Acetogenesis from Carbon Dioxide in Termite Guts

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11.1 Introduction

Since the isolation of *Clostridium aceticum* (Wieringa, 1940), the first bacterium ever shown to derive energy for growth by acetate synthesis from \( \text{H}_2 + \text{CO}_2 \), the phenomenon of acetogenesis from \( \text{C}_1 \) compounds has been of intrinsic interest to microbiologists and biochemists. As seen from other chapters in this volume, work in various laboratories over the years has now led to the isolation of over two dozen different species of such acetogens and to the recognition that these bacteria, united by their unique metabolism, are actually quite diverse phenotypically and phylogenetically. Likewise, detailed studies on the biochemistry of acetogenesis from \( \text{CO}_2 \), conducted mainly with *Clostridium thermoaceticum* by H. G. Wood and his students, have identified each step in the pathway and resulted in the purification and characterization of the relevant enzymes, and in some cases the genes encoding them. Nevertheless, the ecological significance of acetogenesis from \( \text{CO}_2 \) has remained obscure. Certainly, the ability of most acetogens to use \( \text{H}_2 \) as a reductant suggests that they might function as terminal or subterminal "electron sink" organisms in anaerobic microbial food webs, and they are often included in that position in diagrams depicting such webs (e.g., Zinder, 1984). Yet, rarely have habitats been identified in which acetogens outprocess, or are strongly competitive with, other potential \( \text{H}_2 \) consumers such as methanogens and sulfate-reducing bacteria. Hence, their significance in the flow of carbon and reducing equivalents during anoxic decomposition processes has been debatable. In recent years, however, it has been found that the gastrointestinal tract of vertebrates and invertebrates is one type of habitat in which acetogens often appear to be major \( \text{H}_2 \) consumers (Breznak and Kane, 1990;
also see Wolin and Miller Chapter 13). During microbial fermentation in the gut of certain termites, in particular, acetogens not only appear to constitute the primary H₂ sink, but their production of acetate from H₂ + CO₂ makes a major contribution to termite nutrition.

This chapter reviews the phenomenon of acetogenesis from H₂ + CO₂ by termite gut microbes, from the events leading up to its discovery, to the isolation and characterization of some of the acetogenic bacteria. Inasmuch as acetate formation in termite guts can arise by fermentative processes not involving reduction of CO₂, I will hereafter use the prefix "H₂/CO₂" to indicate that reduction of CO₂ (and/or HCO₃⁻) to acetate is with H₂ serving as the electron donor. Included in this chapter are speculations on why H₂/CO₂ acetogens are able to outprocess methanogens as H₂ consumers in guts of certain termites. This is still an unresolved issue for which we have only partial answers. First, however, it is appropriate to begin with a brief introduction to the basic biology of termites, especially those aspects relating to their nutritional ecology. More expanded accounts of the intestinal microecology of termites, and the extent to which gut microbes contribute to termite digestion and nutrition, can be found elsewhere (Breznak, 1982, 1984a, 1990; Breznak and Brune, 1994; O'Brien and Slaytor, 1982; Slaytor, 1993).

11.2 Termites and Their Nutritional Ecology

Termites are insects that belong to the order Isoptera, meaning "equal winged" and reflecting the fact that the forewings and hindwings of reproductivees are similar in size and veination. They are among the most abundant and important of all soil macroinvertebrates. Roughly two-thirds of the Earth's land surface—that occurring between 45° N and 45° S latitude—is inhabited by one or more termite species (Wood and Sands, 1978). However, their populations are greatest in tropical and subtropical regions, where their numbers can exceed 6000/m² and their biomass densities (up to 50 g/m²) often surpass that of grazing mammalian herbivores (0.013–17.5 g/m²; Collins and Wood, 1984; Lee and Wood, 1971).

There exist over 2000 species of termites whose biology, behavior, and nutritional ecology are extremely diverse. Although frequently thought of as feeding on "wood," their diet (depending on the particular species) actually includes a great variety of living or dead plant material (the latter being either sound, or in various stages of decay), as well as dung, and soil rich in organic matter (i.e., humus). Specialized or incidental foods include fungi, algae, lichens, organic-rich portions of termite nests, members (including eggs) of their own colony, and skins or other parts of vertebrate corpses (Wood and Johnson, 1986). Global consumption of plant biomass by termites in all ecological regions has been estimated at 3.36 × 10¹⁵ g annually, which represents about 4% of the plant