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Glucosinolate hydrolysis and bioavailability of resulting isothiocyanates: Focus on glucoraphanin

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ABSTRACT

There is a growing interest in the health benefits of broccoli. Sulforaphane, the major bioactive component in broccoli, is an unstable isothiocyanate stored in the plant as glucoraphanin. Myrosinase enzymes release sulforaphane when the plant is crushed. Extraction during supplement formulation or heat processing can destroy myrosinase. When myrosinase activity is lost, colonic microbiota perform this hydrolysis *in vivo*. Here we review hydrolysis by myrosinase and microbiota. Myrosinase acts fast to generate a bolus of SF that is rapidly absorbed high in the gut and rapidly excreted. Microbial metabolism is slow and delayed. Sulforaphane absorption, distribution and excretion are discussed.

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1. Introduction

Glucosinolates (GSL) are a large family of sulphur- and nitrogen-containing compounds found almost exclusively in plants of the order or *Brassicales*, that includes the families of *Brassicaceae*, *Capparidaceae* and *Caricaceae*. The most studied is the *Brassicaceae* family, that alone has 300 genera and 3000 species, all of which originated from a common ancestral specie of cabbage, *Brassica Oleracea* (Herr & Buchler, 2010). Today, the *Brassicaceae* include many vegetables commonly consumed worldwide, such as broccoli, cabbage, cauliflower, kale, Brussels sprouts, and many more (Herr & Buchler, 2010). GSL are β-Thioglucoside *N*-hydroxysulfates, with a variable side chain and a sulphur-linked β-D-glucopyranose moiety. GSL have been categorized on the basis of the chemical structure of the side-chain, the most common groups of which are aliphatic, aromatic and indolyl, and their biosynthesis has been studied in detail (Clarke, 2010; Halkier & Gershenzon, 2006).

Interest in GSL stems from the bioactivity of their hydrolysis products, both for their anti-herbivory factors that maintain plant health (Halkier & Gershenzon, 2006) and for their positive impact on human health, even at normal dietary levels (Jeffery & Araya, 2009). A diet of 3–5 servings per week is sufficient to cause a 30% or 40% decrease in risk for a number of cancers (Jeffery & Keck, 2008). Animals fed freeze-dried raw crucifers daily show even greater decrease in cancer risk, suggesting that, larger or more frequent servings, may provide greater decreases in cancer risk (Lai, Keck, Wallig, West, & Jeffery, 2008). Dietary GSL are water soluble, although like so many other glycosides, very poorly absorbed (Bheemreddy & Jeffery, 2007). However, not only do intact GSL have no known activity, but once absorbed, they are not hydrolyzed to their bioactive metabolites within the body. Rather, they are excreted unchanged in urine or secreted back into the gut via the bile duct for hydrolysis, Fig. 1 (Bheemreddy & Jeffery, 2007). Thus bioavailability of bioactive hydrolysis products is dependent not only on ingestion of GSL, but on their conversion to their bioactive hydrolysis products, prior to passage across the gut wall. There are two mechanisms for hydrolysis of GSL: the plant contains a group of β-thioglucosidase

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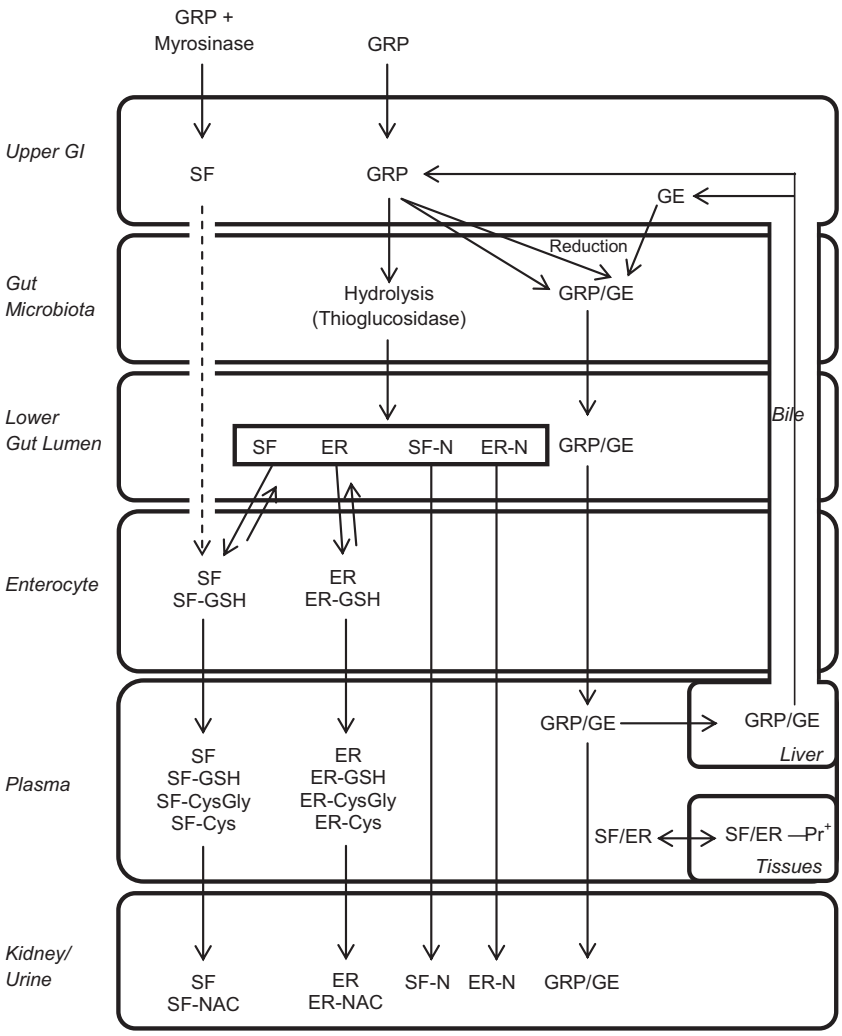

Fig. 1 – Metabolic fate of dietary glucoraphanin. ER, erucin; ER-N, erucin nitrile; ER-NAC, erucin-N-acetyl cysteine; GE, glucoerucin; GI, gastrointestinal; GRP, glucoraphanin; SF, sulforaphane; SF-CYs, sulforaphane-cysteine; SF-CysGly, sulforaphane-cysteine-glycine; SF-GSH, sulforaphane-gluthathione; SF-N, sulforaphane nitrile; SF-NAC, sulforaphane-N-acetyl cysteine; -Pr$^+$, the compound is bound to the protein.

enzymes, commonly called myrosinase, that are able to hydrolyze GSL (Bones & Rossiter, 2006). Alternatively, commensal bacteria appear to hydrolyze GSL, although which bacteria and the extent to which this occurs is an active area of research (Cheng, Hashimoto, & Uda, 2004; Lai, Miller, & Jeffery, 2010; Mullaney, Kelly, McGhie, Ansell, & Heyes, 2013).

2. Myrosinase hydrolysis of glucosinolates

Although there are many enzymes able to hydrolyze the O-glucosidic bond, the myrosinases (E.C. 3.2.3.147) are a family of plant enzymes uniquely able to hydrolyze some S-linked glucosides. The myrosinases are sequestered away from GSL in the growing plant, only coming into contact when the plant tissue is disrupted by crushing or herbivory/chewing. The products formed when GSL are processed by myrosinase, in the presence of water, are glucose and a thiohydroxamate-O-sulphonate, an unstable intermediate that breaks down irreversibly to form one of several different products: isothiocyanates (ITC), thiocyanates, simple nitriles, epithionitriles, oxazolidine-2-thiones or indolyl compounds. The form of product is dependent on the glucosinolate, myrosinase-associated proteins (termed modifier proteins) and the reaction conditions, such as temperature and pH (Bones & Rossiter, 2006). Once formed, there is no interconversion between the different hydrolysis products. There are several myrosinase subfamilies, identified in *Brassica napus* as MA, MB and MC (Bones & Rossiter, 2006). The MB and MC families are typically found associated with modifier proteins, which direct the breakdown of the intermediate. Due to protein complex formation, MB and MC have also been termed insoluble myrosinase (Travers-Martin, Kuhlmann, & Muller, 2008). In brassica, at least two types of modifier proteins exist, Epithiospecifier Protein (ESP) and Epithiospecifier Modifier Protein (ESM1). In the absence of modifier proteins, ITC are typically formed. The ESP directs breakdown of the unstable thiohydroxamate-O-sulphonate toward nitrile formation by binding the sulphur that would otherwise form ITC, and the ESM1 directs breakdown toward isothiocyanate production, possibly by interfering with ESP (Wittstock & Burow, 2007). In the case

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