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Original Research Article

A global survey of low-molecular weight carbohydrates in lentils

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ABSTRACT

Lentils contain a range of low-molecular weight carbohydrates (LMWC); however, those have not been well characterized. The objectives of this study were to (1) determine the concentrations of LMWC in lentils grown in six locations, and (2) identify any genetic and environmental effects on those LMWC concentrations. We analyzed 335 samples from 10 locations throughout 6 countries using high-performance liquid chromatography for sugar alcohols and various mono-, di-, and oligo-saccharides, including raffinose-family oligosaccharides (RFO) and fructooligosaccharides (FOS). Mean LMWC concentrations from each country varied widely: sorbitol, 1250–1824 mg/100 g; mannitol, 57–132 mg/100 g; galactinol, 46–89 mg/100 g; sucrose, 1750–2355 mg/100 g; raffinose + stachyose, 3314–4802 mg/100 g; verbascose, 1907–2453 mg/100 g; nystose, 8–450 mg/100 g; and kestose, from not detected to 244 mg/100 g. The concentrations of many of these LMWC varied with average temperature and precipitation of the region/country of origin. Significant genotype and genotype × location effects contributed to the variability in the concentrations of several LMWC, a feature that could prove useful in breeding lentils for novel agro-ecological environments and for consumer preference. The range of LMWC in lentil may contribute to its survival as a crop and its organoleptic and nutritional properties as a whole food.

1. Introduction

Lentil (*Lens culinaris* Medik.) is an ancient pulse crop, originating from the Mediterranean region and enduring as a staple food in Africa, Europe, South Asia, and Latin America. Varieties of lentil have been adapted for cultivation in diverse regions around the globe, including Asia, Africa, South America, North America, and Australia, enabling lentil production to meet the demands of a growing consumer base. Current world production is 4.9 million tons per annum, the majority of which comes from Canada, India, and Turkey (FAOSTATS, 2015).

Lentil contains a wide array of low-molecular weight carbohydrates (LMWC), such as mono- and di-saccharides, raffinose-family oligosaccharides (RFO), fructooligosaccharides (FOS), and sugar alcohols, all of which are synthesized during seed development (Johnson et al., 2012). Research has repeatedly shown that concentrations of these carbohydrates vary with genotype and growing environment (Johnson et al., 2012; Tahir et al., 2011a). In other words, the plants express different levels of sugars, sugar alcohols, and oligosaccharides depending not only on their genetics but also on their growing environment. For example, concentrations of two sugar alcohols (sorbitol and mannitol) and verbascose were greater in lentil seeds from McClean County, ND vs. Ward County, ND, USA in both 2010 and 2011 (Johnson et al., 2012). In the same study, concentrations of RFO and sugar alcohols were greater in certain lentil genotypes across locations.

Plants require photosynthetic energy for their growth and development. The resulting carbohydrates or sugars from photosynthesis are then utilized as substrates for growth, development, or stored as reserves for survival during abiotic stress (Eveland and Jackson, 2012). Sucrose is the primary transport sugar in plants that can act as a signal directly to these environmental stresses via

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its hexose cleavage products, glucose and fructose (Rolland et al., 2002; Price et al., 2004; Li et al., 2011). For example, sucrose availability from the source tissues decreases during water deficit, acting as a signal to adjust seed growth and development (Eveland and Jackson, 2012). In this way, the plant is able to distribute its resources to maximize its growth and reproduction during environment stress. Additionally, plant species produce RFO from sucrose to enhance drought tolerance (Obendorf, 1997; Clegg et al., 1982).

In addition to their roles in plant physiology, several LMWC, including FOS and RFO, have been extensively studied with respect to dietary interactions with the human gut microbiome and potential health benefits (Bouhnik et al., 2004; Gibson and Roberfroid, 1995; Benno et al., 1987). Such carbohydrates, often called ‘complex,’ ‘non-digestible,’ or ‘prebiotic’ carbohydrates, are not hydrolyzed by brush border enzymes in the small intestine. Microbes in the intestinal tract (especially colon) ferment the carbohydrates, producing short-chain fatty acids and profoundly affecting the ecology of the large intestine and overall human health (Roberfroid, 2007). These interactions are an important aspect of human health and nutrition, emphasizing the need to deepen our understanding of the expression of non-digestible carbohydrates in foods.

Because LMWC concentrations in lentil can vary with growing environment, likely as a means of stress management and survival, it is conceivable that genotypes within a certain environment would use a similar strategy, or pattern, of carbohydrate expression relative to other environments. Recognizing such patterns would be useful in breeding lentils for new and existing environments. For example, lentil growers could target specific genetic material that is well-adapted to a particular environment (i.e., based on the average weather conditions of any locations). Identifying lentil cultivars and growing environments that result in relatively high concentrations of certain carbohydrates, such as prebiotics, could provide a niche for health-food marketing. Thus, the objectives in this study were to (1) determine the concentrations of LMWC in lentils grown in six different countries and (2) identify genotype and growing environments interactions with respect to LMWC concentrations.

2. Materials and methods

2.1. Materials

Carbohydrate standards, reagents, and high-purity solvents used for high-performance liquid chromatographic (HPLC) analyses were purchased from Sigma–Aldrich Co. (St. Louis, MO) and VWR International (Radnor, PA). These were used without any further purification. Water, distilled and deionized (ddH_2O) to a resistance of $\geq$18.2 MΩ (Milli-Q Water System, Millipore, Milford, MA), was used for sample extractions and preparation. Commercially grown lentils (CDC Redberry) finely ground with a cyclone sample mill with 0.25-mm sieve (Udy Corporation, Fort Collins, CO) were used as a laboratory reference standard.

2.2. Lentil seeds

Lentil seed samples were collected from six countries: USA, Lebanon, Morocco, Syria, Turkey, and Ethiopia (Table 1). The lentils were grown in ten locations in 2009, 2011, and 2012, as part of regional variety trials and breeding programs by the International Center for Agricultural Research in the Dry Areas (ICARDA) in Morocco and Washington State University, Pullman, WA. The samples were ground (Udy cyclone sample mill with 0.25-mm sieve) and stored in their original packaging at −40 °C prior to analysis.

Location-specific climatic data – mean annual precipitation and mean temperature during the growing season of the harvest year – were collected for each country and growing year (Table 2). Additionally, national lentil yield and production data for each country were collected from FAOSTAT and reported (Table 2). In Washington, USA, mean annual precipitation ranged from 442 mm in Fairfield to 660 mm in Garfield. Garfield also had the most rainfall (162 mm) during the growing season (compare with Fairfield, 142 mm; Pullman, 112 mm). Average air temperatures were similar across all locations, slightly cooler in Pullman (14 °C) than Fairfied (15 °C) or Garfield (15 °C). Precipitation and temperature patterns were relatively similar among the Mediterranean countries (Lebanon, Morocco, Syria, and Turkey). Mean

Table 1
Country, harvest year, growing location, replicates, and number of genotypes and samples used in the study.

Country	Year	Locations	Coordinates	Replicates	Genotypes	Samples per location	Samples per country
USA	2012	Garfield, WA	47.0092° N 117.1419° W	3	9	27	81
		Fairfield, WA	47.3856° N 117.1739° W	3	9	27	
		Pullman, WA	46.7333° N 117.1667° W	3	9	27	
Lebanon	2011	Terbol	33.49° N 35.59° E	2	30	60	60
Morocco	2009	Jemaat Shaim	32.3500° N 8.8500° W	2	15	30	60
		Marchouche	34.2600° N 4.4700° W	2	15	30	
Syria	2011	Breda	35.56° N 37.10° E	2	15	30	60
	2012	Tel Hadya	36.01° N 36.56° E	2	15	30	
Turkey	2012	Sanliurfa	37.2542° N 39.0425° E	2	22	44	44
Ethiopia	2009	Akaki	8.833° N 38.8333° E	2	15	30	30
Total							335