

# Forage Digestibility: The Intersection of Cell Wall Lignification and Plant Tissue Anatomy

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## Introduction

Ruminants evolved their multi-compartment digestive tract to effectively process plant material containing large amounts of cell wall material. We rely on forages as the sole or major feed resource for domestic ruminant animal production, even in the grain intensive North American beef and dairy systems. Unfortunately, digestibility of forages is extremely variable and almost always less than grains. Because cell wall material is the single largest component of forages, the digestibility of forage cell walls is a primary determinant of animal productivity and efficiency. The plant cell wall is a complex matrix of polymers that surrounds every plant cell. Walls provide the physical support required for plants to grow upright in terrestrial habits and serve many other important functions, such as being a barrier to attack by pathogens and insects. While all cell walls share some basic chemical characteristics, striking differences exist among plant tissues in cell wall concentration, composition, and structural organization. Cell walls of many tissues undergo dramatic shifts in chemical characteristics during maturation. Leaves and stems differ in the types and proportions of tissues they contain, and grasses and legumes differ in cell wall composition and tissue profiles. Growth environment also modulates plant and cell wall development. These sources of variation must be understood if performance of ruminants fed forages is to be accurately predicted. Cellulose and the other cell wall polysaccharides can be completely digested by the rumen microflora, but only when isolated from the wall. Understanding how cell wall component interactions limit microbial digestion is critical. My objective is to integrate knowledge of cell wall composition and structure, plant and tissue anatomy, and plant maturation as factors influencing the digestion of forage cell wall material in the rumen.

## Cell Wall Characteristics

### *Composition*

When we refer to “fiber” in ruminant nutrition we are in fact discussing plant cell wall structure. Typically fiber is measured as neutral detergent fiber (NDF) as part of the detergent fiber analysis system (Van Soest, 1967). For a grass NDF is a reasonably accurate measure of cell wall concentration, as compared to legumes where solubility of pectin in neutral detergent results in a significant under-estimate of cell wall

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concentration by the NDF method (Theander and Westerlund, 1993). Acid detergent lignin (ADL) is a severe under-estimate of actual lignin concentration in grasses, giving lignin concentration estimates that are only one half to one quarter of Klason and acetyl bromide lignin methods (Hatfield and Fukushima, 2005). Lignin is lost in the ADL procedure at the acid detergent fiber (ADF) step because some lignin, particularly for grasses, is soluble in acid at high temperature (Lowry et al., 1994). Because forage hemicellulose and cellulose concentrations are calculated by difference in the detergent system (NDF minus ADF and ADF minus ADL, respectively), the loss of lignin at the ADF step results in concentration over-estimates of these cell wall polysaccharides (Theander and Westerlund, 1993). These comments are not meant to belittle the detergent system as it has been of great value in ruminant nutrition, but only to warn readers that detergent data suffer from known shortcomings.

Cellulose is the single most abundant component in cell walls and composed exclusively of linear glucose chains. The other wall polysaccharides are categorized into two groups, hemicellulose and pectin, that are characterized by extraction methods rather than chemical structure similarities. Hemicelluloses are polysaccharides extracted with alkali from delignified cell walls. Hemicelluloses include xylans, xyloglucans, and mannans (Åman, 1993). Pectins are an even more diverse set of polysaccharides, sharing the trait of being soluble in oxalic acid, and legumes contain more pectins than do grasses. Lignin is a polymer composed of phenylpropanoid monolignol units (Lapierre, 1993). All forages contain both guaiacyl- and syringyl-type lignin, and small amounts of *p*-hydroxyphenyl-type lignin. The hydroxycinnamic acids, ferulic and *p*-coumaric, are the other phenylpropanoid components of grass cell walls but are virtually absent from legume cell walls (Hartley and Ford, 1989). Ferulic acid is esterified to arabinose molecules of arabinoxylans. Some *p*-coumaric acid is similarly esterified to arabinoxylan, but most is esterified to syringyl-type lignin. Arabinoxylan polymers are cross linked through diferulates in grasses (Ralph et al., 1994).

### *Tissue Localization and Development*

All plant cells are surrounded by a primary wall. The primary wall is rich in cellulose, has a relatively random cellulose microfibril orientation, and contains more protein than found in secondary wall layers. Lesser amounts of hemicellulose and pectin are present in primary walls and lignin is initially absent. Some plant tissues never develop walls beyond the initial thin primary wall (Wilson, 1993). Examples of such tissues include mesophyll and phloem tissue in grasses and legume leaves. Thin primary walls are retained by phloem in grass stems and chlorenchyma, secondary phloem, and cambium in legume stems. The epidermis of all plants thickens and develops a waxy exterior layer to prevent desiccation. Vascular tissues (phloem and xylem) are arranged in bundles (Wilson, 1993). These vascular bundles form parallel veins in grass leaves and a branching network in legume leaves. In grass stems the vascular bundles are distributed throughout the stem cross section, but the vascular bundles are more numerous and smaller in size in the exterior portion of the stem referred to as rind. In legume stems the cambium separates the phloem and xylem tissues; and cambial division adds additional xylem tissues (fibers and vessels) as the plant matures, increasing diameter of the stem (Jung and Engels, 2002). Grasses do

not undergo cambial expansion of stem diameter. Secondary wall deposition and lignification do not begin until cells complete growth and elongation. Secondary cell walls are rich in cellulose and hemicellulose, and contain little pectin or protein (Moore and Hatfield, 1994). Once secondary wall thickening begins, the original primary wall is the first region to lignify, with lignification then progressing into the secondary wall (Terashima et al., 1993). The final concentration of lignin is actually higher in primary than secondary wall, but because the secondary wall is larger in volume the total amount of lignin present in secondary wall exceeds that in primary wall (Terashima et al., 1993). Ferulates in grass cell walls act as nucleation sites for lignin deposition to occur (Ralph et al., 1995). Monolignols exported to the cell wall undergo a free-radical reaction with ferulate esters to form a dimer structure to which additional monolignols attach to form the growing lignin polymer (Figure 1). Because only ether linkages of ferulate to lignin can be quantified by current methods (Ralph et al., 1992), cross linking in grass cell walls is under-estimated by ~ 50% (Grabber et al., 1995). Some of the diferulate structures that cross link arabinoxylan chains also become involved in cross links to lignin (Ralph et al., 1998). Although it is thought that cross linking occurs in legume cell walls, such cross linking does not involve ferulates and has not been chemically characterized. Another difference between grasses and legumes is that grass epidermis becomes lignified whereas legume epidermis remains non-lignified.

### *Plant Maturation*

The greatest single factor that impacts the cell wall concentration and composition of forages is the plant maturation process. Accumulation of stem mass exceeds leaf mass addition. Stems contain a higher proportion of thick-walled tissues (sclerenchyma, xylem fiber, and xylem vessel) tissues and less photosynthetic tissues (mesophyll, chlorenchyma) than found in leaves, resulting in stems having a higher cell wall concentration than leaves (Wilson and Kennedy, 1996). Overall herbage cell wall concentration increases as the leaf-to-stem ratio shifts towards a greater proportion of stem. Associated with the increase in herbage cell wall concentration during maturation is a shift towards higher cellulose, xylan, and lignin concentrations, and reduced pectin in the cell wall. These changes in composition reflect the composition of secondary walls compared to primary walls, and the fact that stems contain more tissues that accumulate secondary wall material.

## **Lignification and Digestibility**

### *Lignin Concentration*

Lignin concentration of forages has been reported to be negatively correlated with digestibility of forages for 50 years (Johnson et al., 1962). Although this negative relationship is often reported for dry matter digestibility, lignin is actually impacting cell wall digestibility and not digestion of the non-cell wall nutrients. Generally lignin concentration accounts for 40 to 60% of the variation in cell wall digestion (Figure 2a), with higher correlations observed when data sets are restricted to a single forage species and the range in maturity among samples is great. The negative impact of lignin

on cell wall digestibility of grasses often appears to be greater for grasses than for legumes because of the steeper slope of regressions for digestibility versus lignin for grasses (Smith et al., 1972). At least part of this disparity between forage types is because ADL under-estimates total lignin concentration and this effect is greater for grasses than legumes. When lignin is measured by the more accurate Klason lignin method (Jung et al., 1999b), this difference in relative impact of lignin concentration on digestibility between forages types is greatly reduced. However, correlations of ADL with digestibility are often greater than with Klason lignin (Jung et al., 1997). The chemical nature of the ADL fraction that makes this lignin fraction a better predictor of digestibility is unknown. These observations have led to the accepted dogma that lignin is the primary limitation to forage cell wall digestibility. But if maturity variation is limited, such as occurs when forages are harvested at a specific maturity target in breeding studies and under good management practices, then the relationship between lignin concentration and cell wall digestibility becomes largely non-significant (Figure 2b). This realization resulted in suggestions that lignin structure, cell wall cross linking, and other structural features are additional factors that impact cell wall digestion (Jung and Deetz, 1993).

### *Lignin Structure*

The brown-midrib (*bm*) mutants in corn, sorghum, and pearl millet all share a reddish-brown coloration in the leaf midrib vein and lower stem, reduced lignin concentration, and greater cell wall digestibility (Cherney et al., 1991). In addition to reduced lignin concentration, the *bm* mutants also have alterations in their syringyl-to-guaiacyl (S/G) monolignol composition (Kuc et al., 1968). Variation in monolignol composition will change three-dimensional lignin structure and possibly influence the inhibition of cell wall digestibility by lignin. Jung and Deetz (1993) proposed that S/G monolignol ratio was an additional factor beyond simple lignin concentration that impacts cell wall digestibility; however, recent data have largely excluded S/G ratio as a factor in cell wall digestibility (Jung et al., 1999a). While S/G monolignol ratios do not alter lignin's impact on cell wall digestibility, this does not prove lignin structure has no impact on digestibility. Grabber et al. (1998) found that coniferylaldehyde incorporation into lignin severely reduced enzymatic digestion of cell walls from corn tissue culture. While aldehydes are not normal monolignols, some transgenic plants engineered to reduce lignin concentration accumulated aldehyde units (Jackson et al., 2008). To date aldehyde containing lignins have not decreased cell wall digestibility of transgenic plants; however, this is probably due to the reduced lignin concentrations of the transgenic plants (Kim et al., 2003).

### *Ferulate Cross Linking*

In vitro rumen digestibility of cellulose was decreased when cross linked to polyeugenol (a crude lignin model) compared to simply mixing free polyeugenol with cellulose (Jung and Ralph, 1990). When biosynthesis of ferulate esters on arabinoxylans and subsequent cross link formation to lignin were reduced by manipulating corn cell culture conditions, ferulate cross links inhibited cell wall

digestibility and the impact of cross linking on digestion was independent of lignin concentration in this model system (Grabber, 2005). Casler and Jung (1999) identified individual smooth bromegrass plants that had low or high concentrations of ferulate ether cross links and low and high Klason lignin concentration. In vitro NDF digestibility was greater for plants with low ferulate cross linking or low lignin concentrations; however, the relative impact of ferulate cross linking was larger than the negative impact of lignin. Recently Jung and Phillips (2010) reported the discovery of a corn mutant with reduced ferulate ester deposition in seedling leaves. It was hypothesized that if ferulate ester deposition was reduced by the seedling ferulate ester (*sfe*) mutation, then the number of ferulate cross links that could form in mature tissues would also be lower - thereby improving cell wall digestibility. Corn stover of *sfe* mutant lines harvested at silage maturity had lower ferulate ether cross link concentration and improved in vitro rumen NDF and cell wall polysaccharide digestibility compared to a near-isogenic control line (Jung and Phillips, 2010). When *sfe* corn silage was included in a mixed diet fed to dairy cows, feed intake and milk production were increased (Jung et al., 2011). Cows fed diets containing *sfe* corn silage were less selective against cell wall material in feed consumed and total tract in vivo digestibility of cell wall polysaccharides was increased.

## Tissue Digestion

### *Lignification Effects*

While the preceding discussion focused on the fact that lignin concentration alone does not explain cell wall digestibility, microscopic data clearly illustrate that cell wall lignification is critical to potential digestibility of forage tissues. Non-lignified tissues are always completely digestible; however, if a tissue begins to deposit lignin in its cell wall, then digestibility rapidly declines (Figure 3). Thick, lignified grass sclerenchyma cell walls are extensively digested during prolonged rumen exposure whereas similar thick, lignified legume xylem walls show only minimal digestion. But any tissue with lignified walls is never completely digestible – a thin lignified residual wall always remains even after extremely long rumen exposure times (Engels, 1989). This residual non-digestible, thin lignified wall corresponds to the original, but intensely lignified, primary wall. An important outcome of the intense lignification of primary walls is that these structures become an absolute barrier to rumen bacteria moving from one plant cell to another by digestion of the intervening cell wall. Rumen bacteria digest cell walls from the lumen side (interior) of cells, attacking the lumen side of the secondary wall first and progressively digesting the wall towards the primary wall (Engels, 1989). Digestion halts when the structure of the remaining lignified wall becomes completely non-digestible (Chesson, 1993). In non-lignified tissues rumen bacteria can access adjoining cells by completely digesting the intervening walls (Engels and Jung, 2005).

### *Accessibility*

Building on observations that rumen bacteria cannot access adjoining plant cells by digesting through lignified primary walls, Wilson and Mertens (1995) proposed that

significant amounts of potentially digestible cell wall polysaccharides are unavailable to rumen digestion because cells within forage particles have not been physically ruptured by either chewing or mechanical grinding. A typical size forage particle found in the rumen contains many hundreds of cells and upwards of 1/3<sup>rd</sup> of these cells will not have been ruptured by chewing or grinding. Non-ruptured cells within such forage particles will be inaccessible to rumen bacteria if the cells are surrounded by adjacent cells with lignified primary walls. While the accessibility hypothesis of Wilson and Mertens (1995) was focused on grasses, the concept also holds true for legumes. In vitro rumen digestibility of corn and alfalfa stem cellulose and xylan were increased 47 to 327% by ball milling to pass a 106 µm screen (when almost every cell should have been ruptured), compared to grinding them to pass through a 1-mm screen (Jung et al., 2000). Microscopic analysis of tissue digestion in alfalfa stem pieces (2 mm in length) that had been exposed to rumen bacteria for 24 h showed that the depth of digestion into a stem piece from an exposed end was limited to the average length for each lignified cell type (Engels and Jung, 2005). In contrast to lignified tissues, digestion of non-lignified tissues extended deep into the alfalfa stem particles and through many layers of non-ruptured cells. These results illustrate both how lignified primary walls of non-ruptured cells are an absolute barrier to bacterial digestion and that potentially digestible cell wall material is inaccessible within non-ruptured cells of large forage particles.

## Conclusions

Our understanding of the factors that impact cell wall digestion of forages has improved dramatically in recent years. The old rule that immature forages are the most digestible is still correct, but now we can explain why digestibility declines with forage maturation. Lignin is the most important factor that limits cell wall digestion; however, it is through an understanding of the details of forage lignification and how this impacts the process of digestion that forage quality will be improved. This understanding offers new opportunities to develop forages with greater cell wall digestibility.

## References

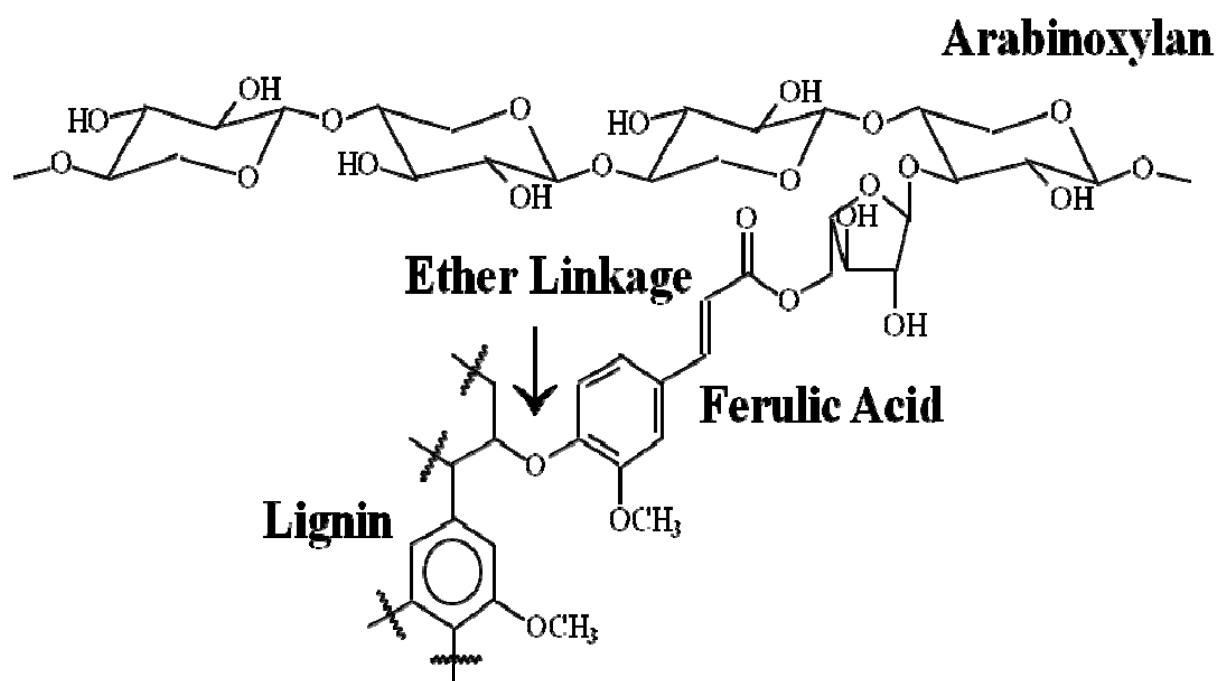
- Åman, P. 1993. Composition and structure of cell wall polysaccharides in forages. p. 183-199, *In* H.G. Jung, D.R. Buxton, R.D. Hatfield, and J. Ralph, eds. Forage Cell Wall Structure and Digestibility. ASA-CSSA-SSSA, Madison, WI, USA.
- Casler, M.D., and H.G. Jung. 1999. Selection and evaluation of smooth bromegrass clones with divergent lignin and etherified ferulic acid concentration. *Crop Sci.* 39:1866-1873.
- Cherney, J.H., D.J.R. Cherney, D.E. Akin, and J.D. Axtell. 1991. Potential of brown-midrib, low-lignin mutants for improving forage quality. *Adv. Agron.* 46:157-198.
- Chesson, A. 1993. Mechanistic models of forage cell wall degradation. p. 347-376, *In* H.G. Jung, D.R. Buxton, R.D. Hatfield, and J. Ralph, eds. Forage Cell Wall Structure and Digestibility. ASA-CSSA-SSSA, Madison, WI, USA.

- Engels, F.M. 1989. Some properties of cell wall layers determining ruminant digestion. p 80-87, *In* A. Chesson and E.R. Orskov, eds. Physico-Chemical Characterization of Plant Residues for Industrial and Feed Use. Elsevier Applied Science, London.
- Engels, F.M., and H.G. Jung. 2005. Alfalfa stem tissues: impact of lignification and cell length on ruminal degradation of large particles. *Anim. Feed Sci. Technol.* 120:309-321.
- Grabber, J.H. 2005. How do lignin composition, structure, and cross-linking affect degradability? A review of cell wall model studies. *Crop Sci.* 45:820-831.
- Grabber, J.H., R.D. Hatfield, J. Ralph, J. Zon, and N. Amrheins. 1995. Ferulate cross-linking in cell walls isolated from maize cell suspensions. *Phytochem.* 40:1077-1082.
- Grabber, J.H., J. Ralph, and R.D. Hatfield. 1998. Severe inhibition of maize wall degradation by synthetic lignins formed with coniferaldehyde. *J. Sci. Food Agric.* 78:81-87.
- Hartley, R.D., and C.W. Ford. 1989. Phenolic constituents of plant cell walls and wall biodegradability. p. 137-145, *In* N.G. Lewis and M.G. Paice, eds. Plant Cell Wall Polymers: Biogenesis and Biodegradation. American Chemical Society, Washington, DC.
- Hatfield, R.D., and R. Fukushima. 2005. Can lignin be accurately measured? *Crop Sci.* 45:832-839.
- Jackson, L.A., G.L. Shadle, R. Zhou, J. Nakashima, F. Chen, and R.A. Dixon. 2008. Improving saccharification efficiency of alfalfa stems through modification of the terminal stages of monolignol biosynthesis. *Bioenerg. Res.* 1:180-192.
- Johnson, R.R., B.A. Dehority, J.L. Parson, and H.W. Scott. 1962. Discrepancies between grasses and alfalfa when estimating nutritive value from in vitro cellulose digestibility by rumen microorganisms. *J. Anim. Sci.* 21:892-896.
- Jung, H.G., and D.A. Deetz. 1993. Cell wall lignification and degradability. p. 315-346, *In* H.G. Jung, D.R. Buxton, R.D. Hatfield, and J. Ralph, eds. Forage Cell Wall Structure and Digestibility. ASA-CSSA-SSSA, Madison, WI, USA.
- Jung, H.G., and F.M. Engels. 2002. Alfalfa stem tissues: cell-wall deposition, composition, and degradability. *Crop Sci.* 42:524-534.
- Jung, H.G., M.A. Jorgensen, J.G. Linn, and F.M. Engels. 2000. Impact of accessibility and chemical composition on cell-wall polysaccharide degradability of maize and lucerne stems. *J. Sci. Food Agric.* 80:419-427.
- Jung, H.G., D.R. Mertens, and A.J. Payne. 1997. Correlation of acid detergent lignin and Klason lignin with digestibility of forage dry matter and neutral detergent fiber. *J. Dairy Sci.* 80:1622-1628.
- Jung, H.G., D.R. Mertens, and R.L. Phillips. 2011. Effect of reduced ferulate-mediated lignin/arabinoxylan cross-linking in corn silage on feed intake, digestibility, and milk production. *J. Dairy Sci.* 94:5124-5137.
- Jung, H.G., W. Ni, C.C.S. Chapple, and K. Meyer. 1999a. Impact of lignin composition on cell-wall degradability in an *Arabidopsis* mutant. *J. Sci. Food Agric.* 79:922-928.
- Jung, H.G., and R.L. Phillips. 2010. Putative seedling ferulate ester (*sfe*) maize mutant: morphology, biomass yield, and stover cell wall composition and rumen degradability. *Crop Sci.* 50:403-418.
- Jung, H.G., and J. Ralph. 1990. Phenolic-carbohydrate complexes in plant cell walls and their effect on lignocellulose utilization. p. 173-182, *In* D.E. Akin, L.G. Ljungdahl,

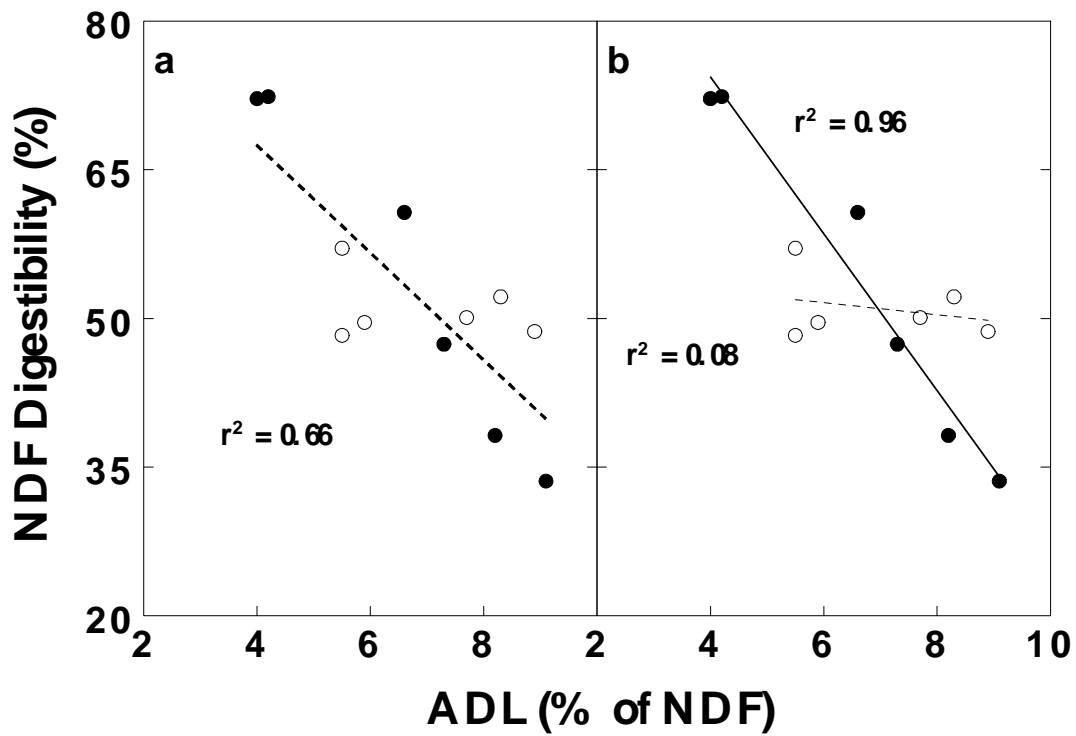
- J.R. Wilson, and P.J. Harris, eds. Microbial and Plant Opportunities to Improve Lignocellulose Utilization by Ruminants. Elsevier, New York, NY.
- Jung, H.G., V.H. Varel, P.J. Weimer, and J. Ralph. 1999b. Accuracy of Klason lignin and acid detergent lignin methods as assessed by bomb calorimetry. *J. Agric. Food Chem.* 47:2005-2008.
- Kim, H., J. Ralph, F. Lu, S.A. Ralph, A.-M. Boudet, J.J. MacKay, R.R. Sederoff, T. Ito, S. Kawai, H. Ohashi, and T. Higuchi. 2003. NMR analysis of lignins in CAD-deficient plants. Part 1. Incorporation of hydroxycinnamaldehydes and hydroxybenzaldehydes into lignins. *Org. Biomol. Chem.* 1:268-281.
- Kuc, J., O.E. Nelson, and P. Flanagan. 1968. Degradation of abnormal lignins in the brown-midrib mutants and double mutants of maize. *Phytochem.* 7:1435-1436.
- Lapierre, C. 1993. Application of new methods for the investigation of lignin structure. p. 133-166, *In* H.G. Jung, D.R. Buxton, R.D. Hatfield, and J. Ralph, eds. Forage Cell Wall Structure and Digestibility. ASA-CSSA-SSSA, Madison, WI, USA.
- Lowry, J.B., L.L. Conlan, A.C. Schlink, and C.S. McSweeney. 1994. Acid detergent dispersible lignin in tropical grasses. *J. Sci. Food Agric.* 65:41-49.
- Moore, K.J., and R.D. Hatfield. 1994. Carbohydrates and forage quality. p. 229-280, *In* J. G.C. Fahey, Jr., M. Collins, D.R. Mertens, and L.E. Moser, eds. Forage Quality, Evaluation, and Utilization. ASA-CSSA-SSSA, Madison, WI, USA.
- Ralph, J., J.H. Grabber, and R.D. Hatfield. 1995. Lignin-ferulate cross-links in grasses: active incorporation of ferulate polysaccharide esters into ryegrass lignins. *Carbohydrate Res.* 275:167-178.
- Ralph, J., R.D. Hatfield, J.H. Grabber, H.G. Jung, S. Quideau, and R.F. Helm. 1998. Cell wall cross-linking in grasses by ferulates and diferulates. p. 209-236, *In* N.G. Lewis and S. Sarkanen, eds. Lignin and Lignan Biosynthesis. ACS, Washington, DC.
- Ralph, J., R.F. Helm, S. Quideau, and R.D. Hatfield. 1992. Lignin-feruloyl ester cross-links in grasses. Part 1. Incorporation of feruloyl esters into coniferyl alcohol dehydrogenation polymers. *J. Chem. Soc. Perkin Trans.* 1:2961-2969.
- Ralph, J., S. Quideau, J.H. Grabber, and R.D. Hatfield. 1994. Identification and synthesis of new ferulic acid dehydrodimers present in grass cell walls. *J. Chem. Soc. Perkin Trans.* 1:3485-3498.
- Smith, L.W., H.K. Goering, and C.H. Gordon. 1972. Relationships of forage composition with rates of cell wall digestion and indigestibility of cell walls. *J. Dairy Sci.* 55:1140-1147.
- Terashima, N., K. Fukushima, L.-F. He, and K. Takabe. 1993. Comprehensive model of the lignified plant cell wall. p. 247-270, *In* H.G. Jung, D.R. Buxton, R.D. Hatfield, and J. Ralph, eds. Forage Cell Wall Structure and Digestibility. ASA-CSSA-SSSA, Madison, WI, USA.
- Theander, O., and E. Westerlund. 1993. Quantitative analysis of cell wall components. p. 83-104, *In* H. G. Jung, D.R. Buxton, R.D. Hatfield, and J. Ralph, eds. Forage Cell Wall Structure and Digestibility. ASA-CSSA-SSSA, Madison, WI, USA.
- Van Soest, P.J. 1967. Development of a comprehensive system of feed analysis and its application to forages. *J. Anim. Sci.* 26:119-128.



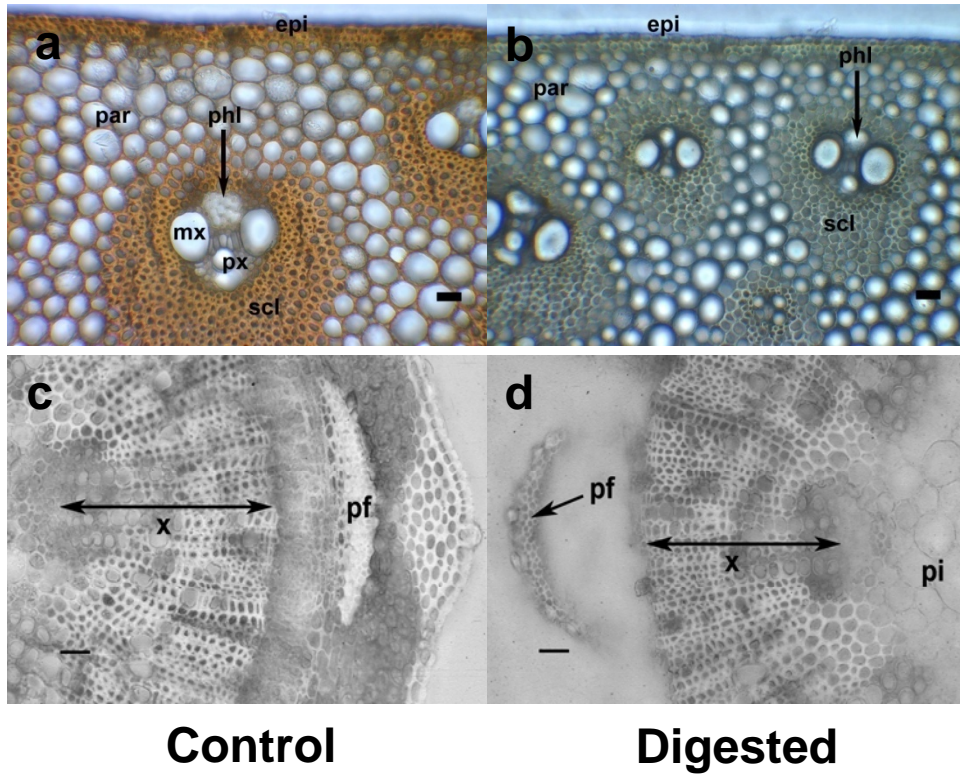
- Wilson, J.R. 1993. Organization of forage plant tissues. p. 1- 32, *In* H.G. Jung, D.R. Buxton, R.D. Hatfield, and J. Ralph, eds. Forage Cell Wall Structure and Digestibility. ASA-CSSA-SSSA, Madison, WI, USA.
- Wilson, J.R., and P.M. Kennedy. 1996. Plant and animal constraints to voluntary feed intake associated with fibre characteristics and particle breakdown and passage in ruminants. *Aust. J. Agric. Res.* 47:199-225.
- Wilson, J.R., and D.R. Mertens. 1995. Cell wall accessibility and cell structure limitations to microbial digestion of forage. *Crop Sci.* 35:251-259.



**Figure 1.** Ferulate cross linking of lignin to hemicellulose in grasses.



**Figure 2.** Relationships between acid detergent lignin (ADL) concentration and in vitro rumen neutral detergent fiber (NDF) digestibility of two grass species harvested at three maturity stages (●) and six genetic lines of one grass species harvested at a single maturity stage (○) when examined across all samples (a) and by individual sample set (b).



**Figure 3.** Digestion of corn (a & b) and alfalfa (c & d) stem tissues by rumen bacteria. Only phloem (phl) tissue in corn stems is non lignified and completely digested, whereas lignified epidermis (epi), parenchyma (par), proto- (px) and meta- (mx) xylem, and sclerenchyma (scl) are partially digestible. In contrast, many alfalfa stem tissues are non-lignified and completely digestible; however, lignified phloem fibers (pf), xylem (x), and pith parenchyma (pi) tissues are largely non-digestible.

# **SESSION NOTES**