



Plant prebiotics and human health: Biotechnology to breed prebiotic-rich nutritious food crops



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ABSTRACT

Microbiota in the gut play essential roles in human health. Prebiotics are non-digestible complex carbohydrates that are fermented in the colon, yielding energy and short chain fatty acids, and selectively promote the growth of *Bifidobacteria* and *Lactobacillae* in the gastro-intestinal tract. Fructans and inulin are the best-characterized plant prebiotics. Many vegetable, root and tuber crops as well as some fruit crops are the best-known sources of prebiotic carbohydrates, while the prebiotic-rich grain crops include barley, chickpea, lentil, lupin, and wheat. Some prebiotic-rich crop germplasm have been reported in barley, chickpea, lentil, wheat, yacon, and Jerusalem artichoke. A few major quantitative trait loci and gene-based markers associated with high fructan are known in wheat. More targeted search in genebanks using reduced subsets (representing diversity in germplasm) is needed to identify accessions with prebiotic carbohydrates. Transgenic maize, potato and sugarcane with high fructan, with no adverse effects on plant development, have been bred, which suggests that it is feasible to introduce fructan biosynthesis pathways in crops to produce health-imparting prebiotics. Developing prebiotic-rich and super nutritious crops will alleviate the widespread malnutrition and promote human health. A paradigm shift in breeding program is needed to achieve this goal and to ensure that newly-bred crop cultivars are nutritious, safe and health promoting.

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1. Introduction

The microbial genome or microbiome includes complex microorganism mixtures that have co-evolved with their human hosts. Humans harbor over 100 trillion cells of microbial communities that populate various sites in their anatomy [1]. Many species of bacteria are found in the gastrointestinal tract especially in the colon, where this flora is largely anaerobic. Diet variation modulates the composition of gut microbiota. The composition of gut microbiota and the metabolic interactions among its species may affect food digestion and energy harvest. An increased understanding of the mechanisms involved in the interactions involving gut microbiota, host and diet will open up the avenues to treat complex human diseases [2,3,4,5].

Prebiotics have been characterized as a group of carbohydrates that resist digestion and absorption in gastrointestinal tract

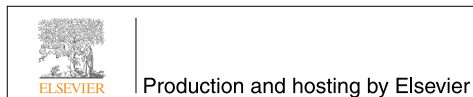
(small intestine); which are fermented by the gut (large intestine) microbiota, selectively promote the growth and activity of a limited number of colonic bacteria, and alter the colonic microflora balance towards a healthier composition [6,7,8]. The prebiotics consumption may enhance immune function, improve colonic integrity, decrease both incidence and duration of intestinal infections, down-regulate allergenic response and improve digestion and elimination [9]. Some cereal grain oligosaccharides may function as prebiotics and increase the levels of beneficial bacteria in the large bowel [8,10,11]. Likewise, prebiotics can also improve uptake of calcium, iron, and zinc, and significantly decrease colon cancer, the level of triglycerides and cholesterol [8,12,13,14,15,16].

Overweight and obesity cause 3.4 million deaths, 3.9% of years of life lost, and 3.8% of disability adjusted life-years (DALYs) worldwide. Populations with a body mass index (BMI) of 25 or greater are more in the developed (up to 38%) than in the developing (up 13.4%) world. Children and adolescents in the developed world are the most affected. Overweight and obesity have therefore become a major global health challenge [17]. Individuals with BMI above 25 are at increased risk of diabetes mellitus, cardiovascular diseases, fatty liver (non-alcoholic), and hypertension [18,19], which significantly impact on public health cost. The evidence to date suggests that gut microbiota are involved in the pathogenesis of obesity [19,20,21]. Obese and lean individuals

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present different microbiota composition profile [22,23,24]. The obese people use more energy from the diet [22,23,25,26]. The dietary intervention (prebiotics) impacts gut microbial diversity and human health, including obesity [19,22,27,28,29].

Higher intake of dietary fibers plays an important role in reducing the risk of cardiovascular disease, regulating weight management and immune function, and shaping microbial diversity in human gastrointestinal tract [30,31,32]. Whole grains are concentrated sources of dietary fiber, resistant starch, oligosaccharides, and carbohydrates that escape digestion in the small intestine and are fermented in the gut. The fibers that escape digestion in the small intestine are fermented in the gut to produce short-chain fatty acids (SCFAs), which are rapidly absorbed in the colon to provide additional energy to the host [30], and prevent the establishment of potentially pathogenic intestinal microbes [33]. SCFA production indicates microbiota metabolic activity. The shift in gut microbiome of humans consuming noble fibers such as polydextrose and soluble corn fiber significantly affects the relative abundance of bacteria at the class, genus and species level [34] as noted in humans who consume a high cruciferous vegetable diet versus those fed with a refined grain diet without vegetables [35]. This finding shows the dominant role of the diet in shaping the gut microbial diversity [30,33,34,35], and provides means for elucidating the role of gut microbiota on the subtle balance between health and disease [30].

This short review article provides an overview on plant prebiotics sources and variability; the genotype \times environment interaction effects, the genetic and molecular basis of synthesis of fructans, and progress towards designing prebiotics-rich and nutritionally-dense food crops, need an interdisciplinary approach among food science, nutrition and genomics-led crop breeding to tap microbiota and plant genetic resources diversity.

2. Prebiotic carbohydrates in plants

To date, fructooligosaccharides (FOS), inulin, and galactooligosaccharides (GOS) from plants are best-known sources of prebiotics. In addition, the raffinose family of oligosaccharides and resistant starch (the type that is not absorbed in the gastrointestinal tract) has also been recognized as prebiotic carbohydrates because these are not absorbed in the intestine and promote the growth of beneficial bacteria in the gut [36,37]. In addition, some polysaccharides found in plant cell walls, such as xylans and pectins, have also been recognized as the potential sources for diverse polysaccharides to produce new prebiotics [38].

3. Novel sources of variation

A literature search (2003–2014) revealed the presence of prebiotic carbohydrates in a number of food crops, with vegetable and root and tuber crops being the predominant sources (Table 1). For example, garlic (*Allium sativum* L.), Jerusalem artichoke (*Helianthus tuberosus* L.), leek (*A. ampeloprasum* L.), okra (*Abelmoschus esculentus* L. Moench), onion (*Allium cepa* L.) and shallot (*A. cepa* L. var. *aggregatum*) among vegetables; dragon fruit (*Hylocereus* species), jack fruit (*Artocarpus heterophyllus* Lam), nectarine (*Prunus persica* L. Batsch), and palm fruit (*Borassus flabellifer* L.) among fruits; chicory (*Chicorium intybus* L.) and yacon [*Smallanthus sonchifolius* (Poepping and Endlicher) H. Robinson] among root crops; or the tuber crops dahliya (*Dahlia* species) and gembili (*Dioscorea esculenta* (Lour.) Burk.) are the major sources of fructans. Yacon accessions with high fructans include AJC 5189, ASL 136 and MHG 923 [39], while those from Jerusalem artichoke are JA 37 and CN 52687 [40]. More recently, the gourd family of vegetables, which includes *Benincasa hispida*, *Lagenaria siceraria*, *Momordica charantia*, *Trichosanthes anguina*, and *Cucurbita maxima* has been reported as good source of digestible and indigestible fibers, with significant prebiotic properties [41]. In addition, mushroom [*Agaricus*

bisporus (J.E. Lange) Emil J. Imbach] has also been reported as potential source of prebiotic carbohydrates [42].

Barley (*Hordeum vulgare* L.), chickpea (*Cicer arietinum* L.), lentil (*Lens culinaris* Medikus), and wheat (*Triticum aestivum* L.) show genetic variability for prebiotic carbohydrates in grain crops (Table 1). Huynh et al. [43] evaluated in glasshouse and in the field 62 bread wheat cultivars and breeding lines of diverse origin for grain fructan. They detected significant genotypic variation for grain fructan, with no evidence of strong genotype \times environment interaction. The fructan contents of field-grown grain samples were positively correlated ($r = 0.83$) with those of glasshouse-grown samples of the same cultivars. The grain fructan content among 19 cultivars varied from 0.66 to 2.27% grain dry weight, while in a set of diverse germplasm it ranged from 0.7 to 2.9%. Cultivars such as Sokoll, Halberd and Cranbrook had the highest levels of grain fructan (glass house: 1.24 to 1.58%, field: 2.2 to 2.27%). Advanced lines had grain fructan above 2%. Marotti et al. [44] detected large differences in dietary fibers among modern and ancient durum wheat cultivars. The insoluble dietary fiber (IDF), soluble dietary fiber (SDF) and total dietary fiber ranged from 102 to 181, 18 to 37, and 127 to 199 g kg⁻¹ dry weight, respectively. Colon bacteria ferment SDF easily, rapidly and completely. In vitro research further revealed that SDF selectively proliferate microbial growth, with fibers from the Kamut@Khorasan (ancient durum wheat) and Solex (modern durum wheat) promoting maximum growth of *Bifidobacterium pseudocatenulatum* B7003 and *Lactobacillus plantarum* L12 strains in the gastrointestinal tract [44]. Sweet wheat [45] – a double mutant lacking *GBSSI* and *SSIIa* genes – had about twice as much total dietary fiber and 7-fold higher concentration of low-molecular-weight soluble dietary fiber, largely fructan, in comparison to parental or wild-type line [46]. Sweet wheat germplasm is an excellent source that may be used to raise fructan levels by crossing it with other high fructan lines [45]. Some einkorn wheat (*Triticum monococcum*) germplasm contain 2 to 3 times greater inulin than maize (24–27 g kg⁻¹) [47]. Likewise, barley cultivars such as KVL 1113 and KVL 1112 are reported to contain grain fructan as high as 3.9 to 4.2 g 100 g⁻¹ [48]. Rye (*Secale cereale* L.) grains are another source of rich dietary fiber. The total dietary fiber among 19 cultivars varied from 147 to 209 g kg⁻¹ dry matter, of which 26 to 41 and 45 to 64 g kg⁻¹ dry matter were arabinoxylans and fructan, respectively [49].

Resistant starches (RS 1, RS 2, RS 3 and RS 4), which escape digestion in small intestine but ferment in the colon by the resident microflora to produce SCFAs, are receiving greater attention due to their potential role in promoting human health [50]. RS 2 and RS 4 promote distinct microflora, impacting colon health [51]. Their content ranges from 12 to 45 g kg⁻¹ dry weight, among ancient and modern durum wheat cultivars.

Grain legumes are rich sources of dietary fiber. Lupin and chickpea kernel-derived fiber stimulates colonic bifidobacteria growth and contributes to colon health [52,53]. Chickpea grains are a good source of α -galactooligosaccharide (α -GOS), which varied from 6.35% to 8.68% dry matter among 19 chickpea cultivars, with ciceritol and stachyose, respectively, accounting for 50% and 35% of the total α -GOS [54]. Chickpea accession '171' had the highest α -GOS (8.68%) and lowest sucrose (2.36%), which may be used to obtain α -GOS for use as a prebiotic in functional foods. Chickpea raffinose, another α -GOS was demonstrated to modulate the intestinal microbial composition to promote intestinal health in humans [55,56]. Johnson et al. [57] reported significant variation for prebiotic carbohydrates, with raffinose, stachyose, sorbitol, and verbascose being predominant sources of prebiotic carbohydrates in lentil. Other plant products with significant prebiotic properties include almond (*Amygdalus communis* L.) seeds and bamboo [*Gigantochloa levis* (Buluh beting)] shoot crude polysaccharides (BSCP), both promote the growth of beneficial microbes in the gut [58,59].

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