

## REVIEW

# The roles and potential of lentil prebiotic carbohydrates in human and plant health

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**Societal Impact Statement**

Lentils are not only rich in protein and micronutrients, but they also have significant amounts of prebiotic carbohydrates, which provide benefits to human health. Beneficial microorganisms ferment lentil prebiotic carbohydrates in the colon, which impart gut health benefits to the consumer. In addition, prebiotic carbohydrates provide benefits to lentil plant health through their roles in carbon transport, storage, and abiotic stress tolerance. Advantageous to both human and plant health, prebiotic carbohydrates should be a prominent target for breeding efforts to improve lentil as a crop, as well as its nutritional value to consumers.

**Summary**

Diet-related ailments, such as obesity and micronutrient deficiencies, have global adverse impacts on society. Lentil is an important staple crop, especially in South Asia and Africa, and has been associated with the prevention of chronic illnesses, including type II diabetes, obesity, and cancer. Lentil, a cool-season food legume, is rich in protein and micronutrients while also containing a range of prebiotic carbohydrates, such as raffinose family oligosaccharides (RFOs), fructooligosaccharides, sugar alcohols (SAs), and resistant starch (RS), which contribute to lentil's health benefits. Prebiotic carbohydrates are fermented by beneficial microorganisms in the colon, which impart health benefits to the consumer. Prebiotic carbohydrates are also vital to lentil plant health, being associated with carbon transport/storage and abiotic stress tolerance. Important to both human and plant health, prebiotic carbohydrates in lentil are a prominent candidate for nutrigenomic breeding efforts. New lentil cultivars could help to combat global health problems, while also proving resilient to climate change. The objectives of this review are to: (a) discuss the benefits lentil prebiotic carbohydrates confer to human and plant health; (b) describe the biosynthesis pathways of two prominent prebiotic carbohydrate families in lentil, RFOs and SAs; and (c) consider the potential of prebiotic carbohydrates in terms of future nutritional breeding efforts.

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## KEYWORDS

biosynthesis, breeding, health, lentil, nutrition, prebiotic, raffinose family oligosaccharides (RFOs), sugar alcohols (SAs)

## 1 | INTRODUCTION

Lentil (*Lens culinaris* Medikus) is an ancient crop. Cultivated lentil dates to before 7000 BCE with likely origin and domestication in southern Turkey and northern Syria (Cubero, Perez de la Vega, & Fratini, 2009). The genus *Lens* contains four species: *L. culinaris* (ssp. *culinaris*, *orientalis*, *tomentosus*, and *odemensis*), *L. ervoides*, *L. lamottei*, and *L. nigricans* (Wong et al., 2015). Lentil is a diploid with seven chromosome pairs ( $2n = 14$ ), with an estimated genome size of 4,063 Mb (Rizvi, Aski, Sarker, Dikshit, & Yadav, 2019). Lentil is a staple crop in much of the world, consumed particularly in South Asia and Africa. World lentil production, led by Canada, India, Turkey, and the United States, exceeded 7.5 million tons in 2017 (FAOSTAT, 2017).

Lentil is commonly consumed as a soup or “dahl,” a Southeast Asian dish typical in India, Nepal, Bangladesh, and Sri Lanka. Lentil has been referred to colloquially as “Poor man's meat,” as it is a rich source of nutrients, composed of 60%–67% carbohydrate, 20%–36% protein, <4% lipid, and 2%–3% ash on a dry basis (Bhatta, 1988). Its nutritional values compare favorably to other significant legumes and cereals, such as chickpea, soybean, rice, and wheat (Table 1). Lentil is an excellent source of energy; it is high in protein (typical of legumes), low in lipids, compared to chickpea and soybean, and rich in minerals and vitamins, compared to rice and wheat (Table 1). Consequently, a diet rich in lentil and other legumes has many health benefits. For example, substituting a half serving of legumes for eggs, bread, rice, or baked potato reduces the risk of developing diabetes (Becerra-Tomás

Nutrient	Lentil	Chickpea	Soybean	Rice	Wheat
Proximate analysis					
Water (g)	8.3	7.7	8.5	11.6	12.4
Energy (kcal)	352	378	446	365	332
Protein (g)	25	20	36	7	10
Total lipid (g)	1.1	6.0	20	0.7	2.0
Carbohydrate (by difference, g)	63	63	30	80	74
Fiber (g)	11	12	9	1	13
Sugars (g)	2.0	11	7	0.1	1.0
Minerals (mg)					
Calcium (Ca)	35	57	277	28	33
Iron (Fe)	6.5	4.3	16	0.8	3.7
Magnesium (Mg)	47	79	280	25	117
Phosphorus (P)	281	252	704	115	323
Potassium (K)	677	718	1,797	115	394
Sodium (Na)	6	24	2	5	3
Zinc (Zn)	3.3	2.8	4.9	1.1	3.0
Vitamins					
Vitamin C (mg)	4.5	4.0	6.0	0.0	0.0
Thiamin (mg)	0.87	0.48	0.87	0.07	0.3
Riboflavin (mg)	0.21	0.21	0.87	0.05	0.19
Niacin (mg)	2.61	1.54	1.62	1.60	5.35
Vitamin B-6 (mg)	0.54	0.54	0.38	0.16	0.19
Folate, dietary folate equivalent (μg)	479	557	375	8	28
Vitamin A, retinol activity equivalents (μg)	2	3	1	0	0
Vitamin E (mg)	0.49	0.82	0.85	0.11	0.53
Vitamin K (μg)	5.0	9.0	47.0	0.1	1.9

**TABLE 1** Nutritional values per 100 g of raw lentil, chickpea, soybean, rice, and wheat

Source: Original data obtained from the USDA Nutrient Database for Standard Reference (2018).

**TABLE 2** Mean carbohydrate concentrations in raw prebiotic-rich foods (lentil, chickpea, onion, and nectarine)

Carbohydrates (g/100 g)	Lentil	Chickpea	Onion	Nectarine
Sugar alcohols				
Sorbitol	0.66 ± 0.056	0.52 ± 0.048	nd	1.08 ± 0.079
Mannitol	0.02 ± 0.008	0.02 ± 0.006	nd	nd
Xylitol	0.02 ± 0.006	0.02 ± 0.002	nd	0.28 ± 0.026
Simple sugars				
Glucose	0.03 ± 0.016	0.03 ± 0.004	0.42 ± 0.01	1.50 ± 0.083
Fructose	0.01 ± 0.009	tr	1.21 ± 0.34	1.15 ± 0.052
Sucrose	1.71 ± 0.435	2.15 ± 0.433	0.43 ± 0.02	3.50 ± 0.198
Raffinose family oligosaccharides				
Raffinose	0.50 ± 0.116	0.44 ± 0.120	0.23 ± 0.011	nd
Stachyose	2.29 ± 0.100	0.53 ± 0.112	nd	nd
Verbascose	1.35 ± 0.437	0.12 ± 0.030	—	—
Fructooligosaccharides				
Kestose	0.33 ± 0.080	0.04 ± 0.018	1.15 ± 0.046	0.18 ± 0.011
Nystose	tr	0.01 ± 0.006	0.77 ± 0.028	0.65 ± 0.015
Soluble fiber	1.44 ± 0.11	tr	—	—
Insoluble fiber	19.0 ± 1.27	13.9 ± 0.09	—	—
Resistant starch	3.25 ± 0.42	3.39 ± 0.96	—	—

Note: Data are expressed as mean ± SD.

Abbreviations: nd, not detected; tr, trace amount.

Sugar alcohol, simple sugar, and oligosaccharide data were obtained from Siva et al. (2019) and Jovanovic-Malinovska, Kuzmanova, and Winkelhausen (2014) for lentil/chickpea and onion/nectarine, respectively. Fiber and resistant starch data were obtained from de Almeida Costa, Silva, Pissini Machado Reis, and Oliveira (2006).

et al., 2018). This effect is in part attributed to the low glycemic index of lentil and other legumes. Red lentil glycemic index (21%) compares favorably to other grain carbohydrate sources, such as multigrain bread (62%), basmati rice (69%), and whole-wheat pasta (55%; Henry, Lightowler, Strik, Renton, & Hails, 2005). A lentil-based diet reduces total and low-density lipoprotein cholesterol and the risk of cardiovascular disease (Abeysekara, Chilibeck, Vatanparast, & Zello, 2012), increases satiety (McCrary, Hamaker, Lovejoy, & Eichelsdoerfer, 2010), and is considered a potential solution to help combat obesity (Siva, Johnson, et al., 2018). Many of lentil's health benefits are likely due to the type and concentration of prebiotic carbohydrates present in the seed and how these change during cooking, cooling, and reheating (Johnson, Thavarajah, Combs, & Thavarajah, 2013).

Prebiotic carbohydrates are specific colonic nutrients that act as biosynthetic precursors for human microbiota activity, which in turn leads to possible health benefits related to combating type II diabetes and obesity. In addition to human health benefits, prebiotic carbohydrates also benefit plant health by increasing leaf raffinose family oligosaccharides (RFOs) to enhance drought (Bartels & Sunkar, 2005), chilling (Nishizawa, Yabuta, & Shigeoka, 2008), and freezing tolerance (Pennycooke, Jones, & Stushnoff, 2003). Sugar alcohols (SAs) also increase chilling (Chiang, Stushnoff, McSay, Jones, & Bohnert, 2005), drought (Pujni, Chaudhary, & Rajam, 2007), and salinity tolerance in a range of plants (Zhifang & Loescher, 2003). These RFOs and SAs

generally act as signaling compounds for both biotic and abiotic stresses (Valluru & Van den Ende, 2011). With climate conditions changing globally, future lentil production might be limited due to increased incidence of drought and higher temperatures. The significance of prebiotic carbohydrates to human and plant health means the type and concentration thereof in lentil are essential traits for nutrigenomic breeding efforts. Nutritionally improved lentil cultivars could help to combat global health problems, while simultaneously enhancing resilience to the effects of climate change (Muehlbauer et al., 2006).

## 2 | PREBIOTIC CARBOHYDRATES

The definition of a *prebiotic* has evolved since its coining in 1995. Complementary to the probiotic concept, Gibson and Roberfroid (1995) originally defined a prebiotic as a "non-digestible food ingredient that beneficially affects the host by selectively stimulating the growth and/or activity of one or a limited number of bacteria already resident in the colon." This definition was revised in 2004 to three criteria that restricted prebiotic foods to ingredients that are (a) resistant to mammalian digestion; (b) fermented by intestinal microflora; and (c) selectively stimulate the growth and/or activity of intestinal bacteria associated with health and well-being (Gibson, Probert, Van, Rastall, & Roberfroid, 2004). The definition was further

broadened in 2008 by the Food and Agricultural Organization of the United Nations to allow the possibility of extraintestinal sites and eliminate the requirement of selective fermentation (Pineiro et al., 2008). The definition was critiqued by Gibson et al. (2010) for this latter omission and also for not adequately excluding antibiotics. Reaffirming selective fermentation and establishing “a niche,” Gibson et al. (2010) defined a *dietary prebiotic* as “a selectively fermented ingredient that results in specific changes in the composition and/or activity of the gastrointestinal microbiota, thus conferring benefit(s) upon host health.” Selective fermentation was again challenged by Bindels, Delzenne, Cani, and Walter (2015), who eliminated this requirement from their definition and again restricted *prebiotic* to the gastrointestinal tract. In 2016, the International Scientific Association for Probiotics and Prebiotics (ISAPP) came to the current consensus definition: “a substrate that is selectively utilized by host microorganisms conferring a health benefit” (Gibson et al., 2017). This current definition has broadened the scope of prebiotics beyond carbohydrate substrates in the gastrointestinal tract by acknowledging the potential for non-gastrointestinal sites and non-carbohydrate substances. However, the definition has retained the selective fermentation component, which the ISAPP sees as vital to the concept of prebiotics (Gibson et al., 2017). While the definition has broadened beyond dietary carbohydrates, research on prebiotics has primarily focused on dietary prebiotic carbohydrates, and, consequently, these are our focus here regarding lentil.

Prebiotic carbohydrates can be categorized based on their degree of polymerization, sugar subunits, and linkage configuration. Naturally occurring prebiotic carbohydrates are divided into two major groups: dietary fiber and SAs (Roberfroid, 2007). Dietary fiber is comprised of starch polysaccharides (RS) and non-starch polysaccharides (RFOs, fructooligosaccharide [FOSs], galactooligosaccharides, xylooligosaccharides, hemicellulose, cellulose, pectin, and inulin; Roberfroid, 2007). These prebiotic carbohydrates are associated with many human health benefits, because they promote satiety, lower high cholesterol, and regulate postprandial blood glucose levels (Beserra et al., 2015). Most naturally occurring prebiotic carbohydrates are found in fresh vegetables, legumes, and fruits at concentrations ranging from trace amounts in wheat, to moderate levels in onion and green bananas, to relatively high concentrations (35.7–47.6 g/100 g) in chicory root (Van Loo et al., 1999).

As a staple part of many diets, legumes, such as lentil and chickpea, provide an excellent source of prebiotic carbohydrates (Table 2). Legumes tend to have higher concentrations of SA, RFO, fiber, and RS than prebiotic-rich fruits and vegetables, which tend to be higher in simple sugars and fructooligosaccharides (Table 2). For example, lentil and chickpea contain mean sorbitol concentrations of 0.66 and 0.52 g/100 g, respectively, compared to not detected and 1.09 g/100 g in onion and nectarine, respectively. With the exception of 0.23 g/100 g of raffinose in onion, nectarine and onion are void of detectable concentrations of RFO. Lentil and chickpea, however, have total RFO concentrations of 4.14 and 1.09 g/100 g, respectively. Although all legumes have merit as prebiotic-rich foods, our focus here is lentil, which is one of the most studied cool-season food legumes.

### 3 | LENTIL PREBIOTIC CARBOHYDRATES

Lentil contains a range of prebiotic carbohydrates including average concentrations of 4,071 mg of RFOs, 1,423 mg of SAs, 62 mg of FOSs, and 7,500 mg of RS per 100 g (Johnson et al., 2013). A recent study reported the prebiotic carbohydrate profile after removing protein and fat from lentil seeds (Table 2: Siva, Thavarajah, Kumar, & Thavarajah, 2019). Among simple sugars, sucrose was the most abundant (1,174–2,288 mg/100 g) followed by glucose (21–61 mg/100 g), fructose (0.2–21.9 mg/100 g), mannose (1.2–7.9 mg/100 g), and rhamnose (0.5–1.0 mg/100 g). For SAs, sorbitol concentrations (606–733 mg/100 g) were the highest followed by mannitol (9–31 mg/100 g) and xylitol (14–31 mg/100 g) regardless of the lentil market class. Among RFOs, stachyose (2,236–2,348 mg/100 g) was more abundant than raffinose (403–646 mg/100 g) and verbascose (581–1,769 mg/100 g). Considering lentil FOSs, kestose levels were higher than nystose levels. Other prebiotic carbohydrates present were arabinose (2,419–2,630 mg/100 g), xylose (1,912–1,936 mg/100 g), and cellulose (611–640 mg/100 g).

Lentil prebiotic carbohydrate concentrations vary by growing location. Johnson, Thavarajah, Thavarajah, Fenlason, et al. (2015) analyzed lentil samples from six countries (Table 3). They observed that total low-molecular weight carbohydrate concentrations were generally the highest in regions with less rainfall, higher temperatures, and higher estimated stress index. This suggests a mechanism of abiotic stress tolerance correlated with the type and level of prebiotic carbohydrates in lentil seeds. Total RFO concentrations ranged from 5,225 mg/100 g in Syria to 7,149 mg/100 g in Morocco. Total SA concentrations ranged from 1,385 mg/100 g in Washington State to 2,019 mg/100 g in Morocco. Further to variability due to location, they noted variation among the nine genotypes analyzed as well as a genotype × location interaction. The significant genotype × growing location interaction supports the hypothesis that increasing the nutritional value of lentil prebiotic carbohydrates can be achieved by selecting ideal growing areas and suitable cultivars for developing nutritionally superior varieties (Johnson, Thavarajah, Thavarajah, Fenlason, et al., 2015).

Concentration of prebiotic carbohydrate can also vary by location and genotype, or by method of food processing (Johnson, Thavarajah, Thavarajah, Payne, et al., 2015; Siva, Thavarajah, & Thavarajah, 2018). Lentils are often cooked, cooled, and reheated before consumption, hence these processes are important considerations in terms of their impact on the prebiotic carbohydrates undergoing these processes prior to consumption. Johnson, Thavarajah, Thavarajah, Payne, et al. (2015) measured prebiotic carbohydrate concentrations in whole and dehulled red and green lentil when raw and after cooking, cooling, and reheating. RFO concentrations decreased with processing (Figure 1), although the differences between raw and reheated lentil were only significant in whole lentil products. Differences in RS concentrations between raw/cooked and cooled/reheated were significant, indicating RS increases when food products are cooled after cooking, likely due to annealing. Siva, Thavarajah, et al. (2018) also showed

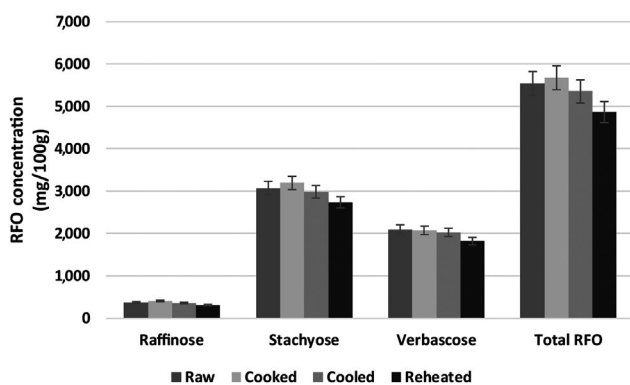
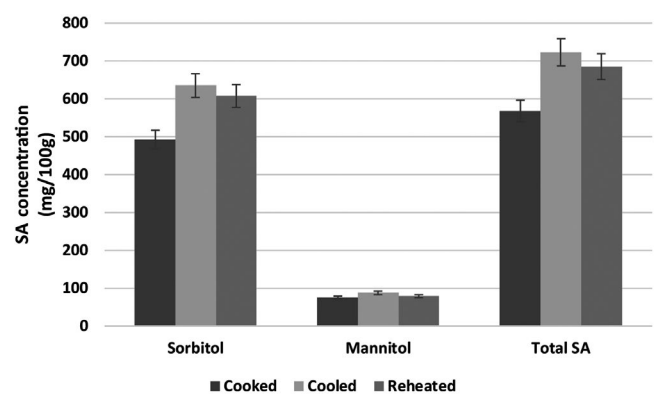
**TABLE 3** Prebiotic carbohydrate concentrations vary by growing location

Country	Sugar alcohols (mg/100 g)			Raffinose family oligosaccharides (mg/100 g)	
	Sorbitol	Mannitol	Galactinol	Raffinose + stachyose	
				Verbascode	
Washington, USA <sup>a</sup>	1,259	57	69	3,956	2,453
Terbol, Lebanon	1,528	117	52	3,314	1,926
Morocco <sup>b</sup>	1,824	132	63	4,802	2,347
Breda, Syria	1,419	87	46	3,318	1,907
Sanliurfa, Turkey	1,328	111	53	3,494	2,273
Akaki, Ethiopia	1,611	118	89	3,774	2,272
Mean	1,509	106	63	3,847	2,266

<sup>a</sup>Mean values of three locations in Washington, USA (Garfield, Fairfield, and Pullman) are reported.

<sup>b</sup>Mean values of three locations in Morocco (Jemaat, Shaim, and Marchouche) are reported.

Original data obtained from Johnson, Thavarajah, Thavarajah, Fenlason, et al. (2015).

**FIGURE 1** Mean raffinose family oligosaccharide (RFO) concentrations of raw, cooked, cooled, and reheated lentil. Original data obtained from Johnson, Thavarajah, Thavarajah, Payne, et al. (2015)**FIGURE 2** Mean sugar alcohol (SA) concentrations of cooked, cooled, and reheated lentil. Original data obtained from Siva, Thavarajah, et al. (2018)

this trend in RS. Additionally, they measured SA concentrations and found that sorbitol and mannitol concentrations significantly increase from cooked to cooled lentil in most market classes and then decrease again with reheating (Figure 2). These studies show that cooking/cooling/reheating processes can increase the health benefits of lentil via modulation of prebiotic carbohydrate concentrations.

#### 4 | LENTIL PREBIOTIC CARBOHYDRATES AND GUT HEALTH

The human gastrointestinal tract, with a surface area of over 300 m<sup>2</sup>, hosts more than 100 trillion microorganisms (Savage, 1977). These microbes, collectively termed “the microbiome”, comprise 10 times more cells than human cells and over 100 times more genetic information than the human genome (Bäckhed, Ley, Sonnenburg, Peterson, & Gordon, 2005). The microbiome is a dynamic ecosystem, with a myriad of interactions between microbes and human tissues that change throughout the course of human growth and development. Increasingly, the microbiome is recognized as an extra-human organ,

capable of protecting the host from invading pathogens, stimulating the immune system, increasing the availability of nutrients, stimulating bowel motility, and improving lipid levels in the body (Holzapfel & Schillinger, 2002). However, gut microbiota are also involved with a host of disease processes, including obesity, diabetes, infections, inflammatory bowel disease, cancer, and many others (Lynch & Pedersen, 2016). Primary determinants of microbiota composition and function include age, environment, genetic factors, diet, health status, and medical interventions, such as the use of antimicrobial agents (Lozupone, Stombaugh, Gordon, Jansson, & Knight, 2012).

The concept of modulating the gut microbiome's composition and function through diet, primarily through prebiotics, has gained enormous attention (Bindels et al., 2015). Prebiotics are fermented by hindgut microflora into active metabolites—short-chain fatty acids, branched-chain fatty acids, vitamins, and bile acid derivatives—that bathe the lumen of the intestinal tract. These compounds, in turn, produce a wide range of important physiological benefits, including anti-inflammatory and immune cell regulation (Arpaia et al., 2013), antineoplastic properties (Furusawa et al., 2013), and metabolic regulation (Gao et al., 2009).

We are now discovering the importance of the microbiome in early childhood growth and development. Moderate acute malnutrition in Bangladeshi children has been related to premature microbiota composition (Subramanian et al., 2014). Supplementation with gut microbial flora from healthy children and with foods rich in several prebiotic ingredients alleviated acute malnutrition with an associated normalization of age-appropriate hindgut microflora (Gehrig et al., 2019). Moreover, an altered gut microbiome has also been implicated in autism spectrum disorder, although this interaction is not yet thoroughly understood (Li, Hu, Ou, & Xia, 2019). Prospective studies with prebiotics in autistic children, when combined with exclusion of a dietary component, have revealed modest improvements in behavioral symptoms; however, randomized controlled trials have not been able to demonstrate these effects (Ng et al., 2019). These discoveries highlight opportunities for further research toward how novel dietary approaches can improve early childhood growth and development. As lentils provide significant levels of prebiotic carbohydrate, we propose they are an ideal food source for increasing prebiotic carbohydrates in people's diets and for imparting the health benefits these may provide. Indeed, the results from a recent study in rats further support the notion that a lentil-rich diet may have significant health benefits because of the superior nutritional value of its prebiotic carbohydrates and the concomitant increase in the activity of hindgut bacteria (Siva, Johnson, et al., 2018). Specifically, rats fed on a lentil diet had a significantly lower mean body weight ( $443 \pm 47$  g/rat) than those fed on control ( $511 \pm 51$  g/rat) or corn ( $502 \pm 38$  g/rat) diets; in addition, mean percent body fat and triglyceride concentration were lower and lean body mass was higher in rats fed on the lentil diet. Moreover, the fecal abundance of *Actinobacteria* and *Bacteroidetes* (beneficial bacteria) was significantly higher and the abundance of *Firmicutes* (pathogenic bacteria) was lower in rats fed the lentil diet versus the control diet.

When considering the impact of diet on the microbiome and chronic disease, we recommend a diet with satisfactory levels of prebiotics. Legumes, such as lentil, are a rich and affordable source of prebiotic carbohydrates with 100 g of lentil providing 12 g of prebiotic carbohydrates (Siva et al., 2019). This recommendation is especially applicable to countries where legumes are often neglected in people's diets. Creativity in processing methods and marketing approaches, such as the recent advance of plant-based burgers, could help to popularize lentil and other legumes in countries where they are not generally widely consumed.

## 5 | PREBIOTIC CARBOHYDRATES AND PLANT HEALTH

As would be expected due to their high concentrations in lentil seed, prebiotic carbohydrates are vital to lentil plant health. Several functions of these carbohydrates have been elucidated. Here we discuss two of the most abundant families of prebiotic carbohydrates in lentil, RFOs and SAs, and their roles as (a) primary photosynthetic products and carbon transport molecules; (b) carbon stores; and (c)

aids of abiotic stress tolerance, namely temperature, drought, and salinity stress.

Raffinose family oligosaccharides and SAs are primary photosynthetic products and carbon transport molecules in many higher plants. Labeled  $^{14}\text{CO}_2$  studies have revealed that the primary soluble carbon products synthesized through photosynthesis in higher plants are sucrose (ubiquitous), RFOs, and SAs (Loescher & Everard, 2000). The orders of plants that utilize RFOs as a photosynthetic product and storage molecule include Lamiales, Cucurbitales, Cornales, and some Celastrales (Sengupta & Majumder, 2015). *Ajuga reptans* L. is the premier example of this type of plant, which uses stachyose as its primary carbon transport molecule. To store carbon, it synthesizes RFO of higher degrees of polymerization (DP), which become trapped for storage purposes (Bachman, Matile, & Keller, 1994). Lentil is not known to synthesize RFOs in leaves as a primary photosynthetic product, and, consequently, also does not transport carbon via RFOs (Obendorf & Gorecki, 2012). Instead, sucrose and SAs function as the transport molecules to the seed during seed filling. RFOs are formed in maturing lentil seeds at high concentrations (Obendorf & Gorecki, 2012). Likewise, for SAs, Grant and ap Rees (1981) showed that approximately 70% of fixed carbon in apple leaves was made into sucrose and sorbitol. Similarly, Loescher, Tyson, Everard, Redgwell, and Bielecki (1992) found that 80%–90% of the fixed carbon was transformed into mannitol and sucrose in celery. Similar patterns of SA accumulation have been shown in lilac and apricot (Loescher & Everard, 2000). Although sucrose is the primary photosynthetic product and carbon transport molecule in legumes, SAs may also function passively in this capacity, being found in both the leaf and seed (Amede, Schubert, & Stahr, 2011; Johnson et al., 2013).

Raffinose family oligosaccharides and SAs also serve as a carbon store. As noted, some plants (i.e., *A. reptans*) store RFOs in their leaves by increasing DP. RFOs are primarily known for their accumulation in seeds during late development (Sengupta & Majumder, 2015) and are especially prevalent in legumes (Obendorf & Gorecki, 2012). RFOs protect the embryo during desiccation. During germination, RFOs are rapidly hydrolyzed by  $\alpha$ -galactosidases but do not appear to be necessary for germination (Peterbauer & Richter, 2001). The use of SAs as a carbon store is largely dependent on tissue type, developmental stage, and environment. For example, apple leaves contain 0.9% sorbitol (dry weight) in June but 4.8% in late July (Loescher & Everard, 2000). Physiologically mature lentil seeds contain significant concentrations of both sorbitol and mannitol (Johnson et al., 2013).

Lastly, RFOs and SAs aid plants experiencing abiotic stress. During abiotic stress, several compounds accumulate, including RFOs and SAs. These compounds aid the plant in survival through these extreme conditions by balancing osmotic pressures and have, therefore, been called "osmoprotectants" (Bohnert & Jensen, 1996). RFOs and SAs substitute for water as compatible solutes; they may provide a medium for enzyme function and protect enzymes from free radicals and consequent denaturing (Smirnov & Cumbes, 1989). Studies using transgenic plants with upregulated RFOs and SAs



**FIGURE 3** Biosynthetic pathway of raffinose family oligosaccharides and sugar alcohols from leaves to seed  
Figure created from Gangola and Ramadoss (2018), Loeschner and Everard (2000), and Dumschott, Richter, Loeschner, and Merchant (2017)

Significant genetic variability exists for lentil prebiotic carbohydrates (Frias, Vidal-Valverde, Bakhsh, Arthur, & Hedley, 1994; Johnson, Thavarajah, Thavarajah, Fenlason, et al., 2015; Tahir, Vandenberg, & Chibbar, 2011), indicating the possibility for genetic manipulation through conventional or molecular breeding approaches. Recent advances in genomic tools and techniques have great potential to accelerate current breeding efforts toward lentil varieties with moderate to high levels of prebiotic carbohydrates (Kumar, Rajendran, Kumar, Hamwieh, & Baum, 2015). Additionally, genome-wide association studies may reveal other genes/QTLs that affect the levels of prebiotic carbohydrates in lentil.

## 7 | CONCLUSION

Lentil is a rich source of prebiotic carbohydrates including SAs, RFOs, FOSs, and other polysaccharides such as cellulose, hemicellulose, and amylose. In addition to the human nutritional benefits, prebiotic carbohydrates have a significant influence on plant health, a feature that will significantly benefit the breeding of pulse crops for climate resilience. Consequently, lentil prebiotic carbohydrates are an important breeding target, requiring further characterization and evaluation of germplasm. Phenotyping diverse lentil mapping populations could identify future genetic markers associated with high levels of prebiotic carbohydrates and thus significantly accelerate nutritional breeding for different growing environments and consumer preference (Varshney et al., 2013). These genetic markers could then be used to screen locally grown varieties as well as to develop new cultivars with special consumer requirements; for example, breeder-friendly genetic markers can be used to develop new varieties with moderate RFOs and increased levels of FOSs and RS to reduce flatulence in populations sensitive to RFOs. Globally, the development and selection of lentil genotypes with enhanced levels of prebiotic carbohydrates could not only provide significant health benefits to society, but could also provide economic benefits through improved crop sustainability and production.

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## AUTHOR CONTRIBUTIONS

N.J. wrote the first draft of the manuscript and edited the final version. C.J. wrote a section of the manuscript and edited the final version. P.T. wrote parts of the manuscript and edited the final version. S.K. wrote parts of the manuscript and edited the final version. D.T. developed the outline with N.J., wrote several sections for the draft, and created/edited the final version.

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