentrate, and 51% SH that were ground (1.5-mm screen), pelleted (0.95 x 7.62-cm die), or not processed (i.e., whole) to lambs and observed that only grinding depressed digestibility of NDF (62, 61, and 56% for whole, pelleted, and ground SH, respectively). However, the negative effects of grinding on digestibility of SH were not evident when larger screen sizes were used (3.2 and 4.8 mm). Likewise, the growth performance of steers fed *ad libitum* a forage-based diet supplemented with either whole or ground SH was not impacted by the physical form of the SH when steers received 1.05 kg/d of SH. In contrast, when the amount of SH increased up to 2.1 kg/d per steer, ground SH resulted in a lower gain-to-DMI ratio than whole SH (0.105 vs. 0.120). Thus, feeding ground SH at high DMI may result in negative associative effects because of reduced ruminal retention time (Anderson et al., 1988). Based on this limited information, it appears that only fine grinding (<1.5 mm) diminishes the feeding value of SH for ruminants.

PERFORMANCE OF LACTATING DAIRY COWS FED SH

Replacing Cereal Grains with SH

The performance of dairy cows fed diets in which SH partially or totally replaced cereal grains is summarized in Table 3. In most studies, SH provided less than 25% of the dietary DM, except for four trials in which SH provided more than 30% of the dietary DM (Conrad and Hibbs, 1961; Nakamura and Owen, 1989; Sarwar et al., 1992; Ipharraguerre et al., 2002a). In 13 of the 15 studies reviewed, the grain supplied in the concentrate mix was either high-moisture or dry ground corn. Nearly all of these experiments, except for those of Pantoja et al. (1994) and Elliott et al. (1995), were conducted to evaluate the effects of replacing a portion of the dietary starch or NSC provided from corn with fiber from SH. However, only in one (Conrad and Hibbs, 1961) was the dietary content of starch reported, in three (Cunningham et al., 1993; Elliott et al., 1995; Stone, 1996) dietary NFC content was calculated, and in three others (Sarwar et al., 1992; Mansfield and Stern, 1994; Ipharraguerre et al., 2002a) dietary NSC or total non-structural carbohydrates was enzymatically determined.

Multiple regression analyses were conducted using data from selected studies to facilitate the interpretation of the relationship between the performance of dairy cows and the substitution of SH for corn grain. Data from 10 studies (Macgregor and Owen, 1976; Nakamura and Owen, 1989; Bernard and McNeill, 1991;

Table 3. Performance of lactating dairy cows fed diets in which soyhulls replaced cereal grains or forages.

Study	DIM	Parity ¹	Dietary treatments ²	DMI	Milk	FCM	Fat	Protein
Soyhulls replaced grains					(kg/d)		(%)	
Conrad and Hibbs (1961) ³	NR	NR	Ct: 44% MH, 16% CM, 28% O	17.4	19.6	19.0	NR	3.08
	NR	NR	T1: 24% MH, 28% CM, 48% SH	16.4	21.4*	18.3	NR	2.89
Wagner et al. (1965) ⁴	NR	NR	Ct: 23% AH, 49% CS, 19.5% CM, 8.5% O	29.7	22.6	21.7	3.73	NR
	NR	NR	T1: 23% AH, 49% CS, 19.5% CM, 8.5% SH	28.3	22.3	21.5	3.74	NR
MacGregor and Owen (1976)	NR	M	Ct: 44% AS, 48% GC	18.1	18.6	19.0	4.18	3.40
			T1: 43% AS, 35% GC, 15% SH	19.1	19.6	19.9	4.09	3.21
			T2: 42% AS, 23% GC, 28% SH	18.6	18.5	18.5	4.04	3.31
Nakamura and Owen (1989)	130	M	Ct: 50% AS, 45% GC	23.4	29.8	27.8	3.13	3.08
			T1: 50% AS, 21% GC, 25% SH	23.8	28.9	28.1	3.33	3.00
			T2: 50% AS, 48% SH	24.0	27.3*	27.1	3.49*	2.84*
Bernard and McNeil (1991)	150	M	Ct: 46% CS, 34% GC	21.3	27.7	NR	3.50	3.39
			T: 48% CS, 11% GC, 23% SH	22.5	27.7	NR	3.67	3.32
Firkins and Eastridge (1992)	28	M, P	Ct: 10% AS, 31% CS, 34% GC	24.4	37.0	33.8	3.50	3.16
			T1: 10% AS, 31% CS, 13% GC, 20% SH, 11% RSB, 0.43% CaS	22.5	38.9	35.6	3.42	2.88†
Sarwar et al. (1992)	57	P	Ct: 22% AS, 22% CS, 38% GC	19.4	24.7	22.7	3.46	3.12
			T1: 22% AS, 22% CS, 20% GC, 19% SH, 7% RSB	19.9	25.9 ^I	24.0 ^L	3.54	3.08 ^{LQ}
			T2: 22% AS, 22% CS, 4% GC, 34% SH, 13% RSB, 1% CaS	20.4	27.7 ^I	25.7 ^L	3.51	2.84 ^{LQ}
Cunningham et al. (1993)	31	M	Ct: 10% AH, 40% CS, 25% HMC	24.1	37.4	34.4	3.48	3.13
			T1: 10% AH, 40% CS, 14% HMC, 12% SH	22.7	35.5	32.3	3.46	3.16
			T2: 10% AH, 40% CS, 2% HMC, 25% SH	23.2	35.8	32.8	3.46	3.14
Pantoja et al. (1994)	43	P	Ct: 16% AS, 24% CS, 34% GC	19.3	29.5	23.6	2.65	2.97
			T: 16% AS, 24% CS, 16% GC, 20% SH	17.8	27.3	24.1	3.21 ^Q	2.82 ^Q
Mansfield and Stern (1994)	78	M	Ct: 14% AH, 6% GH, 32% CS, 28% GC	20.2	28.7	27.9	3.33	2.96
			T: 14% AH, 6% GH, 32% CS, 30% SH	20.7	27.7†	26.9†	3.33	2.90†
Elliott et al. (1995) (Experiment 1, main effects)	29	M, P	Ct: 22% AS, 22% CS, 36% GC	19.8	23.8	25.9	4.61	3.93
			T: 22% AS, 22% CS, 18% GC, 18% SH	19.3	22.8	25.4	4.83	3.90
Elliott et al. (1995) (Experiment 2, main effects)	31	M	Ct: 22% AS, 22% CS, 36% GC	23.5	24.5	24.3	4.02	3.79
	147		T: 22% AS, 22% CS, 18% GC, 18% SH	22.6†	25.7	26.3	4.25*	3.63
Stone (1996)	8	M	Ct: 26% AS, 26% CS, 23% HMC	20.7	40.7	41.2	3.58	2.92
			T: 26% AS, 26% CS, 9% HMC, 14% SH	22.6†	41.7	41.9	3.56	2.89
Stone (1996)	8	P	Ct: 26% AS, 26% CS, 23% HMC	16.6	31.5	32.3	3.70	2.78
			T: 26% AS, 26% CS, 9% HMC, 14% SH	17.1	31.5	31.3	3.71	2.93
Ipharraguerre et al. (2002a)	112	M	Ct: 23% AS, 23% CS, 40% GC	23.8	29.5	29.0	3.60	3.36
			T1: 23% AS, 23% CS, 30% GC, 10% SH	24.8 ^I	29.3	29.0	3.61 ^L	3.28
			T2: 23% AS, 23% CS, 21% GC, 20% SH	24.4 ^I	29.9	30.1	3.67 ^L	3.33
			T3: 23% AS, 23% CS, 11% GC, 30% SH	22.9 ^I	29.3	30.6	3.93 ^L	3.30
			T4: 23% AS, 23% CS, 1% GC, 40% SH	22.7 ^I	28.3	29.7	3.91 ^L	3.31

continued

Table 3. (continued) Performance of lactating dairy cows fed diets in which soyhulls replaced cereal grains or forages.

Study	DIM	Parity ¹	Dietary treatments ²	DMI	Milk	FCM	Fat	Protein
					(kg/d)		(%)	
Soyhulls replaced forages								
Firkins and Eastridge (1992)	28	M, P	Ct: 10% AS, 31% CS, 34% GC	24.4	37.0	33.8	3.50	3.16
			T1: 10% AS, 20% CS, 38% GC, 7% SH	23.5	37.3	33.0†	3.26	3.18
			T2: 10% AS, 20% CS, 37% GC, 7% SH, 1% NaB	23.2	35.1†	31.2†	3.39	3.18
Sarwar et al. (1992)	57	P	Ct: 22% AS, 22% CS, 38% GC	19.4	24.7	22.7	3.46	3.12
			T1: 18% AS, 18% CS, 40% GC, 5% SH	19.8	24.2	22.5	3.57	3.07
			T2: 16% AS, 16% CS, 41% GC, 9% SH	19.4	25.2	23.7	3.61	3.24
Cunningham et al. (1993)	31	M	Ct: 10% AH, 40% CS, 25% HMC	24.1	37.4	34.4	3.48	3.13
			T1: 10% AH, 29% CS, 25% HMC, 12% SH	23.5 ^L	37.3	33.8	3.36	3.18
			T2: 10% AH, 18% CS, 26% HMC, 25% SH	22.3 ^L	35.4	32.6	3.42	3.36
Pantoja et al. (1994)	43	P	Ct: 24% AS, 36% CS, 17% GC	18.3	27.5	22.5	2.79	2.88
			T: 16% AS, 24% CS, 16% GC, 20% SH	17.8	27.3	24.1	3.21 ^Q	2.82 ^Q
Weidner and Grant (1994b)	34	NR	Ct: 30% AS, 30% CS, 17% GC	23.2	31.9	30.0	3.56	3.15
	151		T1: 22% AS, 22% CS, 17% GC, 15% SH	22.5	31.5	28.0*	3.26*	3.14
			T2: 17% AS, 17% CS, 15% GC, 25% SH	23.2	31.8	27.6*	3.20*	2.93*
			T3: 13% AS, 13% CS, 20% AH, 19% GC, 15% SH	22.3	30.0	24.5	2.94	3.15
			T4: 7% AS, 7% CS, 20% AH, 17% GC, 25% SH	25.8*	34.7*	31.6*	3.36*	3.15
Stone (1996)	8	M	Ct: 26% AS, 26% CS, 23% HMC	20.7	40.7	41.2	3.58	2.92
			T: 12% AS, 26% CS, 19% HMC, 14% SH	23.9*	45.9*	44.8	3.41	2.88
Stone (1996)	8	P	Ct: 26% AS, 26% CS, 23% HMC	16.6	31.5	32.3	3.70	2.78
			T: 12% AS, 26% CS, 19% HMC, 14% SH	18.6*	34.1	34.0	3.56	3.13*

¹ Not reported or determined; M = multiparous, P = primiparous.

²AH = alfalfa hay, AS = alfalfa silage, CaS = Ca salts of palm fatty acids, CM = concentrate mix, CS = corn silage, Ct = Control, GC = ground corn, GH = grass hay, HMC = high-moisture corn, MH = mixed hay, NaB = Na bicarbonate, O = oats, RSB = roasted soybeans, SH = soyhulls, T = treatment. Protein, mineral, and vitamin supplements are not included.

³Concentrate and SH were fed as a mixture and to ad libitum intake. Hay was offered in restricted amounts. Dietary treatments reported are the actual ingredient composition of the experimental rations consumed by dairy cows.

⁴Concentrate and SH were fed as a mixture and to supply 454 g of CM/1.4 kg of FCM produced. Forages were fed ad libitum. Dietary treatments reported are the actual ingredient composition of the experimental rations consumed by dairy cows.

*Significant effect ($P < 0.05$).

†Significant effect ($P < 0.10$).

^LSignificant linear effect ($P < 0.05$).

^LSignificant linear effect ($P < 0.10$).

^QSignificant quadratic effect ($P < 0.05$).

^QSignificant quadratic effect ($P < 0.10$).

Cunningham et al., 1993; Mansfield and Stern, 1994; Pantoja et al., 1994; Elliott et al., 1995; Stone, 1996; Ipharraguerre et al., 2002a, 2002b) were pooled based on similar feeding regimens (i.e., corn grain used as energy source, diets fed as TMR, etc.) and replacement strategies (i.e., only corn was replaced with SH). In these 10 studies, cows that ranged from 31 to 150 DIM were fed 25 diets, produced from 19 to 42 kg/d of milk, and consumed from 17 to 25 kg/d of DM (Table 3). Models for DMI, yields of milk and FCM, and fat and CP content of milk were evaluated. Prior to analyses, observations were weighted as described by St-Pierre (2001) to account for unequal replications and variances of the means across studies. Initially, the following independent variables were considered: amount of SH as percentage of the dietary DM, amount of NDF from SH either as percentage of the dietary DM or as percentage of the total NDF in the diet, their quadratic terms, and the two two-way interactions of the amount of SH in the diet by the amount of NDF from SH expressed in either way. The amount of NDF supplied from SH was estimated using the content of NDF in SH reported in the corresponding studies. If the concentration of NDF in SH was not reported, the mean value in Table 1 was used. To reduce unexplained variation and remove patterns in the residuals, the effects of the trials were also included in the models (Steele and Torrie, 1980). No other independent variables were included because of lack of information and/or to avoid overparameterization of the model.

Using the stepwise procedure of SAS (2000), all tested variables, except for trial, were not significant ($P > 0.05$). For DMI, these results might be expected considering that in 13 of 15 studies no significant differences were detected between the control diets and those containing SH (Table 3). In one study, replacing 14% of the DMI supplied as high-moisture corn with SH increased DMI of multiparous cows (~2 kg/d), but did not affect DMI of primiparous cows (Stone, 1996). Stone (1996) suggested that higher-than-recommended dietary levels of starch in the control diet led to subclinical acidosis—subsequently depressing DMI. However, the starch content of the control and experimental diets was not reported. Conversely, when SH were gradually increased in the diet of lactating dairy cows to replace 0, 10, 20, 30, and 40% of the DM supplied as corn, DMI decreased ($P < 0.06$) linearly, but the larger decrease (~1 kg/d) occurred when SH supplied more than 30% of the dietary DM (Ipharraguerre et al., 2002a). Based on data of Batajoo and Shaver (1994), Harmison et al. (1997), Mertens (1997), and Ipharraguerre et al. (2002a, 2002b), it appears that including >30% of dietary DM as SH in high grain diets (≥50%) that have a shortage of physically effective fiber may elevate the concentra-

Figure 1. The relationship between DMI (kg/d) and the amount of dietary NDF supplied from SH (% of dietary DM). Data points correspond to data from different studies (Macgregor and Owen, 1976; Nakamura and Owen, 1989; Bernard and McNeill, 1991; Cunningham et al., 1993; Mansfield and Stern, 1994; Pantoja et al., 1994; Elliott et al., 1995; Stone, 1996; Ipharraguerre et al., 2002a, 2002b).

tion of acids in the rumen and decrease DMI of cows. However, the lack of sufficient data from experiments in which SH supplied more than 30% of the dietary DM limits this analysis.

The NDF content of the experimental diets (Table 3) increased as SH were increased in the diet (NDF ranged from 27 to 58%). It is well known that the dietary concentration of NDF and DMI are inversely and strongly correlated (Hoover, 1986; Mertens, 1994; Armentano and Pereira, 1997). Diets that contain more than about 32% NDF can limit DMI of cows producing approximately 40 kg/d of milk (Mertens, 1994). Considerably more dietary NDF (~44%) is required to restrict DMI of cows producing 20 kg/d of milk. Although the NDF content of several diets in which corn was replaced with SH was similar to or higher than those limits, no relationship between DMI and dietary NDF concentration from SH was evident from the regression and correlation ($P = 0.33$) analyses (Figure 1). Likewise, Armentano and Pereira (1997) pooled data from 32 studies and indicated that the correlation between DMI and the NDF content of diets from nonforage fiber sources was not significant. An explanation for the apparent discrepancy between the effects of forage and nonforage NDF on DMI may be the dissimilar chemical and physical nature of the NDF of forages and SH. First, there is a clear inverse relationship between DMI and dietary NDF concentration from studies in which forages were the major (−0.58 [Hoover, 1986]) or the sole (−0.31 [Armentano and Pereira, 1997]) source of NDF. Second, SH contain a pool of potentially degradable NDF that

is larger than that of most forages used in those studies (e.g., alfalfa silage, corn silage, and alfalfa hay or haylage [Sarwar et al., 1991; Pantoja et al., 1994]). In addition, as discussed previously, NDF from SH can be degraded extensively in the rumen at rates similar to or greater than that of NDF in forages (Firkins, 1997; Table 2). Third, SH have a small particle size and high specific gravity that, compared with forages, could double the passage rate from the rumen (Nakamura and Owen, 1989). Therefore, NDF from SH may not affect DMI to the same extent that NDF from forages does because of differences in their digestion kinetics and physical bulk.

The linear correlation between milk yield and the percentage of SH in the diet from the 10 trials that were pooled was low (-0.12) and nonsignificant ($P = 0.51$). This relationship would be anticipated because only minor changes in milk production have been reported when SH either partially or totally replaced cereal grain in the diet (Table 3). Furthermore, the mechanism by which SH improved milk yield when they replaced grain (Conrad and Hibbs, 1961; Sarwar et al., 1992) could not be identified. For example, Sarwar et al. (1992) reported a linear increase in milk yield of early lactation cows after replacing either 19 or 34% of the DMI supplied as corn with SH. However, roasted SB and inert fats also were added to the SH diets (Table 3); therefore, the effect on milk yield was confounded with the higher fat content of the experimental rations in relation to that of the control ration. Only one study (Nakamura and Owen, 1989) reported a significant decrease in milk yield when SH replaced corn in the diet (Table 3). In that trial, Nakamura and Owen (1989) observed that the complete replacement of corn with SH (48% of dietary DM) in diets containing 50% forage and 50% concentrate decreased milk production by about 2.5 kg/d (Table 3). They suggested that the low starch content of the diet that contained SH limited milk yield, but the lower DM digestibility of the experimental ration (61.3 vs. 69.9% for control) may have also contributed, at least in part, to reduce milk production. Unfortunately, the paucity of data from experiments in which SH supplied more than 25 to 30% of the dietary DM restricts this analysis, as well as any attempt to establish the maximal substitution of SH for corn.

Milk fat content from the 10 pooled trials was not correlated with the concentration of SH in the diet or the dietary NDF from SH. The same lack of correlation between milk fat concentration and those variables was evident after removing the variation due to unequal replications and unequal variation of the means across studies (Figure 2).

Data indicate that the NDF from SH is effective for maintaining or slightly increasing milk fat percentage

Figure 2. The relationship between the weighted content of fat in milk and the amount of dietary NDF supplied from SH (% of dietary DM). Data points correspond to data from different studies (Macgregor and Owen, 1976; Nakamura and Owen, 1989; Bernard and McNeill, 1991; Cunningham et al., 1993; Pantoja et al., 1994; Elliott et al., 1995; Stone, 1996; Ipharraguerre et al., 2002a, 2002b).

when SH are used to replace grain consumed by cows. In effect, in the studies summarized in Table 3 the difference between the control diets and those containing SH averaged $+0.11$ percentage units, and only in four trials were differences among treatments significant (Nakamura and Owen, 1989; Pantoja et al., 1994; Elliott et al., 1995; Ipharraguerre et al., 2002a). In three of those studies, however, the replacement of 18 (Elliott et al., 1995), 20 (Pantoja et al., 1994), or 45% of the dietary DM (Nakamura and Owen, 1989) supplied as corn with SH actually reestablished milk fat content to levels near the average of the breeds (Holstein and Jersey) used in the experiments (Table 3). In addition, the enhanced concentration of fat in the milk of cows fed diets in which increasing amounts of SH replaced corn grain could not be clearly linked to an additive effect of SH on milk fat percentage (Ipharraguerre et al., 2002a).

The lack of consistent effects of dietary SH on milk yield and milk fat in the trials that were included in this analysis resulted in a nonsignificant correlation between the amount of SH used to replace corn and the production of FCM. Only one study (Sarwar et al., 1992) reported a linear increase in FCM yield when the amount of SH that replaced corn increased from 19 to 34% of the dietary DM (Table 3); however, that effect was confounded by the addition of fat to the SH diets. In two of the four studies where SH improved milk fat content (Nakamura and Owen, 1989; Pantoja et al., 1994), milk production decreased and yield of FCM did not differ (Table 3).

Replacing cereal grains with SH significantly (Firkins and Eastridge, 1992; Sarwar et al., 1992; Mansfield and Stern, 1994; Pantoja et al., 1994) or numerically (Conrad and Hibbs, 1961; Macgregor and Owen, 1976; Bernard and McNeill, 1991; Elliott et al., 1995; Ipharraguerre et al., 2002a) depressed the protein content of milk (Table 3). The depression of milk protein concentration ranged from 0.8 to 8% when SH provided from 18 to 48% of the dietary DM, respectively. This response may arise partially because of the low content of NSC in diets that contained high levels of SH, which in turn may limit microbial protein synthesis in the rumen (Sarwar et al., 1992). Nonetheless, Mansfield and Stern (1994) reported that even though the complete replacement of corn with SH (30% of dietary DM) reduced dietary NSC from 33 to 23%, microbial populations in the rumen, microbial N flow to small intestine, and efficiency of microbial protein synthesis were not different. However, milk protein percentage tended ($P < 0.09$) to be depressed and milk protein yield was depressed by the SH diet. More recently, the replacement of increasing amounts of corn grain with SH to supply 0, 10, 20, 30, or 40% of the dietary DM reduced the percentage of dietary NSC from almost 36 to about 16 and also did not affect the synthesis of microbial protein in the rumen of lactating dairy cows (Ipharraguerre et al., 2002b). These data indicate that when SH replace corn to supply 30 to 40% of the dietary DM, changes in the ruminal synthesis of microbial protein are not likely to occur but there might be a reduction in milk protein output.

Based on the higher intestinal availability of NSC in cows fed corn versus SH, Mansfield and Stern (1994) suggested that more glucose for milk synthesis was available when cows consumed corn. Elliott et al (1995), however, found that the plasma concentration of glucose tended ($P < 0.06$) to increase when cows received diets in which ground corn was replaced with SH to supply 18% of the dietary DM. They hypothesized that, although the addition of SH to the diet reduced the molar proportion of propionate, the ruminal concentration of total VFA was enhanced (Table 4); therefore, propionate production and glucose synthesis may have increased if total ruminal VFA production increased. Even though similar shifts in the molar proportion of ruminal VFA were observed, the plasma concentration of glucose in dairy heifers was not affected by the complete replacement of corn with SH, which accounted for 30 and 60% of total dietary DM (Nosbush et al., 1996).

Any increase in milk protein output due to higher energy availability requires an adequate supply of AA to support milk protein synthesis in the mammary gland (Reynolds et al., 1997). Only three studies (Cunningham et al., 1993; Mansfield and Stern, 1994; Iphar-

raguerre et al., 2002b) have measured the AA flows to the small intestine of dairy cows fed diets in which SH replaced corn. In the Mansfield and Stern (1994) trial, feeding SH diets decreased Met as a percentage of the total proportion essential AA reaching the small intestine below that indicated by Schwab et al. (1992) for optimal AA utilization by mid-lactation cows. Likewise, Cunningham et al. (1993) reported a linear decline in the total amount of Met delivered to the small intestine as SH increased from 12 to 25% of the dietary DM, but the proportion of Met in total essential AA in the duodenum was about 4.0% for all diets. Differences were attributed to the lower Met content of SH in relation to corn (Cunningham et al., 1993; Mansfield and Stern, 1994) and to the numerically larger DMI of cows consuming the control diet (Mansfield and Stern, 1994). In contrast, replacing up to 40% of the dietary DM provided as corn with SH did not alter the passage of Met to the duodenum of dairy cows (Ipharraguerre et al., 2002b). These few studies suggest that from early to mid-lactation, diets in which more than 25% of the dietary DM from corn grain is replaced with SH might reduce the output of milk protein by limiting the intake of NSC, the supply of Met to the small intestine, or both. Conversely, it appears that from mid- to late lactation large amounts of dietary SH can be supplied without negatively affecting the concentration of protein in milk; however, the optimum level is unclear.

Replacing Forage with SH

Although the first evaluations of SH as an alternative feed for lactating dairy cows was conducted during the early 1960s (Conrad and Hibbs, 1961; Wagner et al., 1965), the assessment of their ability to replace forages in diets of dairy cattle started almost 30 years later (Table 3). With the exception of two studies (Weidner and Grant, 1994a, 1994b), control diets that contained $\leq 50\%$ of the dietary DM as forage were used to determine the potential reduction of negative associative effects of NSC on ruminal digestion of fiber when SH replaced forages. The amount of SH that replaced forages ranged from 5 to 25% of total dietary DM, and the grain was supplied as ground or high-moisture corn. The forages replaced with SH were alfalfa (hay or silage), corn silage, or a portion of both. Even though the NDF content of the control (29 to 35%) and SH rations (31 to 37%) was similar among treatments across studies, NDF from forages ranged from about 71 to 86% for the control diets and from 40 to 60% for the SH diets. In two experiments (Sarwar et al., 1992; Weidner and Grant, 1994b), the proportion of NDF from roughage was 60% regardless of the dietary level of SH (9 to 15%),

which suggests that caution should be taken when comparing results from different reports.

On average, replacing forage with SH increased DMI 0.3 kg/d, milk yield 0.7 kg/d, and FCM production 0.4 kg/d (Table 3). However, if data are grouped by the NDF concentration from forage for the SH diets and by the forage content of the control diets (DM basis) contrasting inferences can be drawn. First, including SH in diets that contained 60 to 70% NDF from forage did not affect DMI or milk yield regardless of the forage content in the control diet. For instance, Firkins and Eastridge (1992) reported no treatment effects on DMI and milk production when feeding control and treatment diets formulated to contain 62.5% NDF from forage. Eleven percent of the DM in the control diet supplied as corn silage was replaced with 7% SH and 4% ground corn on a DM basis to form the SH diets. Similarly, performance of cows was not affected when an equal mix of corn silage and alfalfa silage was replaced with about 15% SH in diets that contained 60% forage (control), which reduced NDF from forage from 86 to 60% of total dietary NDF (Weidner and Grant, 1994b). Second, replacing 11 and 22% of the DM supplied as corn silage in the control diet (50% forage) with SH decreased NDF supplied as forage from 76% to 58 and 40%, respectively (Cunningham et al., 1993). In that study, as SH increased in the diet, DMI decreased linearly and milk production declined numerically by 2 kg/d per cow (Table 3). Third, when 45 to 50% of the NDF in SH diets and more than 50% of the DM in control diets was supplied as forages, inclusion of SH significantly or numerically improved DMI and milk production. Indeed, Stone (1996) found that the addition of 14% of the dietary DM as SH to replace alfalfa silage in a control diet that contained 53% forage increased DMI and milk production of multiparous Holstein cows. In this experiment, forages provided 71 and 47% of the dietary NDF in the control and SH diets, respectively. When the same dietary treatments were fed to primiparous dairy cows, the SH diet numerically increased DMI and milk yield, but only DMI was significantly enhanced (Stone, 1996). Likewise, DMI and milk production were greater when SH (25%) and alfalfa hay (20%) replaced corn silage (23%) and when alfalfa haylage (23%) and forages supplied 46% of the total dietary NDF, compared with the control diet that contained 60% forage and supplied 62% of the NDF from forage (Weidner and Grant, 1994b).

In general, there was little change in milk composition when cows were fed diets in which SH partially replaced forages (Table 3). Milk protein concentration was increased in one trial (Stone, 1996) and decreased in another (Weidner and Grant, 1994b), but reasons for these changes were not given. As highlighted by

Titgemeyer (2000), two studies (Pantoja et al., 1994; Weidner and Grant, 1994b) reported opposite responses for milk fat percentage in spite of the similar amount of SH and type of forage fed to the cows. Weidner and Grant (1994b) observed that replacing 15 and 25% of the DM supplied as a 1:1 (wt/wt) silage mixture (alfalfa and corn) with SH in a diet that contained 60% forage decreased milk fat content (8 and 10%, respectively). On the other hand, for diets containing 60% forage, the replacement of 8 and 12% of the total DM from alfalfa silage and corn silage with SH (20% of dietary DM) enhanced milk fat concentration by about 15% (Pantoja et al., 1994). In those studies, the contrasting milk fat percentages were positively correlated with opposite changes in the ruminal acetate-to-propionate ratio (Table 4). Interestingly, in the study of Weidner and Grant (1994b) when a portion of the silage mixture was replaced with 20% alfalfa hay (coarsely chopped) in the SH diets, the replacement of the silages with SH increased milk fat percentage (Table 3). They reported that the inclusion of SH decreased the mean particle size of all diets, but less so when long alfalfa hay was added. Furthermore, as dietary SH were increased, total chewing time declined, but the decrease was partially or totally prevented by the addition of coarse hay. Thus, the SH diets used by Weidner and Grant (1994b) and Pantoja et al. (1994) may have presented different physical effectiveness for stimulating rumination and salivation, resulting in opposite changes in ruminal fermentation and milk fat percentage. Stone (1996) replaced 14% of the dietary DM supplied as alfalfa haylage with SH in a diet that contained 53% forage and estimated that the effectiveness of NDF in SH was 53% of that in alfalfa fiber for promoting rumination. Feeding diets with as little as 34% forage (mixture of alfalfa and corn silages) and as much as 23% SH also failed to sustain total chewing activity per unit of NDF consumed (i.e., time spent eating and ruminating per kg of NDF intake; Slater et al., 2000). However, milk fat percentage was depressed only when ruminally degradable starch was increased by the partial replacement of corn (8%) with wheat (12%). Diets that contained only 23% forages, almost 31% SH, and about 27% cereal grain, which was supplied as corn or as mixture of corn (55%) and wheat (45%), did not affect milk fat concentration or milk production of Jersey cows during early lactation (Harmison et al., 1997). In both studies (Harmison et al., 1997; Slater et al., 2000), the lack of a milk fat response coincided with similar ruminal acetate-to-propionate ratios for the control and SH diet. Even though the physical effectiveness of the diet (measured as stimulation of chewing) decreased as SH replaced forage, the potential benefits on ruminal ferment-

tation ("chemical" effectiveness) of NSC dilution with SH may prevent milk fat depression.

These data suggest that SH might be used to replace forages in dairy diets when the supply of effective fiber, which includes a chemical and a physical component, remains adequate after including SH. In cases where forages constitute 50% or less of total dietary DM or have small particle size, their replacement with SH may depress dairy cow performance as a result of an inadequate supply of effective fiber. On the other hand, in situations where forages represent 50% or more of dietary DM and have a particle size that guarantees adequate physical effectiveness, the substitution of SH for forages may not affect or may improve the performance of dairy cows. Furthermore, SH may enhance milk fat percentage because of the replacement of NSC or starch rather than from the stimulation of chewing activity. Therefore, the source, amount, and physical form of forages largely affect the use of SH in dairy diets (Grant, 1997).

RUMINAL FERMENTATION CHARACTERISTICS

The inclusion of SH in dairy diets has resulted in a ruminal fermentation pattern that has either maintained or enhanced the ruminal concentration of total VFA (Table 4). That response has consistently been observed in a number of studies in which different dietary forage-to-concentrate ratios were used or even when forages or grains were replaced with SH. For instance, when Cunningham et al. (1993) added 12 or 25% of the dietary DM as SH to replace similar amounts of either corn silage or high-moisture corn, the concentration of VFA in ruminal fluid increased for the SH diets even though the NFC concentration of these diets was lower (Table 4). Based on similar findings, Mansfield and Stern (1994), Pantoja et al. (1994), and Sarwar et al. (1992) proposed that the high content of fermentable NDF present in SH might allow a more extensive ruminal fermentation, possibly resulting in higher VFA concentrations. In fact, the *in situ* rate and extent of degradation of NDF in SH remained high under a wide range of dietary conditions (Table 2). Furthermore, the amount of dietary NDF apparently digested in the rumen of lactating dairy cows either increased (Pantoja et al., 1994) or did not change (Cunningham et al., 1993) when SH were substituted for forages but consistently increased when SH replaced corn (Cunningham et al., 1993; Mansfield and Stern, 1994; Ipharraguerre et al., 2002b).

In contrast, the replacement of either forages or grains with SH has resulted in dissimilar shifts in the molar proportion of individual VFA, pH, and NH_3N concentration of ruminal fluid (Table 4). Substitution

of SH for corn, which ranged from 12 to 40% of the dietary DM, diminished the molar proportion of propionate and butyrate and enhanced that of acetate (Table 4). Consequently, feeding diets that contained SH has constantly increased the ruminal acetate-to-propionate ratio. Moreover, in all experiments that ratio reached values of 2.5:1, which is greater than the minimum required to sustain normal milk fat percentages (Erdman, 1988). Nonetheless, the molar proportion of total lipogenic VFA (i.e., acetate and butyrate) in ruminal fluid slightly increased or remained unaffected, which may explain, at least in part, the lack of changes in milk fat content observed in most of those studies. Mansfield and Stern (1994) concluded that the above-described changes in the molar proportion of VFA in ruminal fluid revealed a shift from fermentation of NSC to fiber in the rumen. They noted that the replacement of 30% of dietary corn with SH decreased the amount of NSC apparently digested in the rumen by 21% and increased that of NDF by 48%.

Despite the shift in ruminal fermentation, feeding SH in place of grains to ruminants usually failed to affect the pH of the ruminal fluid (Table 4). Sarwar et al. (1992) indicated that replacing 19 and 34% of the total dietary DM supplied as ground corn with SH in high grain diets attenuated the characteristic postfeeding decline of ruminal pH, but that improvement was only significant at 9 h postfeeding. In addition, most reports (Highfill et al., 1987; Anderson et al., 1988; Galloway et al., 1993; Mansfield and Stern, 1994; Elliott et al., 1995) indicate that feeding SH in place of grains resulted in an average ruminal pH (≥ 6.0) that appears to be adequate to support ruminal microflora and cellulolysis (Mould et al., 1983; Mould and Orskov, 1983; Hoover, 1986; Grant and Weidner, 1992).

Replacing forage with SH in dairy diets to supply from 5 to 25% of dietary DM usually increased the molar proportion of propionate in ruminal fluid (Table 4), but alterations in molar percentages of acetate and butyrate were infrequent or inconsistent. In part, these results may have arisen from differences in the amount of forages fed in those experiments. The addition of SH to replace forages in diets that contained more than 50% forage did not affect the molar proportion of acetate and butyrate (Weidner and Grant, 1994a, 1994b; Stone, 1996). Conversely, when forages provided less than 50% of total dietary DM, the inclusion of SH in the diet significantly decreased the molar proportion of acetate (Sarwar et al., 1991, 1992) and butyrate (Sarwar et al., 1992; Cunningham et al., 1993). Hsu et al. (1987) suggested that the highly fermentable fiber of SH might lead to a concentrate-type ruminal fermentation pattern when SH are used to replace forages. That effect

Table 4. Ruminal fermentation characteristics of lactating dairy cows fed diets in which soyhulls replaced cereal grains or forages.

Study	Dietary treatments ¹	pH	NH ₃ N ²	VFA	Ac ³	Pr ⁴	Bu ⁵	Ac:Pr ⁶
			(mg/dl)	(mM/L)		(mol/100 mol)		
Soyhulls replaced grains								
MacGregor and Owen (1976)	Ct: 44% AS, 48% GC	NR ⁷	NR	NR	64.8	18.7	14.8	3.32
	T1: 43% AS, 35% GC, 15% SH	NR	NR	NR	66.5	18.3	15.2	3.63
	T2: 42% AS, 23% GC, 28% SH	NR	NR	NR	65.5	19.7	16.5	3.46
Sarwar et al. (1992)	Ct: 22% AS, 22% CS, 38% GC	NR	NR	113	57.0	23.5	15.0	2.44
	T1: 22% AS, 22% CS, 20% GC, 19% SH, 7% RSB	NR	NR	112	60.4 ^L	21.2 ^{LQ}	14.4 ^L	2.84 ^{LQ}
	T2: 22% AS, 22% CS, 4% GC, 34% SH, 13% RSB, 1% CaS	NR	NR	111	61.4 ^L	22.2 ^{LQ}	12.8 ^L	2.77 ^{LQ}
Cunningham et al. (1993)	Ct: 10% AH, 40% CS, 25% HMC	6.02	13.5	123	59.6	24.9	11.8	2.50
	T1: 10% AH, 40% CS, 14% HMC, 12% SH	5.96	12.8	156 ^Q	62.7 ^L	22.7 ^L	11.3	2.80 ^L
	T2: 10% AH, 40% CS, 2% HMC, 25% SH	5.99	11.7	122	64.8 ^L	21.2 ^L	11.2	3.10 ^L
Pantoja et al. (1994)	Ct: 16% AS, 24% CS, 34% GC	6.05	NR	103	57.0	24.6	13.6	2.34
	T: 16% AS, 24% CS, 16% GC, 20% SH	5.96	NR	106 ^Q	61.4 ^{LQ}	21.9 ^{LQ}	12.8	2.82 ^{LQ}
Mansfield and Stern (1994)	Ct: 14% AH, 6% GH, 32% CS, 28% GC	6.47	20.3	93	61.6	21.6	12.6	2.86
	T: 14% AH, 6% GH, 32% CS, 30% SH	6.36	17.2*	100*	64.9*	20.9	11.0*	3.11*
Elliott et al. (1995) (Experiment 2, main effects)	Ct: 22% AS, 22% CS, 36% GC	6.08	14.5	97	61.9	23.1	11.7	2.74
	T: 22% AS, 22% CS, 18% GC, 18% SH	6.01	15.0	102*	64.1*	21.6*	11.4*	3.02*
Stone (1996)	Ct: 26% AS, 26% CS, 23% HMC	NR	NR	NR	64.3	20.6	11.2	NR
	T: 26% AS, 26% CS, 9% HMC, 14% SH	NR	NR	NR	65.7 [†]	20.2	10.8	NR
Ipharraguerre et al. (2002b)	Ct: 23% AS, 23% CS, 40% GC	6.11	12.6	123	63.7	20.4	11.3	3.20
	T1: 23% AS, 23% CS, 30% GC, 10% SH	6.00 ^I	15.8 ^L	125 ^L	65.0 ^L	19.6 ^I	11.1 ^L	3.38 ^L
	T2: 23% AS, 23% CS, 21% GC, 20% SH	6.09 ^I	15.7 ^L	127 ^L	64.5 ^L	20.2 ^I	10.6 ^L	3.32 ^L
	T3: 23% AS, 23% CS, 11% GC, 30% SH	5.96 ^I	16.3 ^L	131 ^L	65.5 ^L	19.6 ^I	10.6 ^L	3.44 ^L
	T4: 23% AS, 23% CS, 1% GC, 40% SH	6.09 ^I	17.8 ^L	131 ^L	66.2 ^L	19.3 ^I	10.3 ^L	3.48 ^L
Soyhulls replaced forages								
Sarwar et al. (1992)	Ct: 22% AS, 22% CS, 38% GC	NR	NR	113	57.0	23.5	15.0	2.44
	T1: 18% AS, 18% CS, 40% GC, 5% SH	NR	NR	113 ^L	57.1 ^I	23.8 ^L	14.6 ^L	2.44 ^{LQ}
	T2: 16% AS, 16% CS, 41% GC, 9% SH	NR	NR	124 ^L	56.3 ^I	25.2 ^L	14.3 ^L	2.26 ^{LQ}
Cunningham et al. (1993)	Ct: 10% AH, 40% CS, 25% HMC	6.02	13.5	123	59.6	24.9	11.8	2.50
	T1: 10% AH, 29% CS, 25% HMC, 12% SH	6.08	13.5 ^L	136	60.6	23.4 ^Q	12.6 ^{LQ}	2.70
	T2: 10% AH, 18% CS, 26% HMC, 25% SH	5.87	10.4 ^L	128	60.2	26.5 ^Q	10.3 ^{LQ}	2.30
Pantoja et al. (1994)	Ct: 24% AS, 36% CS, 17% GC	6.09	NR	100	59.7	22.4	13.3	2.70
	T: 16% AS, 24% CS, 16% GC, 20% SH	5.96	NR	106 ^Q	61.4 ^{LQ}	21.9 ^{LQ}	12.8	2.82 ^{LQ}
Weidner and Grant (1994a)	Ct: 29% AS, 29% CS, 16% GC	6.22	NR	122	63.8	20.3	12.0	3.16
	T1: 18% AS, 18% CS, 14% GC, 25% SH	5.87 [†]	NR	144	62.6	22.0 [†]	11.8	2.88 [†]
	T2: 7% AS, 7% CS, 20% AH, 18% GC, 25% SH	5.96 [†]	NR	152 [†]	65.0	19.3	11.9	3.38
Weidner and Grant (1994b)	Ct: 30% AS, 30% CS, 17% GC	NR	NR	100	67.5	17.4	11.0	3.95
	T1: 22% AS, 22% CS, 17% GC, 15% SH	NR	NR	94	66.3	19.9*	10.5	3.36*
	T2: 17% AS, 17% CS, 15% GC, 25% SH	NR	NR	101	65.4	21.6*	10.0	3.13*
	T3: 13% AS, 13% CS, 20% AH, 19% GC, 15% SH	NR	NR	123*	67.5	18.3	10.6	3.70
	T4: 7% AS, 7% CS, 20% AH, 17% GC, 25% SH	NR	NR	112*	65.6	20.8*	10.3	3.17*

continued

Table 4 (continued). Ruminal fermentation characteristics of lactating dairy cows fed diets in which soyhulls replaced cereal grains or forages.

Study	Dietary treatments ¹	pH	NH ₃ N ² (mg/dl)	VFA (mM/L)	Ac ³ —	Pr ⁴ (mol/100 mol)	Bu ⁵ —	Ac:Pr ⁶
Soyhulls replaced grains								
Stone (1996)	Ct: 26% AS, 26% CS, 23% HMC T: 12% AS, 26% CS, 19% HMC, 14% SH	NR NR	NR NR	NR NR	64.3 63.5	20.6 22.0†	11.2 10.8	NR NR

¹AH = alfalfa hay, AS = alfalfa silage, CaS = Ca salts of palm fatty acids, CS = corn silage, Ct = control, GC = ground corn, GH = grass hay, HMC = high-moisture corn, RSB = roasted soybeans, SH = soyhulls, T = treatment. Protein, mineral, and vitamin supplements are not included.

²NH₃ N = Ammonia nitrogen.

³Acetate.

⁴Propionate.

⁵Butyrate.

⁶Acetate-to-propionate ratio.

⁷Not reported or determined.

*Significant effect ($P < 0.05$).

†Significant effect ($P < 0.10$).

¹Significant linear effect ($P < 0.05$).

¹Significant linear effect ($P < 0.10$).

^QSignificant quadratic effect ($P < 0.05$).

^qSignificant quadratic effect ($P < 0.10$).

appears to be more pronounced for low forage (<50%) than for high forage (>50%) diets.

The shift in the molar proportion of individual VFA has usually paralleled a decrease in ruminal pH (Kerley et al., 1992; Sarwar et al., 1992; Grigsby et al., 1993; Weidner and Grant, 1994a). The severity of the decline in ruminal pH is largely influenced by the amount and particle size of forages in the diet. For instance, replacement of chopped bromegrass hay with SH to supply 38% of total ration DM sustained ruminal pH above 6.0 (Grigsby et al., 1993). Research with lactating dairy cows, in which long alfalfa hay (20% of dietary DM) replaced a silage mixture in diets that contained 25% SH showed a more rapid postfeeding rise of pH in ruminal fluid (Weidner and Grant, 1994a). In contrast, based on data from Sarwar et al. (1992), SH should be included at much lower rates (<9%) in low-forage (<50%) than in high-forage (>50%) diets to prevent ruminal pH from dropping below 6.0. Part of this response may arise from the poor stimulation of chewing activity and salivation that occurs when diets that contain SH and relatively low amounts of forage or finely processed forages are fed (Weidner and Grant, 1994b).

The concentration of NH₃N in the ruminal fluid of dairy cows fed SH in place of grains was decreased (Sarwar et al., 1992; Mansfield and Stern, 1999), increased (Ipharraguerre et al., 2002b), or unaffected (Cunningham et al., 1993; Elliott et al., 1995). Contrasting results also were found when SH replaced forages in dairy diets (Sarwar et al., 1992; Cunningham et al., 1993). However, in most studies (Table 4) the NH₃N content of ruminal fluid remained above that required for microbial growth or protein synthesis within the rumen (Satter and Slyter, 1974; Hoover, 1986) for all dietary treatments. Furthermore, neither the amount of microbial N flowing to the small intestine (Cunningham et al., 1993; Mansfield et al., 1994; Ipharraguerre et al., 2002b) nor the efficiency of microbial growth (Cunningham et al., 1993; Mansfield and Stern, 1994) was affected by replacing grains or forages with SH in the diet of dairy cows.

EXTENT AND SITE OF DIGESTION

DM and OM Digestion

In general, total-tract digestibility of DM was unaffected for diets of lactating dairy cows in which SH replaced cereal grain (Table 5). Likewise, feeding diets that contained SH did not affect either the percentage (Firkins and Eastridge, 1992; Sarwar et al., 1992; Cunningham et al., 1993; Mansfield and Stern, 1994; Pantaja et al., 1994; Elliott et al., 1995; Ipharraguerre et al., 2002b) or the amount (Cunningham et al., 1993; Ipharraguerre et al., 2002b) of OM apparently digested

Table 5. Nutrient digestion by dairy cows fed diets in which soyhulls replaced cereal grains or forages.

Study	Dietary treatments ¹	DMATTD ²		CPATTD ³		NDFAATD ⁴	
		(%)	△ ⁶	(%)	△	(%)	△
Soyhulls replaced grains							
Conrad and Hibbs (1961) ⁵	Ct: 44% MH, 16% CM, 28% O	69.3		NR ⁷		NR	
	T: 24% MH, 28% CM, 48% SH	76.6	+7.3*	NR		NR	
MacGregor and Owen (1976)	Ct: 44% AS, 48% GC	63.3		64.4		47.6	
	T1: 43% AS, 35% GC, 15% SH	66.3	+3.0	63.5	−0.9	62.6	+15.0 ^L
	T2: 42% AS, 23% GC, 28% SH	64.1	+0.8	65.3	+0.9	61.6	+14.0 ^L
Edionwe and Owen (1989)	Ct: 50% CS, 15% RO, 9% RC	60.5		68.5		45.7	
	T: 50% CS, 22% SH	62.8	+2.3	73.0	+4.5	46.9	+1.2
Nakamura and Owen (1989)	Ct: 50% AS, 45% GC	69.9		66.1		54.5	
	T1: 50% AS, 21% GC, 25% SH	68.6	−1.3 ^L	64.1	−2.0	63.0	+8.5
	T2: 50% AS, 48% SH	61.3	−8.6 ^L	59.4	−6.7	58.7	+4.2
Bernard and McNeil (1991)	Ct: 46% CS, 34% GC	75.7		75.5		60.1	
	T: 48% CS, 11% GC, 23% SH	76.1	+0.4	75.5	0.0	65.1	+5.0*
Firkins and Eastridge (1992)	Ct: 10% AS, 31% CS, 34% GC	NR		NR		52.6	
	T1: 10% AS, 31% CS, 13% GC, 20% SH, 11% RSB, 0.43% CaS	NR		NR		50.3	−2.3
Sarwar et al. (1992)	Ct: 22% AS, 22% CS, 38% GC	NR		64.2		47.6	
	T1: 22% AS, 22% CS, 20% GC, 19% SH, 7% RSB	NR		65.6	+1.4	56.3	+8.7 ^L
	T2: 22% AS, 22% CS, 4% GC, 34% SH, 13% RSB, 1% CaS	NR		64.7	+0.5	59.7	+12.1 ^L
Cunningham et al. (1993)	Ct: 10% AH, 40% CS, 25% HMC	64.8		63.3		41.0	
	T1: 10% AH, 40% CS, 14% HMC, 12% SH	62.5	−2.3	61.9	−1.4	46.3	+5.3 ^L
	T2: 10% AH, 40% CS, 2% HMC, 25% SH	65.3	+0.5	65.9	+2.6	54.9	+13.9 ^L
Pantoja et al. (1994)	Ct: 16% AS, 24% CS, 34% GC	NR		68.4		49.2	
	T: 16% AS, 24% CS, 16% GC, 20% SH	NR		67.5	−0.9	57.5	+8.3 ^Q
Elliott et al. (1995)	Ct: 22% AS, 22% CS, 36% GC	68.6		68.3		52.6	
(Experiment 2, main effects)	T: 22% AS, 22% CS, 18% GC, 18% SH	68.3	−0.3	66.0	−2.3	59.0	+6.4*
Ipharraguerre et al. (2002b)	Ct: 23% AS, 23% CS, 40% GC	72.6		66.8		52.0	
	T1: 23% AS, 23% CS, 30% GC, 10% SH	73.0	+0.4	65.7	−1.1	56.0	+4.0
	T2: 23% AS, 23% CS, 21% GC, 20% SH	73.0	+0.4	67.9	+1.1	58.3	+6.3
	T3: 23% AS, 23% CS, 11% GC, 30% SH	71.2	−1.4	69.6	+2.8	57.6	+5.6
	T4: 23% AS, 23% CS, 1% GC, 40% SH	69.4	−3.2	66.1	−0.7	58.9	+6.9

continued

Table 5 (continued). Nutrient digestion by dairy cows fed diets in which soyhulls replaced cereal grains or forages.

Study	Dietary treatments ¹	DMATTD ²		CPATTD ³		N DFAATD ⁴	
		(%)	Δ ⁶	(%)	Δ	(%)	Δ
Soyhulls replaced forages							
Firkins and Eastridge (1992)	Ct: 10% AS, 31% CS, 34% GC	NR ⁷		NR		52.6	
	T1: 10% AS, 20% CS, 38% GC, 7% SH	NR		NR		46.8	-5.8
	T2: 10% AS, 20% CS, 37% GC, 7% SH, 1% NaB	NR		NR		46.5	-6.1
Sarwar et al. (1992)	Ct: 22% AS, 22% CS, 38% GC	NR		64.2		47.6	
	T1: 18% AS, 18% CS, 40% GC, 5% SH	NR		68.4	+4.2	53.0	+5.4
	T2: 16% AS, 16% CS, 41% GC, 9% SH	NR		66.6	+2.4	51.7	+4.1
Cunningham et al. (1993)	Ct: 10% AH, 40% CS, 25% HMC	64.8		63.3		41.0	
	T1: 10% AH, 29% CS, 25% HMC, 12% SH	68.5	+3.7	67.1	+3.8	50.0	+9.0
	T2: 10% AH, 18% CS, 26% HMC, 25% SH	67.9	+3.1	65.6	+2.3	50.2	+9.2
Pantoja et al. (1994)	Ct: 24% AS, 36% CS, 17% GC	NR		69.8		49.4	
	T: 16% AS, 24% CS, 16% GC, 20% SH	NR		67.5	-2.3	57.5	+8.1 ^Q
Weidner and Grant (1994b)	Ct: 30% AS, 30% CS, 17% GC	66.9		61.8		50.0	
	T1: 22% AS, 22% CS, 17% GC, 15% SH	64.3	-2.6	59.3	-2.5	48.6	-1.4
	T2: 17% AS, 17% CS, 15% GC, 25% SH	72.2	+5.3*	69.6	+7.8*	60.5	+10.5*
Weidner and Grant (1994b)	Ct: 13% AS, 13% CS, 20% AH, 19% GC, 15% SH	71.6		69.3		61.5	
	T: 7% AS, 7% CS, 20% AH, 17% GC, 25% SH	70.8	-0.8	68.9	-0.4	58.0	-3.5

¹AH = alfalfa hay, AS = alfalfa silage, CaS = Ca salts of palm fatty acids, CM = concentrate mix, CS = corn silage, Ct = control, GC = ground corn, HMC = high-moisture corn, MH = mixed hay, NaB = Na bicarbonate, O = oats, RC = rolled corn, RSB = roasted soybeans, RO = rolled oats, SH = soyhulls, T = treatment. Protein, mineral, and vitamin supplements are not included.

²DM apparent total-tract digestibility.

³CP apparent total-tract digestibility.

⁴NDF apparent total-tract digestibility.

⁵Concentrate and SH were fed as a mixture and to ad libitum intake. Hay was offered in restricted amounts. Dietary treatments reported are the actual ingredient composition of the experimental rations consumed by dairy cows.

⁶Treatment effect.

⁷Not reported or determined.

*Significant effect ($P < 0.05$).

^LSignificant linear effect ($P < 0.05$).

^QSignificant quadratic effect ($P < 0.05$).

in the total gastrointestinal tract. These findings were anticipated because extensively fermentable SH were used to replace highly digestible grains (Titgemeyer, 2000). Nevertheless, others (Nakamura and Owen, 1989; Sievert and Shaver, 1993) reported that the digestibility of dietary DM or OM was depressed when SH were used to reduce the starch or NSC content of dairy diets. Those findings are in agreement with the concept that decreasing dietary NFC may hamper fermentation of DM (Stokes et al., 1991b) or OM (Stokes et al., 1991a) by ruminal microflora. In those experiments, however, dietary concentrations of NFC were varied mainly through adjustments of dietary forage components, as highlighted by Mansfield and Stern (1994). Furthermore, replacing corn with SH did not affect microbial protein synthesis (Mansfield and Stern, 1994; Ipharraguerre et al., 2002b) and sustained or even increased the concentration of total VFA (Table 4) in the rumen of dairy cows, indicating that the fermentable OM of SH is as effective as that of corn for supporting ruminal fermentation. On the other hand, replacing large ($\geq 30\%$) amounts of corn with SH in high ($\geq 50\%$) grain diets may affect the site of OM digestion without depressing the amount or proportion of OM apparently digested in the total tract (Ipharraguerre et al., 2002b). This effect may be caused by changes in the rate of passage of SH from the rumen and/or in the supply of NSC in relation to fiber from SH (Nakamura and Owen, 1989; Ipharraguerre et al., 2002b). These data suggest that the digestibility of both DM and OM of diets in which fiber from SH replace NSC from grains may remain unaffected if the amount or the physical form of dietary forages permits increases in ruminal fiber digestion that compensate for the negative effect of increasing ruminal passage rate.

In most cases, the use of SH as a replacement for forage in diets of dairy cattle has either increased (Sarwar et al., 1992; Weidner and Grant, 1994b) or sustained (Firkins and Eastridge, 1992; Cunningham et al., 1993; Pantoja et al., 1994) the percentage of DM and OM apparently digested in the gastrointestinal tract. That response may be partially explained by the highly digestible nature of SH, which generally exceeded the digestibility of the forages used in those experiments. The site of DM and OM digestion was not affected when SH partially replaced forages in diets of lactating dairy cows (Cunningham et al., 1993; Pantoja et al., 1994).

Fiber Digestion

Data from most studies indicate that the replacement of cereal grains with SH increased digestibility of NDF in the total tract (Table 5). However, many factors,

including differences among methodologies and SH sources used in some of the 11 studies, resulted in highly variable estimations of the NDF digestibility of the SH diets. In addition, few trials have evaluated the site of NDF degradation in high-producing cows that were fed SH in place of grains. To facilitate the understanding of the effects of feeding SH on NDF digestion, multiple-regression analyses were conducted using the same procedure and independent variables that were described previously. Once the best-fit model was identified, more accurate parameter estimates for the final equation were obtained using a mixed-model approach (i.e., trial was considered a random effect [St-Pierre, 2001]). Data were analyzed using the MIXED procedure of SAS (2000). Data from only seven (Macgregor and Owen, 1976; Nakamura and Owen, 1989; Bernard and McNeill, 1991; Cunningham et al., 1993; Pantoja et al., 1994; Elliott et al., 1995; Ipharraguerre et al., 2002b) of the 11 studies presented in Table 5 were pooled for the analysis because they used similar feeding regimens (e.g., diets fed as TMR), substitution strategies (only corn was replaced with SH), and experimental designs (Latin square or cross-over design). Additionally, in none of those experiments was attempt made to correct for the lower energy content of the SH diets. Diets contained from 40 to 50% forage that was supplied as mixtures of corn silage and alfalfa silage or hay. The replacement of corn with SH ranged from 12 to 45% of total dietary DM, resulting in a wide range of dietary NDF content (from 27 to 58%). In those experiments, lactating dairy cows used in 20 treatments ranged from 31 to 150 DIM, produced from 18 to 37 kg/d of milk, and consumed from 18 to 24 kg/d of DM.

The regression analysis for NDF digestibility in the total tract resulted in a best-fit model that included terms for the amount of NDF from SH in the diet expressed as percentage of the total dietary NDF (SNDF) and the two-way interaction of this variable and the amount of SH (SNDFSH) in the diet expressed as percentage of the total dietary DM:

Apparent NDF digestibility in the total tract (weighted) = $1.11 + 0.008 (\text{SNDF}) - 0.00014 (\text{SNDFSH})$; $R^2 = 0.99$.

The predicted enhancement in NDF digestibility as SH in the diet increased could be associated with the digestible nature of NDF in SH (Firkins, 1997; Titgemeyer, 2000), the reduction of negative associative effects of corn on fiber digestion (Nakamura and Owen, 1989; Sarwar et al., 1992), or both (Firkins, 1997; Titgemeyer, 2000). The mechanism by which feeding SH in place of corn resulted in a positive associative effect on fiber digestion is not clearly elucidated but, to some extent, appears to be independent of improvements on pH of ruminal fluid. For instance, Cunningham et al.

(1993), Ipharraguerre et al. (2002b), and Pantoja et al. (1994) found that feeding SH numerically decreased ruminal fluid pH below the threshold of 6.0 to 6.2 for maximal fiber digestion (Hoover, 1986; Grant and Weidner, 1992). Although the control diets resulted in a ruminal fluid pH greater than 6.0, significant (Cunningham et al., 1993; Pantoja et al., 1994) or numerical (Ipharraguerre et al., 2002b) increases for NDF digestibility in the total tract were reported when the diets that contained SH were fed to dairy cows (Table 5). Furthermore, NDF digestibility in the total tract increased because more fiber was fermented in the rumen. Using tabulated NSC values (NRC, 2001), it can be estimated that the NSC content of the diets used in those studies ranged from about 36 to 37% for control diets and from 29 to 22% for SH diets. Similarly, the concentration of NSC in the diets fed by Ipharraguerre et al. (2002b) ranged from 35.6% (control) to 15.6% (40% SH on DM basis). In contrast, when the NSC concentration was reduced from 50% (control) to 37 and 27% by adding 12 and 25% of the DM as SH to replace corn in high grain diets, respectively, the linear increase in NDF digestibility in the total tract observed for the diets that contained SH (4 and 12%, respectively) was linked to higher ruminal fluid pH (Sarwar et al., 1992). Firkins (1997) concluded that as the negative associative effects are increased, more potentially digestible fiber is shifted to the lower tract, and thus, more fiber can be fermented postruminally. Unfortunately, the contribution of each site of the gastrointestinal tract to NDF digestibility in the total tract was not determined in the study of Sarwar et al. (1992). Based on data used in this review, a reduction of negative associative effects on fiber digestion related to higher ruminal fluid pH might be expected when SH are added to diets that contain more than about 40% NSC. On the other hand, the regression model for NDF digestibility in the total tract included the interaction between the percentage of dietary SH and the proportion of dietary NDF supplied from SH, which would only increase when the content of dietary SH increase too. Because this interaction term was negative, diminishing returns on NDF digestibility should be anticipated for the effect of increasing SH in the diet. These observations support the earlier discussion as to how a reduced ruminal retention time for diets that contained SH can markedly decrease *in vivo* fiber digestion compared with *in vitro* and *in situ* estimations.

According to several reports, SH did not increase NDF digestibility in the total tract when they were used to replace forage (Table 5). Pooling data mainly from experiments in which SH were used, Firkins (1997) estimated that the NDF from nonforage sources of fiber is about 67% as effective as NDF from forage for increas-

ing fiber digestibility in the total tract. This estimation suggests that as the replacement of forage with SH increased, the amount of potentially fermentable fiber that escaped fermentation in the gastrointestinal tract may also increase due to reduced consistency of the ruminal mat, which in turn may cause a higher rate of passage or negative associative effects. This scenario is most likely to occur when SH are used to replace forage in high grain diets.

NSC Digestion

The effects on NSC digestion of feeding SH to replace either grain or forage in diets of dairy cows have not been adequately explored. Mansfield and Stern (1994) reported that the complete replacement of corn with SH (30% of dietary DM) decreased the amount of NSC apparently digested in the rumen (4.0 vs. 3.0 kg/d) and in the intestines (2.0 vs. 0.7 kg/d) but did not depress the proportion of NSC digested at either site or in the total tract (80 vs. 77%) of lactating dairy cows. Elliott et al. (1995) estimated that NSC digestibility in the total tract of dairy cows was similar (81 vs. 82%) when 18% of the DM from corn was replaced with SH. In these studies, the addition of SH reduced the percentage of NSC in the diet from about 38 to 28 (Elliott et al., 1995) and from 33 to 23 (Mansfield and Stern, 1994). More recently, the replacement of corn with SH to supply 0, 10, 20, 30, and 40% of the dietary DM linearly decreased not only the intake of NSC (from 8.5 to 3.7 kg/d) but also the amount and percentage of these carbohydrates digested in the total tract of dairy cows (Ipharraguerre et al., 2002b). These findings were related to the reduced amount and proportion of NSC digested in the rumen and in the lower digestive tract of cows fed the SH diets. Collectively, these data indicate that replacing cereal grains with SH in the diet depresses the amount of NSC digested in the gastrointestinal tract of dairy cows by reducing the intake of these carbohydrates. Thus, the level of replacement of grains with SH that will produce this effect is partly dictated by the concentration of NSC in the diet before the inclusion of SH. The percentage of NSC digested by dairy cows fed diets containing SH, however, was decreased only when SH provided a large proportion (>30%) of the dietary DM. This decrease in digestibility suggests that factors other than the intake of NSC, such as the rate of passage of SH from the rumen and/or the proportion of highly digestible NSC that pass to the small intestine (Ipharraguerre et al., 2002b), determine this response.

Nitrogen Digestion

In general, data indicate that feeding SH as a replacement either for grain or forage did not alter significantly

the apparent digestibility of N in the gastrointestinal tract of dairy cows (Table 5). When SH replaced corn to provide up to 40% of the dietary DM, the flows to the small intestine of NAN (amount and %), nonmicrobial NAN (amount and %), and microbial N remained unaltered (Ipharraguerre et al., 2002b). However, Mansfield and Stern (1994) found that when SH replaced corn to supply 30% of dietary DM, the flow of NAN (% of total N flow) to the small intestine of dairy cows increased. Because OM digestibility in the rumen and total tract were not decreased, Mansfield and Stern (1994) concluded that a decrease in NH_3N production rather than a shortage of fermentable energy in the rumen caused the changes in N flow elicited by the diets that contained SH. In other research, the addition of SH to replace corn at 12 and 25% of dietary DM also maintained OM digestibility in the rumen but tended to decrease the amount of total N and NAN reaching the small intestine (Cunningham et al., 1993). A slightly lower intake of DM from the diets that contained SH may partially explain that response (Cunningham et al., 1993). Although the addition of SH to the diet markedly reduced NSC in the diet from those two studies (Cunningham et al., 1993; Mansfield and Stern, 1994), neither the flow of microbial N nor the efficiency of microbial growth differed among treatments. Current data suggest that SH are as effective as NSC from corn in providing energy to sustain N digestion and synthesis of microbial protein in the rumen of dairy cows when they do not replace more than 40% of the dietary DM supplied as corn.

Weidner and Grant (1994b) reported an improvement in CP digestibility when a mixture of alfalfa silage and corn silage was replaced with SH to supply 25% of dietary DM (Table 5); however, reasons for the increase were not provided. Based on model predictions, Stone (1996) hypothesized that the replacement of 14% of the alfalfa silage with SH may have enhanced the availability of peptides in the rumen, resulting in increased efficiency of N utilization by ruminal microbes. However, similar rates of replacement of corn silage with SH (12 and 25% of dietary DM) did not augment the extent or the efficiency of microbial protein synthesis in other research (Cunningham et al., 1993).

Mansfield and Stern (1994) reported that feeding a diet in which SH supplied 30% of the DM decreased the intake of Met from 24 to 21 g/d but increased that of Gly from 144 to 176 g/d. Surprisingly, the greater concentration of Lys in SH protein—almost three times more than that in corn protein (Cunningham et al., 1993)—failed to increase the intake of this AA (158 vs. 178 g/d [Mansfield and Stern, 1994]). Conversely, the intake of most individual AA, including Met and Lys, was linearly increased when SH replaced increasing

amounts of corn to supply up to 40% of the dietary DM (Ipharraguerre et al., 2002b), but these differences were confounded partially with numerically higher intakes of N for the cows fed the SH diets. In the study of Mansfield and Stern (1994), feeding the SH diet resulted in similar flows of individual AA to the small intestine. In contrast, in other studies, the addition of SH to replace corn decreased the amounts of Leu, Cys, Asp, and Pro that flowed to the lower tract (Cunningham et al., 1993) but increased those of Lys and Gly (Ipharraguerre et al., 2002b). Cunningham et al. (1993) reported that the amount of Met delivered to the small intestine declined numerically from about 64 to 58 and 52 g/d for diets that contained 0, 15, and 25% SH, respectively. The trends for lower DMI and flow of microbial N to the duodenum when diets that contained SH were fed (Cunningham et al., 1993) might have explained, at least in part, the reduced amount of individual AA, particularly Met, passing to the small intestine. On the other hand, the increased intake of Lys and Gly and the numerical increase in passage to the duodenum of these AA in microbial N probably enhanced their supply to the lower gut (Ipharraguerre et al., 2002b). In addition, the flows of total AA, essential AA, and nonessential AA did not change when part of the high-moisture corn (Cunningham et al., 1993) or ground corn (Mansfield and Stern, 1994; Ipharraguerre et al., 2002b) was replaced with SH.

CONCLUSIONS

Valuable nutritional and economical factors combine to make SH a suitable alternative feed for lactating dairy cows. From a nutritional standpoint, the physicochemical characteristics of SH, such as the high content of digestible fiber, permit the use of this byproduct feed as either a replacement for forage or grain in dairy diets. Data suggest that SH can replace relatively large (<30%) amounts of the DM supplied as corn in high grain diets ($\geq 50\%$ of dietary DM) without negatively affecting either the fermentation and digestion of nutrients in the gastrointestinal tract or the performance of mid- to late lactation dairy cows. Similarly, data suggest that SH might successfully replace considerable amounts ($\leq 25\%$) of the DM provided as forages in dairy diets when the supply of effective fiber, which includes a chemical and a physical component, remains adequate after including SH. However, several factors, as well as their interactions, should be considered in order to understand or predict the performance of dairy cows fed diets containing SH. In the case of lactating cows fed large amounts of both forage and concentrate, it is important to consider the type of carbohydrate being replaced by SH when other ingredients are added to

the diet; the amount, type, and physical form of the dietary forage; and the incidence of either negative or positive associative effects before and after the inclusion of SH to the original diet. Unfortunately, the paucity of data from experiments in which SH constituted more than 25 to 30% of the dietary DM restricts the ability to identify the maximal amount of SH that can be used in dairy diets. In particular, more information is needed to quantify how replacing large (≥ 25 to 30%) amounts of DM supplied as either cereal grains or forages with SH affect the performance of dairy cows. A better understanding and quantification of changes in the ruminal digestion kinetics, particularly in the outflow rate of SH from the rumen, is of crucial relevance. Furthermore, research is needed to clearly identify the site of nutrient digestion, especially of NSC, and to further understand the complexity of the digestive process that occurs when grains or forages are partially replaced with SH in diets for lactating cows.

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