INTRODUCTION

Alfalfa is the primary forage fed to lactating dairy cows; however, there is renewed interest in utilizing grass forages in lactating dairy cow diets particularly because of farm nutrient management issues. Yield and perceived quality is generally lower for grass species compared to legumes while other agronomic factors such as longer stand life, requirement for nitrogen fertilizer, and more tolerance of manure spreading, which allows for greater and more frequent manure application than on alfalfa, may make grasses more desirable. Grasses may also complement diets with high levels of co-products from the ethanol and food industries better than legumes because grasses are generally moderate to low in crude protein (CP) compared to alfalfa and most co-products contain a significant amount of CP. The purpose of this paper is to review some results and limitations of previous lactation studies that have compared the feeding value of grass and legume forages, and provide information on nutritional and cell wall differences between grasses and legumes in order to better understand the utilization of these forages by dairy cows.

HOW DO DAIRY COWS PERFORM WHEN FED GRASS VS. LEGUME DIETS?

As shown in Table 1, comparing legumes to grasses in lactation studies is confounded by the neutral detergent fiber (NDF) differences between the two species. Grasses generally contain more NDF than legumes (Table 2) and, therefore, when diets are formulated to contain an equal amount of forage DM the total dietary NDF concentration will be higher for diets containing grasses compared to legumes. Increasing dietary NDF concentration most often has a negative impact on the amount of DM consumed by lactating dairy cows (Allen, 2000) which generally translates into reduced milk production. The studies reported in Table 1 all had the grass forage higher in NDF compared to the alfalfa fed within the study, but DM intake of cows and milk production was not always compromised by a higher NDF content in the forage. Jung and Allen, (1995) reported the impact of NDF concentration on rumen fill is not always consistent as it also is influenced by the chemical composition and digestibility of the NDF fraction and particle size. The study of Cherney et al. (2004) supports this as the first cutting of both orchardgrass and fescue had a significantly higher (20 to 25% units) NDF digestibility than the first cutting alfalfa (48% NDF digestibility), but milk production and DM intake were not different between diets containing orchardgrass, fescue or alfalfa. The second cuttings of orchardgrass and fescue were similar in NDF digestibility to alfalfa and cows fed diets containing these forages were lower in DM intake and milk production than cows fed the alfalfa diet. Similarly, the study of Weiss and Shockey (1991) reported no difference in milk production or DM intake when comparing orchardgrass with 52% NDF to alfalfa with 40% NDF, but NDF digestibility of the orchardgrass
NDF was 75% compared to 49% for the alfalfa. Unfortunately, none of the studies in Table 1 reported a forage particle size.

When diets are formulated to contain similar forage NDF concentrations, less forage and more concentrate is required in grass as compared to legume diets. Unless concentrate inclusion reaches levels that depress rumen function, a lower forage-to-concentrate ratio typically will increase milk production. Therefore, milk production on grass diets should generally equal or exceed production on legume diets because of the lowered forage-to-concentrate ratio and generally higher energy (concentrate) intake of the grass-containing diet compared to legume diets when formulated for equal NDF. The study by Broderick et al. (2002) clearly illustrates how formulating for an equal dietary NDF concentration increases the concentrate amount in grass diets compared to legume diets, but refutes the premise that milk production and DM intake increase with increasing concentrate feeding (Table 1). In the study by Cherney et al. (2004), lactation diets containing alfalfa, orchardgrass or tall fescue silage were balanced to provide a similar amount of forage NDF as a percent of body weight (0.95% of BW). This resulted in forage inclusion levels of 62, 54, 51, 59, and 48% for alfalfa, orchardgrass first and second cutting and tall fescue first and second cutting, respectively. They reported no difference in DM intake or milk yield for cows fed alfalfa, first-cutting orchardgrass or first-cutting tall fescue silage, but lowered milk production and DM intake for cows fed the second cutting grass silages. The second cutting grass diets had the lowest amount of forage in the diet DM and yet cows produced the lowest amount of milk. The lactation studies of Hansen et al. (1991) and Weiss and Shockey (1991) directly compared grass and legume forage diets formulated on forage to concentrate ratio basis, ranging from 40:60 to 60:40, and found no significant differences between treatments in DM intake or milk production due to forage type or amount of concentrate included in the diet.

Based on the studies reported in Table 1, how to formulate grass based diets to optimize lactation performance isn’t well understood. What is it about grass forages that in some cases result in similar or superior lactation performance compared to legume forages while at other times performance is considerably depressed when grasses are fed? Such deviations in performance are most likely the result of variation in nutrient content and digestibility as affected by forage maturity, leaf-to-stem ratio, and cell wall structure. The following sections will discuss these differences between grass and legume forages.

NUTRIENT COMPOSITION

The nutrient composition of grasses and legumes is variable depending on many factors such as species, maturity, fertilization and soil fertility, growing environment, and harvesting conditions. The nutrient profile of the legume and grass hay and haylages shown in Table 2 is from analyses conducted by Dairyland Laboratories; Arcadia WI on samples submitted in 2006 and 2007 classified as grass or legume species. The average values indicate differences and similarities between grass and legume forages, but do not provide a comprehensive description of how grasses and legumes are different or similar in nutrient composition. The standard deviations give an indication of the greater variability in the nutrient content of samples identified as grass forage compared to legumes. The following brief discussion covers some of the similarities and
differences in fiber, protein, and mineral concentration that generally exist between grass and
legume forages when compared at similar stages of maturity.

Fiber. Grasses contain higher concentrations of NDF and acid detergent fiber than do legumes
(Table 1). The higher fiber concentrations are found in both the leaf and stem fractions of grasses
compared to legumes. Buxton and Redfearn (1997) compared forage species at a similar maturity
and reported that leaves of alfalfa and red clover plants (mid-flowering maturity) were
approximately 25% NDF and stems were 40 to 55% NDF. In contrast, the leaves and stems of
tall fescue, smooth bromegrass, and orchardgrass were approximately 50% and 70% NDF,
respectively. However, the digestibility of NDF at 48 hours as reported by Dairyland
Laboratories is very similar between legume and grass forages. Because of the higher fiber
content of grasses compared to legumes at similar stages of maturity, forage quality indexes
(RFV and RFQ) will always be lower for grasses than legumes.

Protein. The CP concentration of legumes is higher than grasses. The majority of CP in fresh
legumes or grasses is true protein with approximately 10 to 15% as non-protein nitrogen (NPN;
primarily peptides, free amino acids, and nitrates). The amount of NPN increases, as a percent of
the CP, when grasses are heavily fertilized with nitrogen or when either legumes or grasses are
fermented (30 to 65% of CP; Reid, 1994; NRC, 2001). In both hay and haylage, the solubility of
protein tends to be higher in legumes than grasses.

Minerals. Legumes tend to accumulate more total macro and micro-minerals and ash than
grasses. Of the major minerals in forages, legumes contain 2 to 3 times the calcium found in
grasses, while potassium and phosphorus concentration in legumes is only slightly higher or
similar in legumes compared to grasses (Table 1). Across all forage species, the major factors
that impact forage mineral composition include fertilizer application, stage of growth, and
environmental conditions (McDowell and Valle, 2000; Jukenvicius and Sabiene, 2007).

FORAGE FIBER: NEUTRAL DETERGENT FIBER VS. CELL WALL

Fiber, the largest single nutritional fraction of forages, is a major factor which impacts both
intake potential and available energy across all forage species (Jung and Allen, 1995). In
ruminant nutrition, forage fiber is typically measured as NDF using a gravimetric detergent
method developed by Van Soest (1964). However, NDF is only a crude and partial
representation of the cell wall material in forages. The cell wall of forage consists of
hemicellulose, cellulose, lignin and pectin. Pectin is largely soluble in neutral detergent solution
and hemicellulose in non-lignified tissues is also highly soluble (Theander and Westerlund,
1993). The NDF method tends to underestimate cell wall concentration of all forages; however,
because legumes contain more pectin than grasses, NDF underestimates total cell wall
concentration of legumes more than for grasses. Formation of heat-damaged protein which is
neutral detergent insoluble obscures estimates of cell wall concentration by the NDF method
even further. In addition, lignin is only partially recovered by the acid detergent lignin (ADL)
method; grasses have a much poorer lignin recovery in ADL than observed for legumes (Hatfield
et al., 1994). Due to these methodology issues, comparisons between grasses and legumes based
on cell wall concentration would be more useful. The following sections provide information on
grass and legume cell wall structure, and its impact on forage digestibility and digestion kinetics.
CELL WALL STRUCTURE AND IMPACT ON DIGESTIBILITY

Cell walls are complex biochemical structures that surround plant cells to provide physical rigidity, allow water transport, and protect from pest attack. All cell walls are primarily a matrix of three polysaccharides (cellulose, hemicellulose, and pectin) and lignin, but the presence of lignin is variable among plant tissues (mesophyll, parenchyma, phloem, xylem, etc.; Wilson, 1993). Grass and legume forages have distinctly different cell wall characteristics that reflect differences in tissue types, plant parts, and changes that occur during maturation. Digestion of cell wall polysaccharides in the rumen is a function of both physio-chemical characteristics of the polysaccharides themselves and their localization within the cell wall matrix, particularly as related to lignin.

Cellulose is a simple linear polymer of glucose molecules unlike hemicellulose and pectin which are complex multi-polymer groups of linear and branched polysaccharides composed of numerous monosaccharides (e.g., xylose, arabinose, mannose, galactose, rhamnose, fucose, and uronic acids; Moore and Hatfield, 1994). Primary cell walls are the thin walls that surround cells in young tissues and these primary walls are rich in pectin (up to 50% of the wall) with roughly equal amounts of cellulose and hemicellulose. Some plant tissues never develop thick secondary cell walls and such tissues do not lignify, whereas many tissues develop thick secondary walls as they mature and these walls are heavily lignified (Wilson, 1993). Secondary walls account for the majority of the total cell wall material in forages. Photosynthetic tissues have thin, non-lignified primary walls and leaves are richer in these thin walled tissues than stems. As a result, total cell wall concentration of leaves is lower and composition is shifted towards more pectin and less lignin than found in stems. Legumes have particularly large amounts of pectin in primary walls, resulting in more pectin in legume forages than grasses in both leaves and stems. Xylem and sclerenchyma tissues develop very thick secondary walls during plant maturation and these walls become highly lignified in both grasses and legumes (Jung and Engels, 2002; Jung and Casler, 2006a). These secondary cell walls contain little pectin and incorporate large amounts of cellulose and hemicellulose in a ratio of approximately two-to-one. Most tissue types in grasses lignify as they mature whereas most legume tissues do not lignify. In grasses, hemicellulose is cross linked to lignin via ferulic acid molecules (Ralph et al., 1998). Lignin/polysaccharide cross links are thought to occur in legume cell walls, but such cross links have not been identified and do not involve ferulates.

Because relatively few tissue types develop thick secondary walls in legume leaves, the total cell wall concentration of legume leaves does not increase dramatically with maturity as compared to grass leaves (Jung and Engels, 2002). Legume stems deposit large amounts of thick, lignified xylem tissue during maturation and almost all grass stem tissues develop thick, lignified walls; therefore, cell wall concentration and lignification of stem material increases greatly in both legumes and grasses due to maturation. Development of the stem at flowering results in rapid accumulation of cell wall material in grasses whereas legumes add leaf and stem material simultaneously (Åman and Lindgren, 1983; Nordkvist and Åman, 1986). As forages mature, leaf-to-stem ratio of the herbage declines. The overall result of these differences observed in tissues, plant parts, and response to maturation of grasses and legumes account for several patterns observed in whole herbage (Figure 1). Legume herbage contains less total cell wall
material when immature than does grass herbage and the proportion of pectin in the cell wall material is higher. Total cell wall concentration and lignin proportion increase with maturation of both forage types, although the rate of increase can be greater for legumes if leaf losses are significant before or during harvest. Grasses, have a higher hemicellulose-to-cellulose ratio than legumes and this difference is more marked in immature than mature forages. Lignin concentrations are greater in legumes than grasses, but the degree of difference is very lignin method dependent (Hatfield et al., 1994).

While cellulose is composed of simple linear chains of glucose, the individual chains are very tightly packed into large fiber bundles which results in slower cellulose digestion by rumen microbes than digestion rates observed for hemicellulose or pectin (Hatfield and Weimer, 1995; Weimer, 1996). However, all cell wall polysaccharides are completely degradable if non-lignified. Lignification of cell walls dramatically reduces extent of cellulose and hemicellulose digestion but has less impact on pectin digestion, particularly of legumes (Jung and Deetz, 1993). The lesser impact of lignin on pectin digestion in legumes is because tissues which contain large amounts of pectin in legumes never lignify whereas the pectin-rich primary walls of most grass tissues do incorporate at least some lignin (Jung and Engels, 2002; Jung and Casler, 2006a). Ferulate esters of hemicellulose in grasses slow rate of cell wall digestion, but these esters can be cleaved by rumen microorganisms so that potential extent of digestion is not reduced (Grabber et al., 1998). However, ferulate cross links of lignin to hemicellulose cannot be broken; therefore, these cross links reduce potential extent of digestion in grasses.

FIBER AND CELL WALL DIGESTION KINETICS

Extent of cell wall polysaccharide digestion by ruminants is largely a function of rate of digestion and retention time in the rumen (Mertens, 1993). As noted above, cell wall polysaccharides differ in their intrinsic rates of digestion due to their structure even though potential extent of digestion is 100% given sufficient time. Cell wall matrix structure reduces rate and potential extent of digestion below the intrinsic rates of digestion of the polysaccharides due to the impact of ferulates and lignin. Beyond these chemical structure effects at the cell wall level of organization, tissue organization imposes additional limitations on digestion. Rumen bacteria cannot move from interior of one plant cell to the next plant cell by digesting the intervening cell wall if that wall is lignified (Engels, 1989). Therefore cell wall digestion of lignified tissues is limited to the interior edge of the wall for individual plant cells, which is the least lignified layer, and the plant cell must have been ruptured by mastication or mechanical grinding to allow access into the cell by bacteria (Wilson and Mertens 1995). This is in contrast to non-lignified tissues where rumen bacteria can degrade the cell wall completely and move between plant cells via digestion of the intervening walls. When forages are very finely ground to rupture virtually every plant cell, the negative impact of lignified walls to bacterial access is largely removed and cell wall polysaccharide digestibility increased dramatically (Figure 2; (Jung et al., 2000). The cumulative effect of these various factors is that leaves, because they contain larger proportions of non-lignified tissues, will have faster rates of cell wall digestion than stems, and legumes leaves will be much more quickly digested than grass leaves because of the differences in tissue lignification of these forages. Legume stems also exhibit faster rates of cell wall digestion than do grass stems because of the presence of more non-lignified tissues in legume stems, but potential extent of digestion is greater for grass stems (Buxton, 1989). This
difference in ultimate digestibility of stem material is because the thick-walled xylem tissues of legumes are virtually indigestible, even with very long rumen residence times, whereas thick-walled sclerenchyma tissue in grass stems is slowly digestible and a much greater extent of digestion can occur with time (Figure 3; Jung and Engels, 2002; Jung and Casler 2006b). Clearly there is a fundamental difference in lignin’s impact on cell wall polysaccharide digestion between grasses and legumes; however, the nature of this difference and how that controls digestion is unknown.

Retention time of feed particles in the rumen decreases as feed intake increases and particle size of the feed is reduced (Faichney, 1986). Control of feed intake and particle size reduction are complex processes, and are strongly related (Wilson and Kennedy, 1996). Alfalfa disappeared from the rumen of dairy cows more quickly than did perennial ryegrass when offered in two 2-h meals (Waghorn et al., 1989). Similar results were observed with sheep fed alfalfa or Italian ryegrass in a 4-h meal period (Grenet, 1989). A portion of the difference between alfalfa and the grasses was due to the faster rate of digestion of the alfalfa, but particle size reduction was also faster for alfalfa. Because digestion itself accounts for little reduction in particle size (Grenet, 1989); susceptibility of cell walls to mechanical rupture by mastication must also have been greater for the alfalfa than the ryegrass. The greater susceptibility to particle breakdown of legumes compared to grasses is also readily apparent when forages are mechanically ground; grasses tend to shred and produce long, thin pieces whereas legumes typically grind to finer and more cubical shapes. This increased susceptibility to particle size reduction of legumes is likely due to a combination of cell size of plant tissues, tissue organization, and cell wall thickening.

Given the high levels of feed intake and resultant short rumen retention time of dairy cows, the more rapid rate of digestion for legumes than grasses, and the faster particle size breakdown of legumes; one would predict that legumes should be more digestible and result in greater milk production than will grasses. However as described earlier in this paper, milk production is often similar or even greater with diets containing grasses rather than alfalfa. Certainly supplemental ingredients and grain-to-forage ratios strongly influence the outcome, but another factor is the relationship between rumen retention time and digestion kinetics. Satter et al. (1999) provided an analysis based on the model of Waldo et al. (1972) that showed potential extent of digestion had a larger impact than rate of digestion on predicted extent of fiber digestion at rumen retention times beyond 15 h. Incorporating rate of passage into such a model found that all three factors (rate and extent of digestion, and rate of passage) contributed equally to predicting extent of digestion (Jung and Allen, 1995). Therefore, the higher potential extent of grass cell wall digestion may also contribute to better than expected performance of dairy cows fed grass-based diets.

**IMPLICATIONS**

Given the complexity of factors that determine the composition and digestibility of forages; blanket statements claiming superiority of alfalfa or any other forage for milk production are impossible. High levels of performance have been observed for cows fed either legume or grass forages when included as part of a typical total mixed diet with multiple ingredients. The standard advice to feed high quality (low fiber, high digestibility) forages to lactating dairy cows as part of appropriately balanced mixed diets still prevails. However, the criteria or parameters
on which to formulate diets to optimize milk production from grasses is less well understood than it is for alfalfa or corn silages. Current forage analysis methods are incomplete in identifying the chemical or nutritional components in grasses which alter their digestion and support high milk production. Better methods of forage evaluation are needed to discriminate among and between forage species as to their nutritional superiority and quality. While in vitro or in situ NDF digestibility analysis can offer some information about forage quality, this test alone cannot account for all the relevant sources of variation that determine forage quality.

LITERATURE CITED


Table 1. Lactation studies comparing legume and grass forages.

<table>
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<tr>
<th>Reference</th>
<th>Forage Source</th>
<th>Forage: Concentrate</th>
<th>Forage NDF % DM</th>
<th>Diet NDF % DM</th>
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<th>3.5% FCM lb/day</th>
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1 A – alfalfa, B – brome grass, O – orchard grass, F – tall fescue, PR – perennial ryegrass.
2,3 Denotes first and second cuttings, respectively.
a,b – uncommon superscripts within a study differ p < .05
Table 2. Nutrient profile summary of legume and grass hays and haylages from Dairyland Laboratories for 2006 and 2007.

<table>
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<th>Nutrient</th>
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<td>SD¹</td>
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<td>ADF, %</td>
<td>32.0</td>
<td>3.14</td>
<td>34.7</td>
<td>4.24</td>
</tr>
<tr>
<td>NDF, %</td>
<td>40.2</td>
<td>3.91</td>
<td>52.1</td>
<td>6.13</td>
</tr>
<tr>
<td>NDF Digestion 48 hour, %NDF</td>
<td>52.6</td>
<td>4.50</td>
<td>53.2</td>
<td>7.32</td>
</tr>
<tr>
<td>IVTDM Digestion, % 48 hour</td>
<td>81.2</td>
<td>3.00</td>
<td>75.7</td>
<td>5.49</td>
</tr>
<tr>
<td>Lignin, % DM</td>
<td>8.1</td>
<td>1.09</td>
<td>5.8</td>
<td>1.54</td>
</tr>
<tr>
<td>Fat, % DM</td>
<td>3.3</td>
<td>0.59</td>
<td>4.0</td>
<td>0.77</td>
</tr>
<tr>
<td>Sugar, % DM</td>
<td>5.3</td>
<td>1.29</td>
<td>5.5</td>
<td>1.44</td>
</tr>
<tr>
<td>Ash, % DM</td>
<td>11.1</td>
<td>1.61</td>
<td>9.9</td>
<td>2.06</td>
</tr>
<tr>
<td>Calcium, % DM</td>
<td>1.37</td>
<td>0.19</td>
<td>0.65</td>
<td>0.24</td>
</tr>
<tr>
<td>Phosphorus, % DM</td>
<td>0.34</td>
<td>0.04</td>
<td>0.33</td>
<td>0.05</td>
</tr>
<tr>
<td>Potassium, % DM</td>
<td>2.64</td>
<td>0.41</td>
<td>2.64</td>
<td>0.64</td>
</tr>
<tr>
<td>RFV</td>
<td>150</td>
<td>20.4</td>
<td>113</td>
<td>18.0</td>
</tr>
<tr>
<td>RFQ</td>
<td>173</td>
<td>26.7</td>
<td>126</td>
<td>21.0</td>
</tr>
</tbody>
</table>

¹ Standard deviation, ± 1 SD from the average accounts for 66% of the analyzed values reported.
Figure 1. Impact of forage maturity at harvest on concentration of cell wall components in alfalfa and orchardgrass (Åman and Lindgren, 1987; Nordkvist and Åman, 1986).
Figure 2. Increased 96-h in vitro rumen digestibility of cell wall polysaccharides when virtually all plant cells in alfalfa and corn stems were fractured by ballmilling compared to a 1-mm grind where particles contain many intact cells where lignified walls could block bacterial access to non-ruptured cells (Jung et al., 2000).
Figure 3. In vitro rumen digestion of alfalfa and corn stem tissues after 24- and 96-h incubations. Non-lignified tissues are quickly and completely degraded: alfalfa epidermis (epi), collenchyma (coll), and cambium (cam); corn phloem (ph). Lignified phloem fiber (pf) and xylem tissues in alfalfa are only partially digested in 24 h with little further digestion later whereas lignified corn epidermis, parenchyma (par), and sclerenchyma (scl) tissues are substantially thinned over a longer digestion time.