QTL affecting soluble carbohydrate concentrations in stored onion bulbs and their association with flavor and health-enhancing attributes

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Abstract: Onion bulbs accumulate fructans, a type of soluble carbohydrate associated with lower rates of colorectal cancers. Higher fructan concentrations in bulbs are correlated with higher pungency, longer dormancy, and greater onion-induced antiplatelet activity (OIAA). We analyzed replicated field trials of a segregating family for types and concentrations of soluble carbohydrates in onion bulbs 90 days after harvest. Means were adjusted using dry weight as the covariant to reveal highly significant ($P < 0.001$) differences among parents and families for glucose, fructose, sucrose, and the fructans 1-kestose, neokestose, and (6G,1)-nystose. Fructan concentrations showed significant ($P < 0.05$) phenotypic correlations with each other and with sucrose, pungency, and OIAA. These observations are consistent with the hypothesis that onion bulbs accumulating fructans take up or retain less water, concentrating both soluble carbohydrates and thiosulfinates responsible for pungency and OIAA. Interval mapping of family means from the covariant analyses revealed regions on linkage groups A and D significantly (LOD > 2.68) affecting soluble carbohydrate concentrations. The enzyme catalyzing the first step of fructan polymerization, 1-sucrose-sucrose fructosyltransferase (1-SST), mapped independently of these genomic regions. One region on linkage group D near an acid-invertase gene was significantly (LOD = 3.45) associated with sucrose concentrations. This study reveals that the accumulation of sucrose in stored onion bulbs may allow for the combination of sweeter flavor with significant OIAA.

Key words: quantitative trait locus, fructans, thiosulfinates, reducing sugars.

Résumé : Les bulbes de l'oignon accumulent des fructanes, un type de glucide soluble qui est associé à un taux d'incidence réduit de cancer colorectal. Des concentrations accrues en fructanes chez les bulbes sont corrélées avec une plus grande âcreté, une dormance prolongée et une plus grande activité antiplaquettes (OIAA ; « onion-induced antiplatelet activity »). Les auteurs ont analysé une famille en ségrégation pour les types de glucides solubles et leurs teneurs chez des bulbes 90 jours après la récolte (provenant de plusieurs essais répliqués en champ). Les moyennes ont été ajustées sur la base du poids sec (comme covariable) et des différences très significatives ($P<0,001$) ont été observées entre les parents et les familles pour les teneurs en glucose, fructose, saccharose ainsi que pour les fructanes 1-kestose, neokestose et (6G,1)-nystose. Les concentrations en fructanes étaient significativement ($P<0,05$) corrélées les unes avec les autres ainsi qu'avec la teneur en saccharose, l'âcreté et l'OIAA. Ces observations sont conformes à l'hypothèse voulant que les bulbes qui accumulent davantage de fructanes accumulent ou retiennent moins d'eau, ce qui aurait pour effet de concentrer les glucides solubles et les thiosulfinates responsables de l'âcreté et de l'OIAA. Une cartographie par intervalles s'appuyant sur la moyenne des familles issue de l'analyse de covariance a révélé des régions sur les groupes de liaison A et D qui montraient un effet significatif ($LOD>2,68$) sur la concentration en glucides solubles. L'enzyme catalysant la première étape de polymérisation des fructanes, 1-sucrose-sucrose fructosyltransferase (1-SST), a montré une ségrégation indépendante par rapport à ces régions génomiques. Une région sur le groupe de liaison D, située à proximité d'un gène codant pour une invertase acide, montrait une association significative ($LOD = 3,45$) avec la concentration en saccharose. Cette étude montre que l'accumulation de saccharose dans les bulbes d'oignon

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entreposés pourrait entraîner le cumul d'une saveur plus douce et d'une OIAA significative.

Mots clés : locus d'un caractère quantitatif, fructanes, thiosulfinates, sucres réducteurs.

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Introduction

The primary storage carbohydrates in onion bulbs are low-molecular-weight fructans and account for up to 65% of the non-structural carbohydrates (Bacon 1957; Kahane et al. 2001; Jaime et al. 2002). Fructans are a significant source of soluble dietary fiber (Delzenne et al. 1995; Kleessen et al. 1997) and their consumption has been correlated with lower rates of colorectal cancers (Roberfroid and Delzenne 1998) and decreased levels of serum cholesterol, phospholipids, and triglycerides (Wun 1996). Onion is the second major food source of naturally occurring fructans and oligofructose in the American diet, providing about 25% of these compounds (Moshfegh et al. 1999).

Higher fructan concentrations in bulbs are correlated with greater soluble solids content (SSC) (Sinclair et al. 1995), higher pungency (Bedford 1984; Lin et al. 1995; Simon 1995; Galmarini et al. 2001), longer bulb dormancy (Foskett and Peterson 1950; Suzuki and Cutcliffe 1989), and higher onion-induced antiplatelet activity (OIAA) (Debaene et al. 1999; Galmarini et al. 2001). Galmarini et al. (2001) analyzed a segregating family from BYG15-23 × AC43 for quantitative trait loci (QTL) affecting dry weights (DW), SSC, pungency, and OIAA and revealed strong genetic and phenotypic correlations among these traits. Galmarini et al. (2001) recognized that the significant correlations among these traits may be due to the pleiotrophic effects of carbohydrate concentrations in the onion bulb, as previously suggested by Darbyshire and Henry (1979, 1981). According to this hypothesis, polymerization of fructans reduces water retention by onion bulbs concentrating both soluble carbohydrates and the thiosulfinates responsible for pungency and OIAA (Darbyshire and Henry 1979; Jaime et al. 2001; Galmarini et al. 2001; Kahane et al. 2001). The strong correlations among higher pungency, higher SSC, and higher OIAA represent a challenge to the health-functionality of onion because consumers are often unwilling to consume fresh onions that are highly pungent. Cooking onion reduces the pungency, but also decreases OIAA by driving off beneficial thiosulfinates (Ali et al. 1999; Chen et al. 2000). Therefore to enjoy the health-enhancing attributes of onion, consumers must eat more lower pungency or lightly cooked onions.

Previous research has established phenotypic differences for bulb carbohydrate concentrations among onion germplasms across environments (Kahane et al. 2001); however, there are no reports of analyses of segregating families from crosses between low- and high-solids populations. In this study, we analyzed soluble carbohydrates in onion bulbs from replicated trials of the BYG15-23 × AC43 segregating family (Galmarini et al. 2001; King et al. 1998) to reveal major quantitative trait loci (QTL) affecting carbohydrate concentrations and correlated phenotypic variation for pungency and OIAA. We also mapped 1-sucrose-sucrose fructosyltransferase (1-SST), the enzyme catalyzing the first step in fructan biosynthesis from sucrose (Vijn and Smeekens 1999), to assess its association with soluble carbohydrate concentrations.

Materials and methods

Plant materials

The genetic map of onion using the BYG15-23 × AC43 segregating family has been previously described (King et al. 1998). Individual F_2 plants were self pollinated to produce F_3 families; F_3-massed (M) families were produced by intercrossing among F_3 progenies from individual F_2 plants. Galmarini et al. (2001) described the analyses of replicated plots of these F_3M families over environments for SSC, pungency, and OIAA. Ten bulbs from each plot were randomly selected 90 days after harvest, cut, and juiced together. Galmarini et al. (2001) allowed the juice to sit on the laboratory bench for 20 min to produce enzymatically derived pyruvate for pungency evaluations (Schwimmer and Weston 1961). Samples of juices were frozen at –20 °C for pungency evaluations (Schwimmer and Weston 1961) and SSC measurements (Mann and Hoyle 1945). Second samples of the incubated onion juice were centrifuged at 4400 *g* for 10 min and supernants frozen at –80 °C for determinations of OIAA (Galmarini et al. 2001). Because carbohydrate degradation may have occurred in onion juices prepared by Galmarini et al. (2001) after incubation on the lab bench for 20 min and before freezing at –80 °C, we produced bulbs in 2001 in replicated plots of F_3M families, harvested, stored, and juiced as described by Galmarini et al. (2001). Replicate samples of onion juices were immediately boiled or allowed to sit on the bench for 20 min, followed by centrifugation and freezing at –80 °C as previously described. Juices extracted by Galmarini et al. (2001) 90 days after harvest and frozen at –80 °C from replicated plots at Randolph, Wis., in 1997 and Palmyra, Wis., in 1998 were also sampled. After HPLC analyses of fructans (described below), we calculated the correlations among carbohydrate concentrations in onion juices prepared by Galmarini et al. (2001) with onion juices extracted and immediately boiled in 2001 to determine if significant degradation of fructans had occurred in the incubated onion juices (Galmarini et al. 2001).

Samples were filtered through 0.2-μm nylon filters (Millipore, Bedford, Mass.) and diluted 1:100 and 1:500 in sterile distilled water containing 0.1% sodium azide (to inhibit microbial growth). Carbohydrates were separated on a CarboPac PA-1 column (250 × 4 mm, Dionex, Sunnyvale, Calif.) using a Shimadzu HPLC (VP series HPLC C system). The elution gradient was from 99.5% A (100 mM sodium hydroxide) and 0.5% B (100 mM sodium hydroxide in 600 mM sodium acetate) to 43% A : 57% B over 20 min, followed by a 10 min wash with 99.5% A : 0.5% B. Separated carbohydrates were detected and quantified with a pulsed electrochemical detector (ESA coulochem II, Chelmsford, Mass.)

using a gold electrode. The starting potential, 0.050 V, was applied for 0.4 s and integration was from 0.3 to 0.4 s. The cleaning cycle was from 0.41 to 0.61 s at 0.75 V, followed by –0.19 V from 0.62 to 1.02 s. Separated carbohydrates were identified by cochromatography with standards and were quantified using a response curve generated for five concentrations of each sugar. Purification and characterization of fructans with three to five degrees of polymerization were completed as described by Henson and Livingston (1996).

Statistical analyses

Statistical analyses of soluble carbohydrate (glucose, fructose, sucrose, 1-kestose, neokestose, and (6G,1)-nystose) concentrations were completed using PROC GLM of SAS (SAS 1990) with bulb dry weights (DW) as the covariant and treating onion families and environments as random variables. Phenotypic correlations among soluble carbohydrate concentrations were calculated from least-square family means and compared with least-square family means of SSC, DW, pungency, and OIAA from Galmarini et al. (2001) adjusted using DW as the covariant. Because of the large number of correlation coefficients calculated, levels of significance were determined using the Bonferroni–Holm sequential test (Holm 1979; Rice 1989). Simple and composite interval mapping of chromosome regions affecting nonstructural carbohydrate concentrations were completed using the onion genetic map (King et al. 1998) and Plab(QTL) (Utz and Melchinger 1996). A minimum LOD score of 2.68 was chosen as significant based on genome-wide threshold LOD values after 50 permutation tests as described by Churchill and Doerge (1994).

Mapping of 1-SST

The full-length onion cDNA clone of 1-SST (Vijn et al. 1998) was the gift of Dr. S. Smeekens, University of Utrecht, Holland, and was hybridized (Bark and Havey 1995) to DNA gel blots of BYG15-23 and AC43 digested singly with *Alu*I, *Apa*I, *Asc*I, *Ava*I, *Ava*II, *Bam*HI, *Ban*I, *Bgl*I, *Bgl*II, *Bst*EII, *Dde*I, *Dra*I, *Eco*RI, *Eco*RV, *Fsp*I, *Hae*III, *Hinc*II, *Hin*dIII, *Kpn*I, *Mbo*I, *Msp*I, *Nae*I, *Nco*I, *Nde*I, *Not*I, *Pst*I, *Pvu*II, *Sac*I, *Sal*I, *Sca*I, *Spe*I, *Swa*I, *Xba*I, *Xho*I, and *Xmn*I to identify restriction fragment length polymorphisms (RFLPs) and to reveal complexity of banding patterns. RFLPs were mapped using the BYG15-23 × AC43 family (King et al. 1998) and Map Manager software (Manly et al. 2001).

Results

Carbohydrates in onion juice

We observed highly significant ($P < 0.01$) correlations ($r = 0.869$) among carbohydrate concentrations in onion juices prepared and frozen at –80 °C by Galmarini et al. (2001) versus juices extracted from bulbs produced in 2001, immediately boiled, and frozen at –80 °C, demonstrating that no significant fructan degradation had occurred in the onion juices prepared by Galmarini et al. (2001). Therefore, the onion juices extracted from bulbs 90 days after harvest by Galmarini et al. (2001) were used for this study. HPLC analyses showed that glucose and fructose concentrations were always greater than sucrose or fructans for both parents and progenies (Table 1), as previously reported by other researchers (Darbyshire 1978; Darbyshire and Henry 1979; Jaime et al. 2002). Neokestose was the most common fructan and represented 69% of total fructans; 1-kestose and (6G,1)-nystose were the next most concentrated at approximately 10% each. More complex fructans of degrees of polymerization > 3 comprised relatively minor components of the fructans, each at 3% or less. Onion juice from AC43 possessed significantly less soluble carbohydrates than BYG15-23 (Table 1). Family means adjusted to mean DW showed highly significant ($P < 0.001$) differences for SSC, glucose, fructose, sucrose, 1-kestose, neokestose, and (6G,1)-nystose (Table 2), indicating that carbohydrate differences among families were not simply the result of water retention by the bulbs. Environments were significant for all traits except glucose; none of the family-by-environment interactions were significant (Table 2). The concentrations of SSC, sucrose, 1-kestose, neokestose, and (6G,1)-nystose showed significant ($P < 0.05$) phenotypic correlations (Table 3). Neokestose was significantly correlated with pungency and OIAA and sucrose with OIAA (Table 3). Concentrations of glucose and fructose showed significant phenotypic correlations with each other, but not with SSC, pungency, OIAA, or the other carbohydrates (Table 3).

Genetics of carbohydrate accumulation in segregating family from AC43 × BYG15-23

Interval mapping of family means from the covariant analyses revealed one region on linkage group A significantly (LOD = 2.81) affecting (6G,1)-nystose concentrations and one region on linkage group D significantly associated with sucrose (LOD = 3.45) concentrations (Table 4). These chromosome regions were previously shown by Galmarini et al. (2001) to affect SSC or DW. The QTL on linkage group D is near an acid-invertase gene (API89) and had a major effect on sucrose concentrations, explaining 29% of the phenotypic variation with the chromosome region from BYG15-23 significantly increasing sucrose concentrations (Table 4). The region on linkage group E (API92 to AOB236) previously shown to affect DW, pungency, and OIAA (Galmarini et al. 2001) had no significant associations with carbohydrate concentrations.

Mapping of 1-SST in onion

1-SST initiates fructan synthesis by transferring one fructose from one sucrose to another sucrose to produce the trisaccharide 1-kestose (G1–2F1–2F) (Vijn and Smeekens 1999). Hybridization of 1-SST to onion DNA gel blots produced simple patterns (autoradiograms not shown), indicating that this enzyme is not duplicated in the onion genome, and revealed RFLPs with *Sca*I and *Xho*I digests. 1-SST mapped to the end of linkage group G at 2.3 cM from AOB156-E1-4.3 (King et al. 1998); thus phenotypic variation for soluble carbohydrates in the BYG15-23 × AC43 family was not associated with this chromosome region.

Discussion

This is the first study to evaluate segregating progenies from a cross of low- (AC43) and high- (BYG15-23) solids

Table 1. Least-square means ± standard error for carbohydrate concentrations in bulbs from AC43 and BYG15-23 and ranges of progenies from segregating family of BYG15-23 × AC43.

Entry	SSC	GLU	FRU	SUC	KES	NEO	NYS
AC43	4.6±0.8*a*	16.2±2.3*a*	13.3±2.2*a*	2.4±1.9*a*	0.3±0.2*a*	1.4±0.1*a*	0.4±0.3*a*
BYG15-23	8.7±0.6*b*	15.4±1.6*a*	19.7±1.6*b*	12.8±1.4*b*	0.7±0.2*b*	5.9±1.0*b*	0.4±0.2*a*
Progeny range	5.6 to 8.9	11.7 to 24.4	14.0 to 25.3	2.5 to 17.5	0.0 to 2.3	0.4 to 10.5	0.0 to 2.0

Note: Least-square mean calculated using dry weights as the covariant and expressed as micrograms per microliter of onion juice. Parental means in columns followed by the same letter were not significantly different at P < 0.01**.** Abbreviations are dry weights (DW), soluble solids content (SSC), glucose (GLU), fructose (FRU), sucrose (SUC), 1-kestose (KES), neokestose (NEO), and (6G,1)-nystose (NYS). Values for SSC were previously reported by Galmarini et al. (2001) and are included here for convenience only.

Table 2. Level of significance among families, environments, and their interaction for carbohydrate concentrations in bulbs of a segregating family of BYG15-23 × AC43.

SV	SSC[a]	GLU	FRU	SUC	KES	NEO	NYS
Families	0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Environments	<0.001	0.866	<0.001	0.042	0.002	0.003	<0.001
Family × Environment	0.948	0.257	0.968	0.989	0.497	0.072	0.365

Note: Means were adjusted using dry weights as the covariant.
[a]Significances and ranges for SSC were previously reported by Galmarini et al. (2001) and are included here for convenience only. See Table 1 for abbreviations.

Table 3. Phenotypic correlations among means adjusted using dry weight as the covariant for individual carbohydrates, flavor, and onion-induced antiplatelet activities of onion juice from the segregating family of BYG15-23 × AC43.

	SSC[a]	PYR	OIAA	GLU	FRU	SUC	KES	NEO
PYR	**0.575**							
OIAA	**0.381**	**0.573**						
GLU	–0.104	–0.006	0.177					
FRU	–0.049	0.187	0.235	**0.726**				
SUC	**0.648**	0.358	**0.447**	0.06	0.025			
KES	**0.588**	0.311	0.289	0.03	–0.287	**0.778**		
NEO	**0.66**	**0.39**	**0.37**	0.128	–0.034	**0.807**	**0.871**	
NYS	**0.487**	**0.487**	0.233	0.125	–0.265	**0.605**	**0.953**	**0.796**

[a]See Table 1 for abbreviations. Correlation coefficients shown in bold were significant at $p < 0.05$ using the Bonferroni–Holm sequential test (Holm 1979; Rice 1989). PYR, enzymatically derived pyruvate activity; OIAA, onion-induced antiplatelet activity (Galmarini et al. 2001).

Table 4. Linkage groups significantly (LOD > 2.68) affecting carbohydrate concentrations in onion juice after adjusting to a mean dry weight (DW) for a segregating family from the cross of high- (BYG15-23) and low-solid (AC43) parents.

Linkage Group	Region[a]	Carbohydrate	LOD[b]	R^{2b}	Additive effect[c]
A	API18–AOB77	(6G,1)-nystose	2.81	24	10
D	AJK84–API89	Sucrose	3.45	28.7	3.2

[a]Linkage groups and marker positions were reported by King et al. (1998).
[b]LOD indicates log of odds ratio; R^2, coefficient of determination.
[c]Additive effect of increasing carbohydrate concentration in micrograms per microliter of onion juice after substitution of an allele from BYG15-23.

onions over environments for types and amounts of soluble carbohydrates in bulbs. Significant differences were observed among parental and progeny means for fructose, sucrose, 1-kestose, and neokestose using DW as the covariant (Tables 1 and 2). Jaime et al. (2001) also showed that the low-solids cultivar 'Grano de Oro' possessed significantly less sucrose and fructans than high-solids onions. In agreement with our study, numerous researchers (Darbyshire and Henry 1979; Jaime et al. 2001, 2002; Kahane et al. 2001) previously reported the relatively high proportion of 1-kestose and neokestose in onion bulbs. Darbyshire (1978) observed a predominance of these trisaccharides after 90-day storage of 'Golden Brown Lockyer', an onion from a background similar to BYG15-23 (Bark and Havey 1995), and attributed their accumulation to low-temperature hydrolysis of more complex fructans during storage. Family-by-environment interactions were not significant (Table 2); Kahane et al. (2001) also reported low environmental effects on soluble carbohydrate concentrations among onion germplasms.

We revealed significant phenotypic correlations among SSC, sucrose, 1-kestose, neokestose, and (6G,1)-nystose in

onion (Table 3). Concentrations of glucose and fructose were highly correlated with each other, but not with any of the other traits (Table 3). The significant phenotypic correlation between glucose and fructose concentrations were in agreement with Jaime et al. (2001), but in disagreement with Kahane et al. (2001) who reported significant phenotypic correlations between glucose and fructans with degrees of polymerizations (DP) of 5 or 6, as well as between fructose and fructans with DP of 3 or 4. The differences with our study may be due to the specific germplasms used to generate our segregating family, whereas Kahane et al. (2001) surveyed a range of germplasms.

QTL on linkage groups A and D were significantly associated with fructan and sucrose concentrations (Table 4), in the same regions previously shown to affect SSC or DW (Galmarini et al. 2001). Phenotypic variation for soluble carbohydrates in our segregating family was not associated with the chromosome region carrying 1-SST, the enzyme catalyzing the first step in fructan polymerization from sucrose (Vijn and Smeekens 1999). Galmarini et al. (2001) identified a region on linkage group E significantly associated with DW, SSC, pungency, and OIAA. However, this region showed no significant (LOD < 2.68) effects on any of these traits when analyzing family means adjusted to a mean DW, indicating that the QTL on linkage group E may affect relative water content of bulbs. The cDNA of a sucrose transporter (API66, Genbank accession number BE205593) mapped to this position on linkage group E (King et al. 1998; Galmarini et al. 2001). These observations are consistent with two previous hypotheses regarding soluble carbohydrate accumulation in onion. The first proposes that sucrose in onion is a transient molecule either degraded by invertases to glucose and fructose or used for fructan biosynthesis (Darbyshire and Henry 1981; Vijn and Smeekens 1999). The second hypothesis proposes that the significant phenotypic correlations among the thiosulfinates (responsible for pungency and OIAA) and soluble carbohydrates in onion bulbs are due to the relative water content of bulbs (Darbyshire and Henry 1979, 1981; Galmarini et al. 2001). The region on linkage group E near API66 may control sucrose availability. In the high-solids onion, sucrose would be available for fructan biosynthesis, allowing these bulbs to accumulate more fructans, take up or retain less water, and concentrate both thiosulfinates and soluble carbohydrates to produce the significant correlations among pungency, OIAA, and soluble carbohydrates (Table 3). If sucrose were unavailable, either owing to restricted transport or degradation, fewer fructans would be synthesized and these bulbs would retain more water, thereby causing the relatively low soluble carbohydrate concentrations to correlate with lower pungency and OIAA.

The region on linkage group D had a highly significant (LOD 3.45) effect on sucrose concentrations (Table 4). An RFLP revealed by API89, an onion cDNA with high similarity to acid invertase (Genbank accession AA451558), mapped to this region (Galmarini et al. 2001). In tomato, Fridman et al. (2000) reported that a major QTL controlling sucrose accumulation also mapped at an acid-invertase gene. The significantly higher sucrose concentrations in the high-solids parent and progenies were likely produced by low-temperature hydrolysis of previously accumulated fructans during the 90-day storage period (Darbyshire 1978).

In conclusion, our analyses of soluble carbohydrates in stored onion bulbs support the hypothesis that the accumulation of fructans are associated with greater thiosulfinate concentrations, yielding the strong phenotypic correlations among soluble carbohydrates, pungency, and OIAA. Our study also revealed that the accumulation of sucrose in stored onion bulbs may be a unique way to combine sweeter flavor with significant OIAA.

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