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# 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 promotes 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, yacón, 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 suggest 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.

**Keywords:** Germplasm, gut microbiota, human health, non-digestible fibers, transgene

## 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 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 play an important role in reducing the risk of cardiovascular disease, regulate weight management, immune function, and in 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]. SCFAs 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, which needs 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 (*A. 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] have 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 amongst 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 $\alpha$-galactooligosaccharide ($\alpha$-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 $\alpha$-GOS [54]. Chickpea accession ‘171’ had the highest $\alpha$-GOS (8.68%) and lowest sucrose (2.36%), which may be used to obtain $\alpha$-GOS for use as a prebiotic in functional foods. Chickpea raffinose, another $\alpha$-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 plants 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].

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 (Figure 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 x 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 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 *y-vacuolar processing enzyme* (*y-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 increase 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 arabinoxylans 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-fructosyltransferase (1-SST) and fructan:fructan 1-fructosyltransferase (1-FFT) [80] with a chain length of up to 200 degree 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 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 fructans 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 $21^{rst}$ 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 ß-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 ß-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 grains 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 (Figure 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 fructans 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 offers 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 crops 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.

## Author's contributions

Sangam Dwivedi (SLD) and Rodomiro Ortiz (RO) proposed the theoretical frame for this review article, SLD, RO, Kanwar Sharawat and Naveen Puppala wrote the paper after analyzing the cited literature in the text.

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**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 $kg^{-1}$) | 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

**Table 2**

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

| Jerusalem artichoke | Accession number | Shallot | Accession number |
|---|---|---|---|
| Institute of Field and Vegetable Crops Novi Sad, Serbia | 120 | Science and Advice for Scottish Agriculture, United Kingdom | 707 |
| North Central Regional Plant Introduction Station, USA | 107 | Leibniz Institute of Plant Genetics and Crop Plant Research, Germany | 329 |
| Leibniz Institute of Plant Genetics and Crop Plant Research, Germany | 102 | Station d'Amélioration Pomme de Terre et Plantes à Bulbes, France | 319 |
| **Onion** | | **Leek** | |
| National Res. Centre for Onion and Garlic, India | 1,300 | Agriculture and Food Research Council, United Kingdom | 128 |
| Northeast Regional Plant Introduction Station, Cornell University, USA | 1,156 | Leibniz Institute of Plant Genetics and Crop Plant Res., Germany | 95 |
| Royal Botanic Gardens, Kew, United Kingdom | 976 | The Netherlands Plant Research International, Netherlands | 88 |
| **Garlic** | | **Okra** | |
| National Res. Centre for Onion and Garlic, India | 750 | Regional Station Akola, NBPGR, India | 2,286 |
| Vegetable Section Olomouc, Czech Republic | 623 | University of Georgia, USA | 2,220 |
| Asian Vegetable Research and Development Center, Taiwan, China | 505 | University of the Philippines, Los Baños College, Philippines | 942 |
| **Jack fruit** | | **Dahlia** | |
| Laboratoire d'Ecologie Moléculaire, Université de Pau, France | 81 | Research Institute of Landscaping and Ornamental Gardening, Czech Republic | 224 |
| Regional Station Thrissur, NBPGR, India | 72 | Vytautas Magnus University, Lithuania | 115 |
| Department of Agriculture Sabah, Malaysia | 57 | National Plant Material Center USDA/SCS, USA | 15 |
| **Dragon fruit** | | **Gembili** | |
| Programa de Recursos Genéticos Nicaragüenses, Nicaragua | 50 | Dry-lowlands Research Programme, Papua New Guinea | 149 |
| Southern Fruit Research Institute, Viet Nam | 24 | Dodo Creek Research Station, Solomon Islands | 112 |

| | | | |
|---|---|---|---|
| Departamento Nacional de Recursos Fitogenéticos y Biotecnología, Ecuador | 18 | University of the Philippines, Los Baños College, Philippines | 73 |
| **Yacón** | | **Chicory** | |
| Estación Experimental Agraria Baños del Inca, Peru | 123 | Station de Génétique/Amélioration des Plantes, INRA, France | 400 |
| Universidad Nacional de Cajamarca, Peru | 110 | Unité Expérimentale d'Angers, Groupe d'Étude et de contrôle des Variétés et des Semences (GEVES), France | 251 |
| Estación Experimental Agraria Andenes, Peru | 89 | Leibniz Institute of Plant Genetics and Crop Plant Res., Germany | 223 |

718

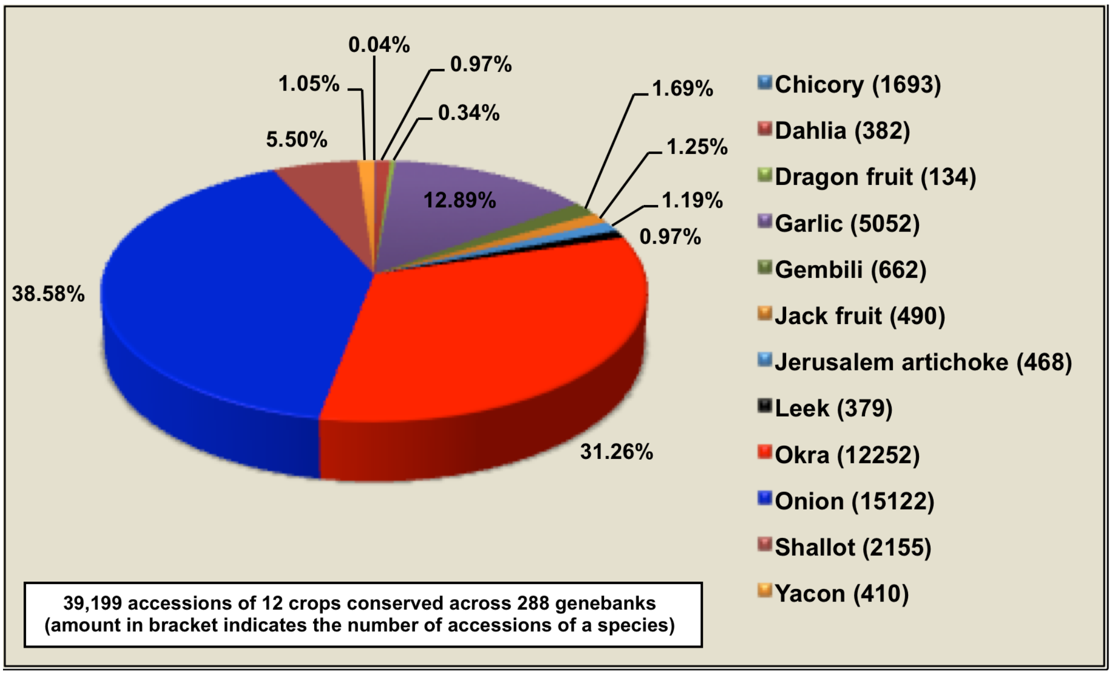

**Fig. 1.** Proportion of accessions representing 12 fruit, vegetable, root and tuber crops preserved across 288 genebanks globally (Source: http://apps3.fao.org/wiews/)