Contents lists available at ScienceDirect

Electronic Journal of Biotechnology

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

CrossMark

Sangam Dwivedi [a,b], Kanwar Sahrawat [b], Naveen Puppala [a], Rodomiro Ortiz [c,*]

[a] Agricultural Science Center at Clovis, New Mexico State University, 2346 SR 288, NM 88101, USA
[b] International Crops Research Institute for the Semi-Arid Tropics, Patancheru PO 502324, Andhra Pradesh, India
[c] Swedish University of Agricultural Sciences, Sundsvagen 14 Box 101, SE 23053 Alnarp, Sweden

ARTICLE INFO

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.

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].

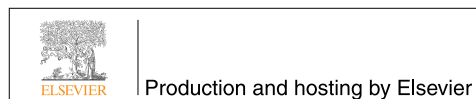Prebiotics have been characterized as a group of carbohydrates that resist digestion and absorption in gastrointestinal tract (small intestine); which are fermented by the gut (large intestine) microbiota, selectively promote the growth and activity of a limited number of colonic bacteria, and alter 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 lever (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

ELSEVIER Production and hosting by Elsevier

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 × 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 sonchifoliu* (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 × 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].

Table 1
Genetic variation for prebiotic carbohydrates reported in cereal and legume, root and tuber, and fruit and vegetable crops.

Crop species	Summary of variation reported	Reference
Cereal and legume crops		
Barley (20)	Grain fructan, 0.9 to 4.2 g 100 g^{-1}, KVL 1113 and KVL 1112 being highest	[48]
Lentil (10)	Sorbitol, 1039 to 1349 mg 100 g^{-1}; mannitol, 160 to 294 mg 100 g^{-1}; raffinose and stachyose, 2319 to 2793 mg 100 g^{-1}; verbascose, 922 to 1968 mg 100 g^{-1}; and nystose, 52 to 79 mg 100 g^{-1}	[57]
Durum wheat (10)	Insoluble dietary fiber, soluble dietary fiber and total dietary fiber 102–181, 18–37 and 127–199 g kg^{-1} dry weight, respectively	[44]
Lentil (22)	Raffinose, stachyose, and verbascose 1.6 to 2.4 g, 1.7 to 2.9 g, and 1.2 to 1.9 g 100^{-1} dry matter, respectively	[89]
Chickpea (19)	α-galactooligisaccharide (α-GOS), 6.35 to 8.68%, Ciceritol the main sugar	[54]
Wheat (62)	Grain fructan in cultivars 0.66 to 2.27% dry weight; germplasm 0.7 to 2.9% dry weight; advanced lines >2% dry weight	[43]
Einkorn wheat, maize and rice	Inulin 55–85, 24–27, and 1.7 to 8.4 g kg^{-1} in einkorn wheat, maize and rice, respectively	[47]
Rye (19)	Arabinoxylans 26 to 41 and fructan 45 to 64 g kg^{-1} dry matter	[49]
Root and tuber crops		
Dahlia, yam and gembili	Dahlia and gembili tubers high in inulin type fructan, 78% and 68%, respectively, than that of yam tubers (49%)	[90]
Yacon (23)	Ploidy level significantly impacted the content and distribution of fructooligosaccharides (FOS); 11 lines high in short chain-FOS, while 12 lines high in long chain-FOS	[91]
Yacon (35)	Fructooligosaccharide (FOS), 6.4 to 65 g 100^{-1} dry matter, AJC 5189 high in FOS	[39]
Yacon (4)	Oligofructans, 42.84 to 49.13 mg g^{-1} fresh tubers	[92]
Yacon (4)	Inulin content, 141–289 mg kg^{-1} dry matter, with tubers having greater levels than rhizomes	[93]
Yacon (10)	Fructan, 31–89 g kg^{-1} fresh root weight; ASL136, MHG923 and MHG927 being highest in fructan (72–89 g fructan kg^{-1})	http://www2.cipotato.org/publications/program_reports/97_98/51yacon.pdf
Fruit and vegetable crops		
Jerusalem artichoke (79)	Inulin, 55.3 to 74.0% dry weight, JA 37 and CN 52867 promising for both yield and inulin	[40]
Fruits (32) and vegetables (41)	Most fruits, except nectarine (0.89 mg g^{-1} fresh weight), contain low amount of FOS; vegetables with high FOS: scallion 4.1 mg g^{-1}, onion 2.24 mg g^{-1}, garlic 1.76 mg g^{-1}, and Jerusalem artichoke 1.6 mg g^{-1} fresh weight	[94]
Varieties of plant foods (47)	Garlic and Jerusalem artichoke had high inulin-type fructan (19.4 to 29.2 g 100 g^{-1} fresh weight) than shallot and red onion (3.6 to 8.8 g 100 g^{-1} fresh weight); FOS highest in Jerusalem artichoke (5.2 g 100 g^{-1} fresh weight)	[95]
Bulb (3) and roots/tubers (7)	Inulin type fructan 27 to 42% dry weight in garlic, shallot and onion; sweet potato, white radish, cassava and yam bean contain 0.42 to 2.14%	[96]
Fruits and vegetables (13)	Jackfruit (flesh, 98 mg g^{-1}; seeds, 29 mg g^{-1} dry extract), okra (49 mg^{-1} dry extract), and palm fruit (pericarp, 14 mg g^{-1}; flesh, 47 mg g^{-1}; embryo, 34 mg g^{-1} dry extract) rich in oligosaccharides	[97]
Pitaya (dragon fruit)	Red-fleshed dragon fruits contain more oligosaccharides 89.6 g kg^{-1} than white-fleshed types, 86.2 g kg^{-1} fresh fruit weight	[98]
Onion (15)	Fructan 0.84 to 3.04%, San Juan de la Rambla being highest in fructan	[99]
Fruits (43) and vegetables (60)	High fructan vegetables: garlic, artichoke, shallots, leek bulb, and onions (1.2 to 17.4 g 100 g^{-1} fresh weight); fruits with detectable fructan: longon, peach, persimmon, and melon (0.21 to 0.46 g 100 g^{-1} fresh weight)	[100]

Figure in bracket within the first column refers to either the number of accessions within a crop or number of different crop species evaluated for prebiotic compounds.

Research on identifying genetic variation for prebiotic carbohydrates in most of these crops is in its infancy. However, there is a growing awareness to develop "wholesome" functional food for improving human health. Core [60] and mini core [61] collections that represent diversity of the entire collection of a given species preserved in a genebank are reported in most of the grain crops [62,63]; thus suggesting that these could be used as resource to identify prebiotic-rich germplasm for use in crop breeding. Likewise, many genebanks have large germplasm collections of fruits, vegetables, and root and tuber crops (Fig. 1 and Table 2), which were previously reported as source of high fructans (Table 1). There is a need to develop representative subsets in these crops, which could be systematically evaluated for prebiotic carbohydrates.

4. Genotype × environment interaction

Research to date suggests that most of the nutritional traits are highly influenced by environment (location) and genotype × environment interaction effects, with environments having major effects [64]. In a trial involving 10 lentil cultivars evaluated at two locations for two years, Johnson et al. [57] reported significant year and location effects for sorbitol, mannitol and verbascose, and year × location × cultivar effects for sorbitol, while Putta et al. [40] detected genotype ×

environment interaction for inulin content in Jerusalem artichoke. The environment effects in both the trials were the most significant. Genotype × environment interaction ($P \leq 0.001$) is also reported for rafinnose family of oligosaccharides [65]. These results reinforce the need for multilocation evaluation of germplasm/cultivars to identifying those with high prebiotic carbohydrates for use in plant breeding.

5. Genomic regions associated with prebiotics

Quantitative trait loci (QTL) associated with fructan and inulin is known in wheat [66]. QTL on chromosomes 2B, 3B, 5A, 6D and 7A have been associated with high fructan in a double haploid (DH) mapping population involving a high-fructan breeding line (Berkut) and the low-fructan cultivar Krichauff [66]. *QGfc.aww-6D.2* and *QGfc.aww-7A.1* had the largest effects (17 and 27% of the total phenotypic variation, respectively). Validation in another mapping population involving Sokoll and Krichauff confirmed that *QGfc.aww-6D.2* and *QGfc.aww-7A.1* show similar effects. Gene-based single nucleotide polymorphism (SNP) markers have successfully been mapped to a major QTL (*QGfc.qww-7A.1*) [66], which affects the accumulation of fructan in wheat grains [68]. Furthermore, the alleles controlling high- and low-fructan were associated in fructan production in a diverse set of 128 wheat lines [67]. Stem-water soluble carbohydrate (SWSC) in
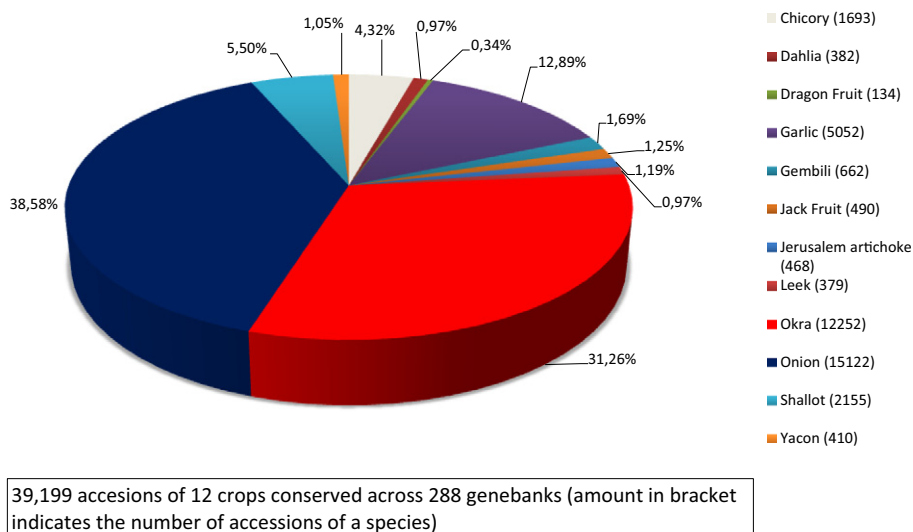
Fig. 1. Proportion of accessions representing 12 fruit, vegetable, root and tuber crops preserved across 288 genebanks globally (Source: http://apps3.fao.org/wiews/).

wheat consists mainly of fructans and sucrose and can serve as a source for grain development and fructan synthesis [68]. It is likely that genes affecting SWSC [69] could affect grain fructan accumulation. Likewise, two major QTL for inulin content, *Xgcag9* on chromosome 2BL-2 and *Xgwm499* on chromosome 5BS contributed respectively 20 and 15% of the phenotypic variation in a DH population involving AC Reed and Grandin [66]. There are QTL with major effects on the fructan level of the vegetative tissues of barley, onion and ryegrass [70,71,72].

Arabinoxylans represent the major dietary fibers present in wheat bran and its hydrolysis leads to the formation of arabinoxylan oligosaccharides (AXOS) [73], which has a strong prebiotic effect [74]. QTL mapping and validation revealed that *QGax.aww-2A.1* and *QGax.aww-4D.1* had a major effect on wheat grain arabinoxylan accumulation [75], which are apparently different at two QTL with large effects on grain fructan that are in chromosome 6D and 7A [66].

Fructans, the major component of water-soluble carbohydrate temporarily reserved in the stem are used for grain filling by temperate cereals. Research shows that sucrose:sucrose 1-fructosyltransferase (1-SST), sucrose:fructan 6-fructosyltransferase (6-SFT), and fructan–fructan 1-fructosyltransferase (1-FFT) enzymes are involved in fructan synthesis in barley and wheat [76,77,78]. More recently, Kooiker et al. [79] investigated the effect of *TaMYB13-1* gene and its influence on fructan synthesis in transgenic wheat. *TaMYB13-1* overexpression resulted in up-regulation of all three families of fructosyltransferases and *γ-vacuolar processing enzyme* (*γ-VPE-1*) involved in the maturation of fructosyltransferases in the vacuole. The overexpression of these target genes was highly correlated in recombinant inbred lines and during stem development as well as the transgenic and non-transgenic wheat, supporting a direct regulation of these genes by wheat transcription factor TaMYB13-1. Further *TaMYB13-1* overexpression in wheat led to enhanced fructan accumulation in the leaves and stems and also increased spike weight and grain weight per spike in transgenic plants under water-limited environments. This finding suggests that TaMYB13-1 plays an important role in coordinated up-regulation of genes necessary for fructan synthesis and can be used as a molecular tool to improve the high fructan trait.

6. Designing prebiotic-rich and super-nutritious crops

Marker-assisted selection (MAS) is used in plant breeding to speed and increases the precision of genetic progress; and when integrated into optimized molecular breeding strategies, it can also lower the cost of selection [63]. As noted above few validated QTL with major

effects and associated with grain fructan or arabinoxylans are known in wheat. Nguyen et al. [75] identified microsatellite marker *gpw-95001-4D* nearest at grain arabinoxylans QTL (*QGax.aww-4D.1*), while Huynh et al. [66] reported microsatellite marker *gwm681-7A*, closely associated with a major grain fructan QTL (*QGfc.aww-7A.1*). Huynh et al. [67] successfully mapped gene-based SNPs, *Ta1-FFT*, *Ta6-SFT*, and *TaWIVRV*, co-located with each other and with the grain fructan QTL, *QGfc.aww-7A.1* [66]. SNP alleles controlling high or low fructan are associated with fructan production in diverse 128 wheat lines [66]. These markers are available for indirect selection of segregants with high grain fructan or arabinoxylan concentrations in wheat. For example, the validated QTL *QGfc.aww-7A.1* with a major effect and SNP-based markers may be used for targeted enhancement of grain fructan in wheat.

Chicory, artichoke and onion are good sources of inulin molecules, which are synthesized by two enzymes, sucrose:sucrose 1-SST and fructan:fructan 1-FFT [80] with a chain length of up to 200° of polymerization [81]. Tubers of transgenic potato (*Solanum tuberosum* L.) containing *1-SST* and *1-FFT* genes had full spectrum of inulin molecules present in globe artichoke, with no adverse effect on plant growth or tuber yield [82]. The inulin containing tubers however display a reduction in starch content, which means that synthesis of inulin does not increase tuber storage capacity. Hellwege et al. [82] found that inulin produced in potato tubers is indistinguishable from inulin isolated from artichoke roots. More recently, Stoop et al. [83] produced transgenic maize and potato containing *1-SST* and *1-FFT* from Jerusalem artichoke. Transgenic maize expressing *1-SST* or *1-SST* and *1-FFT* driven by endosperm-specific promoter produced 3.2 mg g^{-1} kernel inulin type fructan, with no adverse effect either on kernel development or in germination. Potato tubers expressing *1-SST* accumulated 1.8 mg inulin g^{-1} tuber, while the tubers with a combined expression of *1-SST* and *1-FFT* accumulated 2.6 mg inulin g^{-1} tuber. The introduction of fructan biosynthetic pathway in a high-sucrose maize background increased inulin accumulation to 41 mg g^{-1} kernel, indicating that sucrose availability is limiting fructan production in transgenic maize.

Sugar beet (*Beta vulgaris* L.) is an economically important crop but lacks enzymes to produce fructans. It is a rich source of sucrose that accumulates in the vacuole of its taproot cells. Transgenic sugar beet containing onion fructosyltransferases *1-SST* and *6G-FFT* had an efficient conversion pathway of sucrose into complex, onion-type fructans, without any adverse effect on taproot growth or the loss of storage carbohydrate content [84,85]. More recently, Hanlie Nell

Table 2
Select genebanks holding major germplasm collections of chicory, dahlia, dragon fruit, gembili, garlic, jack fruit, Jerusalem artichoke, leek, okra, onion, shallot and yacon.

	Accession number
Jerusalem artichoke	
Institute of Field and Vegetable Crops Novi Sad, Serbia	120
North Central Regional Plant Introduction Station, USA	107
Leibniz Institute of Plant Genetics and Crop Plant Research, Germany	102
Onion	
National Res. Centre for Onion and Garlic, India	1300
Northeast Regional Plant Introduction Station, Cornell University, USA	1156
Royal Botanic Gardens, Kew, United Kingdom	976
Garlic	
National Res. Centre for Onion and Garlic, India	750
Vegetable Section Olomouc, Czech Republic	623
Asian Vegetable Research and Development Center, Taiwan, China	505
Jack fruit	
Laboratoire d'Ecologie Moléculaire, Université de Pau, France	81
Regional Station Thrissur, NBPGR, India	72
Department of Agriculture Sabah, Malaysia	57
Dragon fruit	
Programa de Recursos Genéticos Nicaragüenses, Nicaragua	50
Southern Fruit Research Institute, Viet Nam	24
Departamento Nacional de Recursos Fitogenéticos y Biotecnología, Ecuador	18
Yacon	
Estación Experimental Agraria Baños del Inca, Perú	123
Universidad Nacional de Cajamarca, Perú	110
Estación Experimental Agraria Andenes, Perú	89
Shallot	
Science and Advice for Scottish Agriculture, United Kingdom	707
Leibniz Institute of Plant Genetics and Crop Plant Research, Germany	329
Station d'Amélioration Pomme de Terre et Plantes à Bulbes, France	319
Leek	
Agriculture and Food Research Council, United Kingdom	128
Leibniz Institute of Plant Genetics and Crop Plant Res., Germany	95
The Netherlands Plant Research International, Netherlands	88
Okra	
Regional Station Akola, NBPGR, India	2286
University of Georgia, USA	2220
University of the Philippines, Los Baños College, Philippines	942
Dahlia	
Research Institute of Landscaping and Ornamental Gardening, Czech Republic	224
Vytautas Magnus University, Lithuania	115
National Plant Material Center USDA/SCS, USA	15
Gembili	
Dry-lowlands Research Programme, Papua New Guinea	149
Dodo Creek Research Station, Solomon Islands	112
University of the Philippines, Los Baños College, Philippines	73
Chicory	
Station de Génétique/Amélioration des Plantes, INRA, France	400
Unité Expérimentale d'Angers, Groupe d'Étude et de contrôle des Variétés et des Semences (GEVES), France	251
Leibniz Institute of Plant Genetics and Crop Plant Res., Germany	223

succeeded in introducing the *1-SST* and *1-FFT* from *Cynara scolymus* in sugarcane (*Saccharum officinarum* L.). Transgenic sugarcane plants accumulated inulin up to 165 mg g^{-1} fresh weight, which is comparable to that found in native plants; therefore, exhibiting great potential as a future industrial inulin source. It seems therefore feasible to introduce fructan biosynthesis pathways in both staple and industrial crops, as already noted in transgenic maize, potato, sugar beet, and sugarcane health-imparting prebiotics for use in functional food to promote human health.

Malnutrition is widespread and casts enormous negative socio-economic impact at the individual, community, and national levels [86]. The world population by 2050 is expected to be around 9 billion; and providing enough food that is nutritious (protein and prebiotic-rich and micronutrients dense) and safe (free from toxic compounds and microbial toxins) to humankind is the greatest challenge in the 21st century. To date, the research has shown that nutritional traits can be combined into improved genetic background using both conventional and nonconventional plant breeding. For example, seed iron-dense beans and rice, maize with high tryptophane and lysine, or β-carotene rich maize and sweet potato cultivars have been developed and are commercially grown in some areas of Africa, Asia, Central and South America, while "Golden Rice 2" variants (containing high β-carotene) have been developed using transgenic breeding and are being introgressed into several Asian rice cultivars [64].

Advances in prebiotic research have conclusively demonstrated that fructans, and the fructooligosaccharides – including inulin – are nondigestible fibers promoting the growth of beneficial microbiota in the gut, which positively impact micronutrient absorption and utilization in humans [7,8,11,13,16]. Exploratory research to date suggests that it is possible to identify prebiotic-rich genetic resources, as evidenced in barley, wheat, chickpea and lentil among grain crops. Likewise, some fruit, vegetable, root and tuber crops have also been identified as rich sources of prebiotic carbohydrates. A global search of genebank data repository revealed that many of the latter group of crops (fruit, vegetable, root and tuber) have large germplasm collections (Fig. 1 and Table 2), which needs to be scientifically scrutinized to form representative subsets and evaluated for prebiotic carbohydrates. A paradigm shift in plant breeding is needed to incorporate nutritional quality (prebiotic rich and nutrient dense) as important objective that ensures that newly developed cultivars are not nutritionally inferior [64].

7. Perspectives

Humans are confronted today with diet-related health problems that in ancient times were of minor importance [87]. Human gut microbiota is populated by an array of bacterial species, which has established multiple mechanisms to influence human health. Diet has a dominant role in shaping the gut microbial diversity and human health. Inulin and fructan are the best-characterized prebiotics obtained from plants. Limited search has revealed sufficient genetic variation for inulin and fructan in barley and wheat grains. Prebiotic compounds are abundant in vegetable, root and tuber crops as well in some fruit crops. Targeted search for identifying genetic variability for prebiotics is yet to begin. Genebanks are the repository of large collection of plant germplasm. Reduced subsets representing diversity of entire germplasm collection of a given species preserved in the genebanks are available in most of the grain crops, which need evaluation to identifying novel germplasm rich in prebiotic carbohydrates for use in plant breeding. Crops lacking such representative subsets require developing these germplasm samples to capture the diversity available in the genebank.

Chicory, artichokes and onion are good sources of fructan. Transgenic maize and potato containing *1-SST* and *1-FFT* genes from Jerusalem artichoke, transgenic sugar beet containing *1-SST* and *6G-FFT* genes from onion, and transgenic sugarcane containing *1-SST* and *1-FFT* from globe artichoke have shown high fructan with no adverse effect on plant development, which clearly indicates that it is feasible to introduce fructan biosynthesis pathways in both staple and industrial crops, to produce health-imparting prebiotics to promote human health.

The evidence to date strongly suggests that manipulation of gut microbiota represents a novel approach in treating obesity and related metabolic disorders. Culture-independent assays and modern high-throughput sequencing and bioinformatics tools (not the subject

of this review) provide opportunities to investigate taxonomic and functional diversity of the gut microbiota. These developments are powerful means of understanding the contribution of the human microbiome to health and its potential as a target for therapeutic interventions [88]. The dietary interventions (prebiotics) to induce microbial change offer a great opportunity towards improved human health [20,21,22,27]. Increasing in the levels of prebiotics together with other quality traits (fat, protein, minerals, and vitamins) in staple food crops is therefore an important strategy to enhance nutrition and health of malnourished people worldwide.

Research to date suggests that it is feasible to develop nutritionally dense crop cultivars to fight widespread malnutrition, more specifically in the developing world. It is encouraging to note that plant breeders are aware that other quality traits such as micronutrients, vitamins and now prebiotics are equally important as are oil and protein. They are progressively taking a holistic approach to breed crops that provide wholesome food promoting human health at large. A multidisciplinary approach involving all stakeholders is needed to develop nutritionally dense and prebiotic-rich cultivars adapted to diverse agro-ecosystems.

Financial support

Author contributions

Proposed the theoretical frame: SLD, RO; Wrote the paper: SLD, RO, KS, NP.

References

[1] Trivedi B. Microbiome: The surface brigade. Nature 2012;492:S60–1. http://dx.doi.org/10.1038/492S60a.
[2] Laparra JM, Sanz Y. Interactions of gut microbiota with functional food components and nutraceuticals. Pharmacol Res 2010;61:219–25. http://dx.doi.org/10.1016/j.phrs.2009.11.001.
[3] Schwartz S, Friedberg I, Ivanov IV, Davidson LA, Goldsby JS, Dahl DB, et al. A metagenomic study of diet-dependent interaction between gut microbiota and host in infants reveals differences in immune response. Genome Biol 2012;13:32.
[4] Tremaroli V, Bäckhed F. Functional interactions between the gut microbiota and host metabolism. Nature 2012;489:242–9. http://dx.doi.org/10.1038/nature11552.
[5] Leone V, Chang EB, Devkota S. Diet, microbes, and host genetics: The perfect storm in inflammatory bowel diseases. J Gastroenterol 2013;48:315–21. http://dx.doi.org/10.1007/s00535-013-0777-2.
[6] Gibson GR, Roberfroid MB. Dietary modulation of the human colonic microbiota: Introducing the concept of prebiotics. J Nutr 1995;125:1401–12.
[7] Roberfroid MB. Prebiotics: The concept revisited. J Nutr 2007;137:830S–7S.
[8] Miremadi F, Shah NP. Applications of inulin and probiotics in health and nutrition. Int Food Res J 2012;19:1337–50.
[9] Sharma S, Agrawal N, Verma P. Miraculous health benefits of prebiotics. Int J Pharm Sci Res 2012;3:1544–53.
[10] Topping C. Cereal complex carbohydrates and their contribution to human health. J Cereal Sci 2007;46:220–9. http://dx.doi.org/10.1016/j.jcs.2007.06.004.
[11] Zhang N, Huang X, Zeng Y, Wu X, Peng X. Study on prebiotic effectiveness of neutral garlic fructan in vitro. Food Sci Hum Wellness 2013;2:119–23. http://dx.doi.org/10.1016/j.fshw.2013.07.001.
[12] Delzenne N, Aertssens J, Verplaetse H, Roccaro M, Roberfroid M. Effects of fermentable fructo-oligosaccharides on mineral, nitrogen and energy digestive balance in the rat. Life Sci 1995;57:1579–87. http://dx.doi.org/10.1016/0024-3205(95)02133-4.
[13] Coudray C, Bellanger J, Costiglia-Delavaud C, Remesy C, Vermorel M, Rayssignuier Y. Effects of soluble or partly soluble dietary fibres supplementation on absorption and balance of calcium, magnesium, iron, and zinc in healthy young men. Eur J Clin Nutr 1997;51:375–80.
[14] Pedersen A, Sandström B, Van Amersvoort JMM. The effect of ingestion of inulin on blood lipids and gastrointestinal symptoms in healthy females. Br J Nutr 1997; 78:215–22. http://dx.doi.org/10.1079/BJN19970141.
[15] Davidson MH, Maki KC, Synecki C, Torri SA, Deenman KB. Effects of dietary inulin on serum lipids in men and women with hypercholesterolemia. Nutr Res 1998; 3:503–17. http://dx.doi.org/10.1016/S0271-5317(98)00038-4.
[16] Yeung CK, Glahn RE, Welch RM, Miller DD. Prebiotics and iron bioavailability — Is there a connection? J Food Sci 2005;70:R88–92. http://dx.doi.org/10.1111/j.1365-2621.2005.tb09984.x.
[17] Ng M, Fleming T, Robinson M, Thomson B, Graetz N, Margono C, et al. Global, regional, and national prevalence of overweight and obesity in children and adults during 1980–2013: A systematic analysis for the global burden of disease study 2013. Lancet 2014. http://dx.doi.org/10.1016/S0140-6736(14)60460-8.
[18] Yeo SK, Ooi LG, Lim TJ, Liong MT. Antihypertensive properties of plant-based prebiotics. Int J Mol Sci 2009;10:3517–30. http://dx.doi.org/10.3390/ijms10083517.
[19] Parekh PJ, Arusi E, Vinik AI, Johnson DA. The role and influence of gut microbiota in pathogenesis and management of obesity and metabolic syndrome. Front Endocrinol 2014;5. http://dx.doi.org/10.3389/fendo.2014.00047 [article 47].
[20] Moreira APB, Teixeira TFS, Peluzio MCG, Alfenas RCG. Gut microbiota and the development of obesity. Nutr Hosp 2012;27:1408–14. http://dx.doi.org/10.3305/nh.2012.27.5.5887.
[21] Shen J, Obin MS, Zhao L. The gut microbiota, obesity and insulin resistance. Mol Asp Med 2013;34:39–58. http://dx.doi.org/10.1016/j.mam.2012.11.001.
[22] DiBaise JK, Frank DN, Mathur R. Impact of the gut microbiota on the development of obesity: Current concepts. Am J Gastroenterol Suppl 2012;1:22–7. http://dx.doi.org/10.1038/ajgsup.2012.5.
[23] Bervoets L, Van Hoorenbeeck K, Kortleven I, Van Noten C, Hens N, Vael C, et al. Differences in gut microbiota composition between obese and lean children: A cross-sectional study. Gut Pathog 2013;5:10. http://dx.doi.org/10.1186/1757-4749-5-10.
[24] Ferrer M, Ruiz A, Lanza F, Haange SB, Oberbach A, Till H, et al. Microbiota from the distal guts of lean and obese adolescents exhibit partial functional redundancy besides clear differences in community structure. Environ Microbiol 2013; 15:211–26. http://dx.doi.org/10.1111/j.1462-2920.2012.02845.x.
[25] Cani PD, Bibiloni R, Knauf C, Waget A, Neyrinck AM, Delzenne NM, et al. Changes in gut microbiota control metabolic endotoxemia-induced inflammation in high-fat diet-induced obesity and diabetes in mice. Diabetes 2008;57:1470–81. http://dx.doi.org/10.2337/db07-1403.
[26] Murphy EF, Cotter PD, Healy S, Marques TM, O'Sulliva O, Fouhy F, et al. Composition and energy harvesting capacity of the gut microbiota: Relationship to diet, obesity and time in mouse models. Gut 2010;59:1635–42. http://dx.doi.org/10.1136/gut.2010.215665.
[27] Cani PD, Joly E, Horsmans Y, Delzenne NM. Oligofructose promotes satiety in healthy human: A pilot study. Eur J Clin Nutr 2006;60:567–72. http://dx.doi.org/10.1038/sj.ejcn.1602350.
[28] Arora T, Loo RL, Anastasovska J, Gibson GR, Tuohy KM, Sharma RK, et al. Differential effects of two fermentable carbohydrates on central appetite regulation and body composition. PLoS ONE 2012;7:e43263. http://dx.doi.org/10.1371/journal.pone.0043263.
[29] Tilg H, Gasbarrini A. Prebiotics for obesity: A small light on the horizon. Gut 2012; 62:1096–7. http://dx.doi.org/10.1136/gutjnl-2012-303908.
[30] De Filippo C, Cavalieri D, Di Paola M, Ramazzotti M, Poullet JB, Massart S, et al. Impact of diet in shaping gut microbiota revealed by a comparative study in children from Europe and rural Africa. Proc Natl Acad Sci U S A 2010;107:14691–6. http://dx.doi.org/10.1073/pnas.1005963107.
[31] Kendall CWC, Esfahani A, Jenkins DJA. The link between dietary fibre and human health. Food Hydrocoll 2010;24:42–8. http://dx.doi.org/10.1016/j.foodhyd.2009.08.002.
[32] Slavin J. Fiber and prebiotics: Mechanisms and health benefits. Nutrient 2013; 5:1417–35. http://dx.doi.org/10.3390/nu5041417.
[33] Hermes RG, Molist F, Yawazaki M, Nofrarías M, Gomez De Segura A, Gasa J, et al. Effect of dietary level of protein and fiber on the productive performance and health status of piglets. J Anim Sci 2009;87:3569–77. http://dx.doi.org/10.2527/jas.2008-1241.
[34] Hooda S, Boler BMV, Serao MCR, Brulc JM, Staeger MA, Boileau TW, et al. 454 pyrosequencing reveals a shift in fecal microbiota of healthy adults men consuming polydextrose or soluble corn fiber. J Nutr 2012;142:1259–65. http://dx.doi.org/10.3945/jn.112.158766.
[35] Li F, Hullar MAJ, Schwarz Y, Lampe JW. Human gut bacterial communities are altered by addition of cruciferous vegetables to a controlled fruit- and vegetable-free diet. J Nutr 2009;139:1685–91. http://dx.doi.org/10.3945/jn.109.108191.
[36] Fuentes-Zaragoza E, Sánchez-Zapata E, Sendra E, Sayas E, Navarro C, Fernández-López J, et al. Resistant starch as prebiotic: A review. Starch-Starke 2011;63:406–15. http://dx.doi.org/10.1002/star.201000099.
[37] Van den Ende W. Multifunctional fructans and raffinose family oligosaccharides. Front Plant Sci 2013;4:247. http://dx.doi.org/10.3389/fpls.2013.00247.
[38] Yoo H-D, Kim D, Paek S-H. Plant cell wall polysaccharides as potential resources for the development of novel prebiotics. Biomol Ther (Seoul) 2012; 20:371–9.
[39] Campos D, Betallulez-Pallardel I, Chirinos R, Aguilar-Galvez A, Noratto G, Pedreschi R. Prebiotic effects of yacon (Smallanthus sonchifolius Poepp. & Endl), a source of fructooligosaccharides and phenolic compounds with antioxidant activity. Food Chem 2012;135:1592–9. http://dx.doi.org/10.1016/j.foodchem.2012.05.088.
[40] Putta R, Jogloy S, Wangsomnuk PP, Srijarani S, Kesmala T, Patanothai A. Genotypic variability and genotype by environment interactions for inulin content of Jerusalem artichoke germplasm. Euphytica 2012;183:119–31. http://dx.doi.org/10.1007/s10681-011-0520-0.
[41] Sreenivas KM, Lele SS. Prebiotic activity of gourd family vegetable fibers using in vitro fermentation. Food Biosci 2013;1:26–30. http://dx.doi.org/10.1016/j.fbio.2013.01.002.

[42] Aida FMNA, Shuhaimi M, Yazid M, Maaruf AG. Mushroom as a potential source of prebiotics: A review. Trends Food Sci Technol 2009;20:567–75. http://dx.doi.org/10.1016/j.tifs.2009.07.007.

[43] Hyunh B-L, Palmer L, Mather DE, Wallwork H, Graham RD, Welch RM, et al. Genotypic variation in wheat grain fructan content revealed by a simplified HPLC method. J Cereal Sci 2008;48:369–78. http://dx.doi.org/10.1016/j.jcs.2007.10.004.

[44] Marotti I, Bregola V, Aloisio I, Di Gioia D, Bosi S, Silvestro RD, et al. Prebiotic effect of soluble fibres from modern and old durum-type wheat varieties on Lactobacillus and Bifidobacterium strains. J Sci Food Agric 2012;92:2133–40. http://dx.doi.org/10.1002/jsfa.5597.

[45] Nakamura T, Shimbata T, Vrinten P, Saito M, Yonemaru J, Seto Y, et al. Sweet wheat. Genes Genet Syst 2006;81:361–5.

[46] Shimbata T, Inokuma T, Sunohara A, Vrinten P, Saito M, Takiya T, et al. High levels of sugars and fructan in mature seed of sweet wheat lacking GBSSI and SSIIa enzymes. J Agric Food Chem 2011;59:4794–800. http://dx.doi.org/10.1021/jf200468c.

[47] Genc Y, Humphries JM, Lyons GH, Graham RD. Exploiting genotypic variation in plant nutrient accumulation to alleviate micronutrient deficiency in populations. J Trace Elem Med Biol 2005;18:319–24. http://dx.doi.org/10.1016/j.jtemb.2005.02.005.

[48] Nemeth C, Andersson AAM, Andersson R, Mangelsen E, Sun C, Åman P. Relationship of grain fructan content to degree of polymerization in different barleys. Food Nutr Sci 2014;5:581–9. http://dx.doi.org/10.4236/fns.2014.56068.

[49] Hansen HB, Rasmussen CV, Knudsen KEB, Hansen A. Effect of genotype and harvest year on content and composition of dietary fibre in rye (Secale cereale L.) grain. J Sci Food Agric 2003;83:76–85. http://dx.doi.org/10.1002/jsfa.1284.

[50] Cummings JH, Beatty ER, Kingman SM, Bingham SA, Englyst HN. Digestion and physiological properties of resistant starch in the human large bowel. Br J Nutr 1996;75:733–47. http://dx.doi.org/10.1079/BJN19960177.

[51] Martínez I, Kim J, Duffy PR, Schlegel VL, Walter J. Resistant starches types 2 and types 4 have differential effects on the composition of the fecal microbiota in human subjects. PLoS ONE 2010;5:e15046. http://dx.doi.org/10.1371/journal.pone.0015046.

[52] Smith SC, Choy R, Johnson SK, Hall RS, Wildeboer-Veloo ACM, Welling GW. Lupin kernel fiber consumption modifies fecal microbiota in healthy men as determined by rRNA gene fluorescent in situ hybridization. Eur J Nutr 2006;45:335–41. http://dx.doi.org/10.1007/s00394-006-0603-1.

[53] Madhukumar MS, Muralikrishna G. Fermentation of xylo-oligosaccharides obtained from wheat bran and Bengal gram husk by lactic acid bacteria and bifidobacteria. J Food Sci Technol 2012;49:745–52. http://dx.doi.org/10.1007/s13197-010-0226-7.

[54] Xiaoli X, Liyi Y, Shuang H, Wei L, Yi S, Hao M, et al. Determination of oligosac-charide contents in 19 cultivars of chickpea (Cicer arietinum L.) seeds by high performance liquid chromatography. Food Chem 2008;111:215–9. http://dx.doi.org/10.1016/j.foodchem.2008.03.039.

[55] Fernando WMU, Hill JE, Zello GA, Tyler RT, Dahl WJ, Van Kessel AG. Diets supplemented with chickpea or its main oligosaccharide component raffinose modify fecal microbial composition in healthy adults. Benefic Microbes 2010; 1:197–207. http://dx.doi.org/10.3920/BM2009.0027.

[56] He J-Y, Zhang Y, Li W, Sun Y, Zheng X-X. Prebiotic function of alpha-galactooligosaccharides from chickpea seeds. Food Sci 2011;32:94–8.

[57] Johnson CR, Thavarajah D, Combs Jr GF, Thavarajah P. Lentil (Lens culinaris L.): A prebiotic-rich whole food legume. Food Res Intl 2013;51:107–13. http://dx.doi.org/10.1016/j.foodres.2012.11.025.

[58] Mandalari G, Nueno-Palop C, Bisignano G, Wickham MSJ, Narbad A. Potential prebiotic properties of almond (Amygdalus communis L.) seeds. Appl Environ Microbiol 2008;74:4264–70. http://dx.doi.org/10.1128/AEM.00739-08.

[59] Azmi AFMN, Mustafa S, Hashim DM, Manap YA. Prebiotic activity of polysaccharides extracted from Gigantochloa levis (Buluh beting) shoots. Molecules 2012; 17:1635–51. http://dx.doi.org/10.3390/molecules17021635.

[60] Frankel OH. Genetic manipulations: Impact on man and society. In: Arber WK, Llimensee K, Peacock WJ, Starlinger P, editors. Genetic perspective of germplasm conservation. Cambridge, United Kingdom: Cambridge University Press; 1984. p. 161–470.

[61] Upadhyaya HD, Ortiz R. A mini core subset for capturing diversity and promoting utilization of chickpea genetic resources in crop improvement. Theor Appl Genet 2001;102:1292–8. http://dx.doi.org/10.1007/s00122-001-0556-y.

[62] Dwivedi SL, Upadhyaya HD, Balaji J, Buhariwalla HK, Blair MW, Ortiz R, et al. Using genomics to exploit grain legume biodiversity in crop improvement. Plant Breed Rev 2006;26:171–357. http://dx.doi.org/10.1002/9780470650325.ch6.

[63] Dwivedi SL, Crouch JH, Mackill DJ, Xu Y, Blair MW, Ragot M, et al. The molecularization of public sector crop breeding: Progress, problems, and prospects. Adv Agron 2007;95:163–318. http://dx.doi.org/10.1016/S0065-2113(07)95003-8.

[64] Dwivedi SL, Sahrawat KL, Rai KN, Blair MW, Andersson MS, Pfeiffer W. Nutritionally enhanced staple food crops. Plant Breed Rev 2012;36:169–292. http://dx.doi.org/10.1002/9781118358566.ch3.

[65] Gangola MP, Khedikar YP, Gaur PM, Bâga M, Chibbar RN. Genotype and growing environment interaction shows a positive correlation between substrates of raffinose family oligosaccharides (RFO) biosynthesis and their accumulation in chickpea (Cicer arietinum L.) seeds. J Agric Food Chem 2013;61:4943–52. http://dx.doi.org/10.1021/jf3054033.

[66] Huynh B-L, Wallwork H, Strangoulis JCR, Graham RD, Willsmore KL, Olson S, et al. Quantitative trait loci for grain fructan concentration in wheat (Triticum aestivum L.). Theor Appl Genet 2008;117:701–9. http://dx.doi.org/10.1007/s00122-008-0811-6.

[67] Huynh B-L, Mather DE, Schreiber AW, Toubia J, Baumann V, Shoaei Z, et al. Clusters of genes encoding fructan biosynthesizing enzymes in wheat and barley. Plant Mol Biol 2012;80:299–314. http://dx.doi.org/10.1007/s11103-012-9949-3.

[68] Ruuska SA, Rebetzke GJ, Van Herwaarden AF, Richards RA, Fettell NA, Tabe L, et al. Genotypic variation in water-soluble carbohydrate accumulation in wheat. Funct Plant Biol 2006;33:799–809. http://dx.doi.org/10.1071/FP06062.

[69] Yang DL, Jing RL, Chang XP, Li W. Identification of quantitative trait loci and environmental interactions for accumulation and remobilization of water-soluble carbohydrates in wheat (Triticum aestivum L.). Genetics 2007;176:571–84. http://dx.doi.org/10.1534/genetics.106.068361.

[70] Hayes PM, Blake T, Chen THH, Tragoonrung S, Chen F, Pan A, et al. Quantitative trait loci on barley (Hordeum vulgare L.) chromosome 7 associated with components of winterhardiness. Genome 1993;36:66–71. http://dx.doi.org/10.1139/g93-009.

[71] Mccallum J, Clark A, Pither-Joyce M, Shaw M, Butler R, Brash D, et al. Genetic mapping of a major gene affecting onion bulb fructan content. Theor Appl Genet 2006;112:958–67. http://dx.doi.org/10.1007/s00122-005-0199-5.

[72] Turner LB, Cairns AJ, Armstead IP, Ashton J, Skøt K, Whittaker D, et al. Dissecting the regulation of fructan metabolism in perennial ryegrass (Lolium perenne) with quantitative trait locus mapping. New Phytol 2006;169:45–58. http://dx.doi.org/10.1111/j.1469-8137.2005.01575.x.

[73] Broekaert WF, Courtin CM, Verbeke K, Van de Wiele T, Verstraete W, Delcour JA. Prebiotic and other health-related effects of cereal-derived arabinoxylans, arabinoxylan-oligosaccharids, and xylooligosaccharides. Crit Rev Food Sci Nutr 2011;51:178–94. http://dx.doi.org/10.1080/10408390903044768.

[74] Neyrinck AM, Van Hée VF, Piront N, De Backer F, Toussaint O, Cani PD, et al. Wheat-derived arabinoxylan oligosaccharides with prebiotic effect increase satietogenic gut peptides and reduce metabolic endotoxemia in diet-induced obese mice. Nutr Diabetes 2012;2:e28. http://dx.doi.org/10.1038/nutd.2011.24.

[75] Nguyen V-L, Huynh B-L, Wallwork H, Stangoulis J. Identification of quantitative trait loci for grain arabinoxylan concentration in bread wheat. Crop Sci 2011; 51:1143–50. http://dx.doi.org/10.2135/cropsci2010.08.0484.

[76] Müller J, Aeschbacher RA, Sprenger N, Boller T, Wiemken A. Disaccharide-mediated regulation of sucrose: Fructan-6-fructosyltransferase, a key enzyme of fructan synthesis in barley leaves. Plant Physiol 2000;123:265–74. http://dx.doi.org/10.1104/pp.123.1.265.

[77] Kawakami A, Yoshida M. Molecular characterization of sucrose:sucrose 1-fructosyltransferase and sucrose:fructan 6-fructosyltransferase associated with fructan accumulation in winter wheat during cold hardening. Biosci Biotechnol Biochem 2002;66:2297–305. http://dx.doi.org/10.1271/bbb.66.2297.

[78] Kawakami A, Yoshida M. Fructan:fructan 1-fractosyltransferase, a key enzyme for biosynthesis of graminan oligomers in hardened wheat. Planta 2005;223:90–104. http://dx.doi.org/10.1007/s00425-005-0054-6.

[79] Kooiker M, Drenth J, Glassop D, Mcintyre CL, Xue G-P. TaMYB13-1, a R2R3 MYB transcription factor, regulates the fructan synthetic pathway and contributes to enhanced fructan accumulation in bread wheat. J Exp Bot 2013;64:3681–96. http://dx.doi.org/10.1093/jxb/ert205.

[80] Edelman J, Jefford TG. The mechanism of fructosan metabolism in higher plants as exemplified in Helianthus tuberosus. New Phytol 1968;67:517–31. http://dx.doi.org/10.1111/j.1469-8137.1968.tb05480.x.

[81] Praznik W, Beck RHF. Application of gel permeation chromatographic systems to the determination of the molecular weight of inulin. J Chromatogr A 1985; 348:187–97. http://dx.doi.org/10.1016/S0021-9673(01)92452-5.

[82] Hellwege EM, Czapla S, Jahnke A, Willmitzer L, Heyer AG. Transgenic potato (Solanum tuberosum) tubers synthesize the full spectrum of inulin molecules naturally occurring in globe artichoke (Cynara scolymus) roots. Proc Natl Acad Sci U S A 2000;97:8699–704. http://dx.doi.org/10.1073/pnas.150043797.

[83] Stoop JM, Van Arkel J, Hakkert JC, Tyree C, Caimi PG, Koops AJ. Develop-mental modulation of inulin accumulation in storage organs of transgenic maize and transgenic potato. Plant Sci 2007;173:172–81. http://dx.doi.org/10.1016/j.plantsci.2007.04.011.

[84] Sévenier R, Van Der Meer IM, Bino R, Kooops AJ. Increased production of nutrients by genetically engineered crops. J Am Coll Nutr 2002;21:199S–204S. http://dx.doi.org/10.1080/07315724.2002.10719266.

[85] Weyens G, Ritsema T, Van Dun K, Meyer D, Lommel M, Lathouwers J, et al. Production of tailor-made fructans in sugar beet by expression of onion fructosyltransferase genes. Plant Biotechnol J 2004;2:321–7. http://dx.doi.org/10.1111/j.1467-7652.2004.00074.x.

[86] Stein AJ. Global impacts of human mineral malnutrition. Plant Soil 2010; 335:133–54. http://dx.doi.org/10.1007/s11104-009-0228-2.

[87] Eaton SB, Konner M. Paleolithic nutrition: A consideration of its nature and current implications. N Engl J Med 1985;312:283–9. http://dx.doi.org/10.1056/NEJM198501313120505.

[88] Morgan XC, Huttenhower C. Human microbiome analysis. PLoS Comput Biol 2012; 8:e1002808. http://dx.doi.org/10.1371/journal.pcbi.1002808.

[89] Tahir M, Lindeboom N, Bâga M, Vandenberg A, Chibbar R. Composition and correlation between major seed constituents in selected lentil (Lens culnaris Medik) genotypes. Can J Plant Sci 2011;91:825–35. http://dx.doi.org/10.4141/cjps2011-010.

[90] Zubaidah E, Akhadiana W. Comparative study of inulin extracts from dahlia, yam, and gembili tubers as prebiotic. Food Nutr Sci 2013;4:8–12. http://dx.doi.org/10.4236/fns.2013.411A002.

[91] Fernández EC, Rajchl A, Lachman J, Čížková H, Kvasnička F, Kotíková Z, et al. Impact of yacon landraces cultivated in the Czech Republic and their ploidy on the short- and long-chain fructoologosaccharides content in tuberous roots. LWT Food Sci Technol 2013;54:80–6. http://dx.doi.org/10.1016/j.lwt.2013.05.013.

[92] Kateřna V, Lebeda A, Doležalová I, Jirovský D, Simonovska B, Vovk I, et al. The biological and chemical variability of yacon. J Agric Food Chem 2006;54:1347–52. http://dx.doi.org/10.1021/jf052645u.

[93] Lachman J, Havrland B, Fernández EC, Dudjak J. Saccharides of yacon [Smallanthus sonchifolius (Poepp. et Endl.) H. Robinson] tubers and

rhizomes and factors affecting their content. Plant Soil Environ 2004; 50:383–90.

[94] Jovanovic-Malinovska R, Kuzmanova S, Winkelhausen E. Oligosaccharide profile in fruits and vegetables as sources of prebiotics and functional foods. Int J Food Prop 2014;17:949–65. http://dx.doi.org/10.1080/10942912.2012.680221.

[95] Judprasong K, Tanjor S, Puwastein P, Sunpuag P. Investigation of Thai plants for potential sources of inulin-type fructans. J Food Compos Anal 2011;24:642–9. http://dx.doi.org/10.1016/j.jfca.2010.12.001.

[96] Moongngarm A, Trachoo N, Sirigungwan N. Low molecular weight carbohydrates, prebiotic content, and prebiotic activity of selected food plants in Thailand. Adv J Food Sci Technol 2011;3:269–74.

[97] Wichienchot S, Thammarutwasik P, Jongjareonrak A, Chansuwan W, Hmadhlu P, Hongpattarakere T, et al. Extraction and analysis of prebiotics from selected plants from southern Thailand. Songklanakarin J Sci Technol 2011;33:517–23.

[98] Wichienchot S, Jatupornpipat M, Rastall RA. Oligosaccharides of pitaya (dragon fruit) flesh and their prebiotic properties. Food Chem 2010;120:850–7. http://dx.doi.org/10.1016/j.foodchem.2009.11.026.

[99] Galdón BR, Rodríguez CT, Rodríguez EMR, Romero CD. Fructans and major compounds in onion cultivars (Allium cepa). J Food Compos Anal 2009;22:25–32. http://dx.doi.org/10.1016/j.jfca.2008.07.007.

[100] Muir JG, Shepherd SJ, Rosella O, Rose R, Barrett JS, Gibson PR. Fructan and free fructose content of common Australian vegetables and fruit. J Agric Food Chem 2007;55:6619–27. http://dx.doi.org/10.1021/jf070623x.