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A 100-Year Review: Carbohydrates—Characterization, digestion, and utilization[1]

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ABSTRACT

Our knowledge of the role of carbohydrates in dairy cattle nutrition has advanced substantially in the 100 years of the publication of the *Journal of Dairy Science*. In this review, we trace the history of scientific investigation and discovery from crude fiber, nitrogen-free extract, and "unidentified factors" to our present analytical schemes and understanding of ruminal and whole-animal utilization and effects of dietary carbohydrates. Historically, advances in research and new feeding standards occurred in parallel with and fostered by new methods of analysis. The 100 years of research reviewed here has bequeathed to us an impressive legacy of information, which we will continue to grow.
Key words: carbohydrates, digestion, utilization, 100-year review

INTRODUCTION

In preparing this review on the role of carbohydrates (**CHO**) in the nutrition of dairy cattle, we were fascinated and humbled by the full scope of work done before and after 1917 that helped to set the stage for our current understanding and use of insoluble fiber and nonfiber CHO (the CHO not included in insoluble fiber). The seeds of most, if not all, of the concepts about CHO that we currently use for dairy cow nutrition were discovered and planted early, and research in the *Journal of Dairy Science* (**JDS**) served to grow and prune them (Appendix Table A1; Figure 1).

Our knowledge about the characterization, digestion, and utilization of dietary CHO has changed dramatically during the 100 years that JDS has been published. Among the nutrients, CHO are unique because they have both digestive and physiological roles. They have the broadest range in digestibility of any nutrient, ranging from 100% for sugars to 0% for indigestible fiber and they, with lignin, typically make up the greatest portion of diets (70 to 80%). The rumen evolved to selectively retain fiber for optimal utilization; both the chemical and physical attributes of CHO affect rumen function, the pattern of ruminal fermentation, and ultimately the metabolism and production of the dairy cow. Thus, nutritional characteristics of CHO have a tremendous impact on digestible nutrients and net energy. The accuracy of the characterization of CHO for their varied effects similarly has greatly influenced the utility of research, nutrient recommendations, and diet formulation for dairy cows.

Papers published in JDS are products of their time. The journal began in the era of feeding recommendations by Armsby (1917), Haecker (1913), Henry and Morrison (1915), and Savage (1913). Although researchers knew about the diversity of CHO, the most commonly reported fractions were crude fiber (**CF**) and nitrogen-free extract (**NFE**). There was some discussion of net energy, but "total digestible nutrients" was the primary "energy" descriptor used for diets. It was not until Moore et al. (1953) unequivocally demonstrated that the relationship of TDN to estimated net energy overvalued low-TDN feeds such as forages that the need to change methods of evaluating feeds, including CHO analyses, became indisputable. During the 100 yr that JDS has published, we moved from a dairy NRC (1945) in which CHO were not mentioned to the most recent dairy NRC (2001) in which a whole chapter is devoted to CHO. Such change is reflective of the changing research information and concepts that were available. Reid (1956), in an excellent review for the 50th anniversary of the American Dairy Science Association, noted at the time that the chemical nature of nutrient groups was better understood than their biochemical, physiological, and pathological effects.

In the early years of JDS, methods were often not very well described; for example, "The proximate constituents... were determined by the recognized methods" (McCandlish, 1920). As more analyses became available and procedures were better defined, method descriptions improved. In the early years, papers gave

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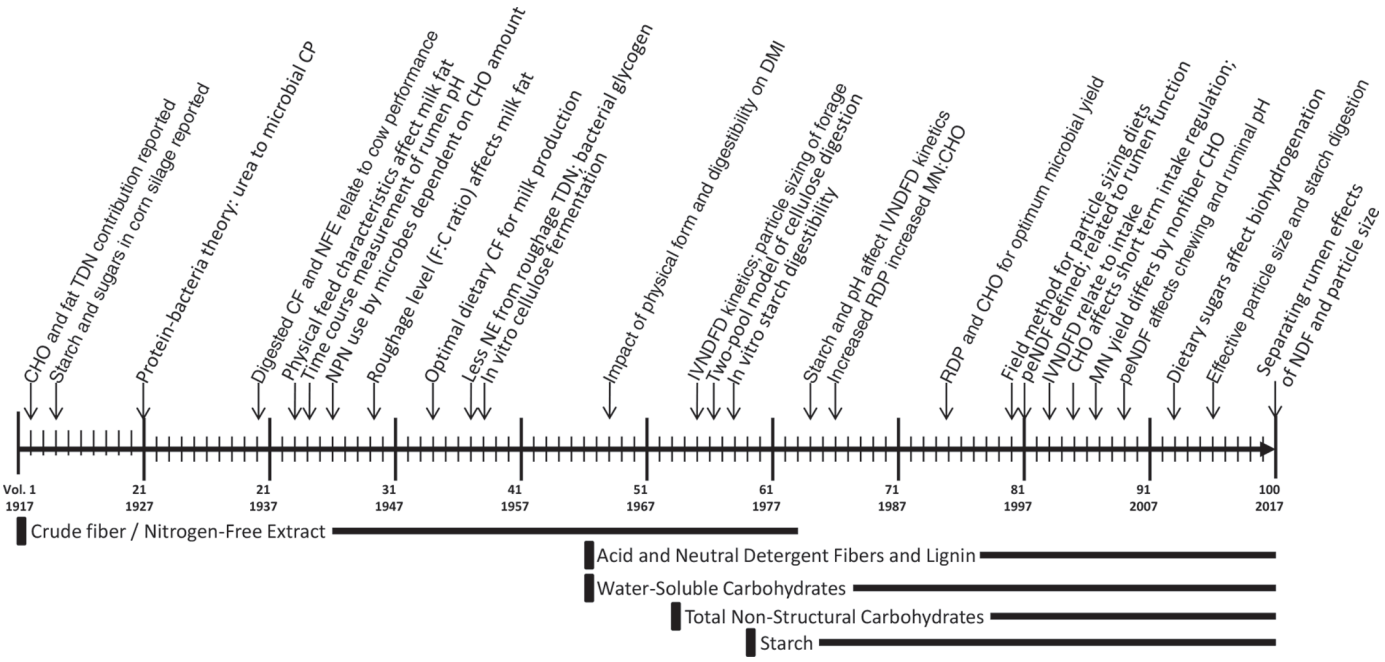

Figure 1. A timeline showing the periods in which different analyses were used (see also Appendix Table A1). CF = crude fiber, CHO = carbohydrate, F:C = forage-to-concentrate ratio, IVNDFD = in vitro neutral detergent fiber digestibility, MN = microbial nitrogen, NFE = nitrogen-free extract.

no description of statistics performed or significance of results: in 1917 when JDS began publication, Fisher's (1925) and Snedecor's (1937) seminal works on statistics were not yet published. Researchers were limited on the chemical and statistical analyses that they could perform. Historically, advances in research and new feeding standards occurred in parallel with and were fostered by new methods of analysis. This simply illustrates that research progress relies on analytical measurements that allow description of biological processes of interest.

Where work with CHO started and how it evolved in JDS is a function of the base of information available and the introduction and evaluation of new insights and methods. Our goal was to review the publications in JDS that had significant impact and were milestones in the characterization, digestion, and utilization of CHO. In some instances, we will discuss research work published in other journals to provide perspective and context.

CHEMICAL CHARACTERIZATION OF CARBOHYDRATES

Insoluble Fiber

Although methods have changed, the concept of nutritional, insoluble fiber has been relatively constant for nearly 200 years as a feed fraction that was indigestible or resistant to digestion. That nutritional fiber is an empirical measurement is not a failure of understanding or technique, but the result of attempting to measure the nutritional concept of "fiber" using chemical solubility or bioavailability methods. Accordingly, measurement of fiber is defined *only* by the method of analysis, which in turn places extra burden on analysts to follow the method exactly to produce results reflective of the empirical analyte of interest. For ruminants, nutritional, insoluble fiber can be defined as "the slowly digesting or indigestible organic matter of a feed or diet that occupies space in the rumen" (adapted from Mertens, 1997). This is essentially a definition of insoluble fiber that relates to the original desire to measure the indigestible fraction of feeds, with the recognition that slowly digesting matter is resistant to digestion, and that fiber represents the "filling effect" of diets.

The fiber method in place in 1917 was CF, which was developed by Henneberg and Stohmann (1860, 1864) to describe indigestible material in the feed and was part of the Weende or proximate system of analysis. However, Tollens (1897) found that CF was partially digested by ruminants and did not capture all lignin, and there was a variable distribution of lignin and CHO between CF and NFE. Since its inception, the proximate analysis system was considered imperfect and provisional, with Henneberg and Stohmann (1864) and Tollens (1897)