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Review

The Metabolism of the Fructooligosaccharides in Onion Bulbs: A Comprehensive Review

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Abstract: In the past two decades, there has been vast expansion in the research of fructooligosaccharides (FOS), including their chemistry, biochemistry and enzymology in higher plants. However, in spite of these considerable advances in fructan science, many other aspects of the mechanisms of fructan metabolism have not been fully understood. The bulbing and yield of dry onion cultivars vary, but they depend on the contents of the high dry matter and non-structural carbohydrates (fructooligosaccharides) which contribute to keepability. The knowledge of the mechanisms of the synthesis and the degradation of the FOS occurring during growth and storage are of great interest. Important progress has been made in the research area of onion FOS, and in addition to their role as accessible reserve carbohydrates in bulbs during sprouting, FOS participate in many physiological processes of production, protection and preservation of the bulbs. This review aims to contribute to a better understanding of the metabolism of FOS in onion bulbs, based on recent investigations. The activities of the main enzymes involved in the synthesis and the hydrolysis of the FOS during the pre-harvest (growth) and post-harvest (storage) life of the bulbs are reviewed, although present knowledge is too limited to explain clearly the mechanisms triggering the enzymes activities or the mechanisms by which FOS contribute to quality and long keepability of the bulbs.

Key words: catabolism, anabolism, fructooligosaccharides, *Allium cepa*

The onion bulb, like other *Alliums*, is widely used for culinary and medicinal purposes. Besides its remarkable medicinal powers, the onion is generally consumed for its flavor; its nutritive value has been appreciated only recently.[1] During cultivation, harvesting, handling, transportation, packaging and storage, onion bulbs are exposed to different treatments, atmospheric conditions and temperatures, all of which can affect their growth,[2] their quality and their physiological characteristics.[3,4] The results of these effects could be responsible for several reactions and for stress causing important biochemical changes in the bulb tissues.[3,5]

Carbohydrates in onion bulbs account for a major portion of their dry matter, contributing as much as 65 to 80% of the dry weight. The principle components of the non-structural carbohydrates are glucose, fructose, sucrose and a series of fructooligosaccharides (fructosyl polymers) with degrees of polymerization (DP) up to 12.[6−8]

The fructooligosaccharides (FOS), also known as fructans, polyfructosylsucroses of varying molecular size, are the main carbohydrate reserve of onions, as well as of other vegetative organs and plants including alliaceous organs (bulbs). FOS are accumulated during the bulbing stage, then are catabolized during the regrowth and the sprout development of the bulbs.[7] FOS may have functions other than carbon storage: they have been implicated in protecting plants against water deficit by drought or low temperature, in inducing resistance to drought or cold stress,[9−11] and as osmoregulators,[9,12,13] but the molecular mechanisms behind these putative roles still remains unclear. In studies of Jerusalem artichoke tubers and barley leaves, FOS and their metabolizing enzymes were found to be localized in the vacuoles of the protoplasts.[14,15] However despite the physiological and biochemical roles of FOS in bulbs (and tubers), little has been done on the enzymology and regulation of their degradation, and their catabolism in onion bulbs during growth, dormancy and sprouting has scarcely been investigated.

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1. Fructooligosaccharides in onion bulbs.

The occurrence of FOS in some *Allium* species has been known since 1894 as reported by Archbold.[16] The content, distribution and structure were first investigated during the 1970s by Bacon[17] and Darbyshire and Henry.[18,19] Later, FOS content and distribution were studied by Jaime *et al*.[20] and Campbell *et al*.[21] However, these studies were characterized by a relative lack of data because chemical and/or enzymatic methods were used to assess and to deduce high polymerized FOS on one hand, and techniques used for analyses did not allow the separation or identification of higher polymerized FOS on the other hand. Recently, new techniques for separating and determinating the structural composition of the different FOS in onions have been developed. Shiomi *et al*.[22−24] separated the FOS of onion and asparagus bulbs using the HPAEC-PAD technique (Fig. 1), while Stahl *et al*.[25] used simultaneous MALDI-MS and HPAEC methods and obtained similar results. These advanced techniques led to an ideal separation and identification of the different FOS found in onion bulb tissues as shown in Table 1.

Furthermore, the composition of the FOS has important

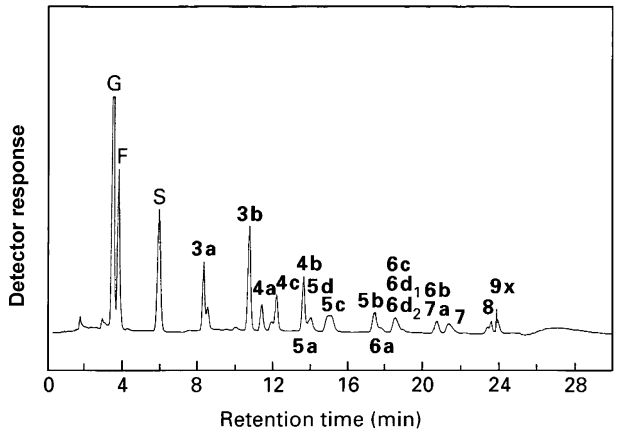

Fig. 1. Separation of neutral soluble carbohydrates of onion bulbs by high performance anion exchange chromatography and pulsed amperometric detection (HPAEC-PAD).[22]

G: glucose; F: fructose; S: sucrose; 1^F-β-D-fructofuranosylsucrose (3a, 1-kestoe); 6^G-β-D-fructofuranosylsucrose (3b, neokestose); 1^F(1-β-D-fructofuranosyl)$_2$ sucrose (4a, nystose); 6^G(1-β-D-fructofuranosyl)$_2$ sucrose (4b); 1^F, 6^G-di-β-D-fructofuranosyl sucrose (4c); 1^F(1-β-D-fructofuranosyl)$_3$ sucrose (5a); 6^G(1-β-D-fructofuranosyl)$_3$ sucrose (5b); 1^F(1-β-D-fructofuranosyl)$_2$-6^G-β-D-fructofuranosyl sucrose (5c); 1^F-β-D-fructofuranosyl-6^G(1-β-D-fructofuranosyl)$_2$ sucrose (5d); 1^F(1-β-D-fructofuranosyl)$_4$ sucrose (6a); 6^G(1-β-D-fructofuranosyl)$_4$ sucrose (6b); 1^F(1-β-D-fructofuranosyl)$_3$-6^G-β-D-fructofuranosyl sucrose (6c); 1^F-β-D-fructofuranosyl-6^G(1-β-D-fructofuranosyl)$_3$ sucrose ($6d_1$); 1^F(1-β-D-fructofuranosyl)$_2$-6^G(1-β-D-fructofuranosyl)$_2$ sucrose ($6d_2$); 1^F(1-β-D-fructofuranosyl)$_5$ sucrose (7a); 1^F(1-β-D-fructofuranosyl)$_m$-6^G(1-β-D-fructofuranosyl)$_n$ sucrose (7, $m+n=5$)1^F(1-β-D-fructofuranosyl)$_m$-6^G(1-β-D-fructofuranosyl)$_n$ sucrose (8, $m+n=6$); 1^F(1-β-D-fructofuranosyl)$_m$-6^G(1-β-D-fructofuranosyl)$_n$ sucrose ($9x$, $m+n\geq 7$).

implications for the physiology during bulbing, maturation, dormancy and sprouting of the bulbs.[6,7,26] However, this composition varies, although slightly, according to the type of onion (green or dry onion), cultivar, dry matter content and stage of maturity,[27] and the distribution of the FOS is variable from the outer (old) to the inner (young) scales[19] as shown in Fig. 2. It has been noted that content of low-DP FOS is correlated to that of dry matter (DM$<$ 10%),[28] while in high dry matter onion bulbs, the maximum degree of polymerization is between 10 and 15.[8,29]

Table 1. The structural composition of the different fructooligosaccharides of onion bulb separated by HPAEC.

	Structure
1-Kestose (3a)	1^F-β-D-fructofuranosylsucrose
Neokestose (3b)	6^G-β-D-fructofuranosylsucrose
Nystose (4a)	1^F(1-β-D-fructofuranosyl)$_2$ sucrose
4b	6^G (1-β-D-fructofuranosyl)$_2$ sucrose
4c	1^F, 6^G-di-β-D-fructofuranosyl sucrose
5a	1^F(1-β-D-fructofuranosyl)$_3$ sucrose
5b	6^G (1-β-D-fructofuranosyl)$_3$ sucrose
5c	1^F(1-β-D-fructofuranosyl)$_2$-6^G-β-D-fructofuranosyl sucrose
5d	1^F-β-D-fructofuranosyl-6^G(1-β-D-fructofuranosyl)$_2$ sucrose
6a	1^F(1-β-D-fructofuranosyl)$_4$ sucrose
6b	6^G(1-β-D-fructofuranosyl)$_4$ sucrose
6c	1^F(1-β-D-fructofuranosyl)$_3$-6^G-β-D-fructofuranosyl sucrose
$6d_1$	1^F-β-D-fructofuranosyl-6^G(1-β-D-fructofuranosyl)$_3$ sucrose
$6d_2$	1^F(1-β-D-fructofuranosyl)$_2$-6^G(1-β-D-fructofuranosyl)$_2$ sucrose
7a	1^F(1-β-D-fructofuranosyl)$_5$ sucrose
7	1^F(1-β-D-fructofuranosyl)$_m$-6^G(1-β-D-fructofuranosyl)$_n$ sucrose ($m+n=5$)
8	1^F(1-β-D-fructofuranosyl)$_m$-6^G(1-β-D-fructofuranosyl)$_n$ sucrose ($m+n=6$)
$9x$	1^F(1-β-D-fructofuranosyl)$_m$-6^G(1-β-D-fructofuranosyl)$_n$ sucrose ($m+n\geq 7$)

2. *Anabolism of FOS in onion bulb tissues.*

As stated above, the synthesis of the fructooligosaccharide polymers is localized in the vacuoles of the cells. The FOS consist of polymers of fructose attached to sucrose molecules. In onion, as in liliaceous plants, special types of FOS called the inulin neoseries are produced. In these types of FOS, the fructose residues are linked to 1-OH of fructofuranose residue and 6-OH glucopyranose residue. For this synthesis as shown in Fig. 3, three enzymes are required.[30–32] The sucrose: sucrose 1-fructosyltransferase (1-SST, EC 2.4.1.99) initiates FOS synthesis by catalyzing the transfer of a fructosyl residue from sucrose to another sucrose molecule, resulting in the formation of the trisaccharide 1-kestose (1^F-β-D-fructofuranosylsucrose or G1-2F1-2F). After that, the fructan: fructan 1-fructosyltransferase (1-FFT, EC 2.4.1.100) elongates the chain, while the fructan: fructan 6^G-fructosyltransferase links one fructosyl residue by (2→6) initiating the formation of inulin neoseries FOS. Whereas the involvement of two different enzymatic proteins (6G-FFT and 1-FFT) has been

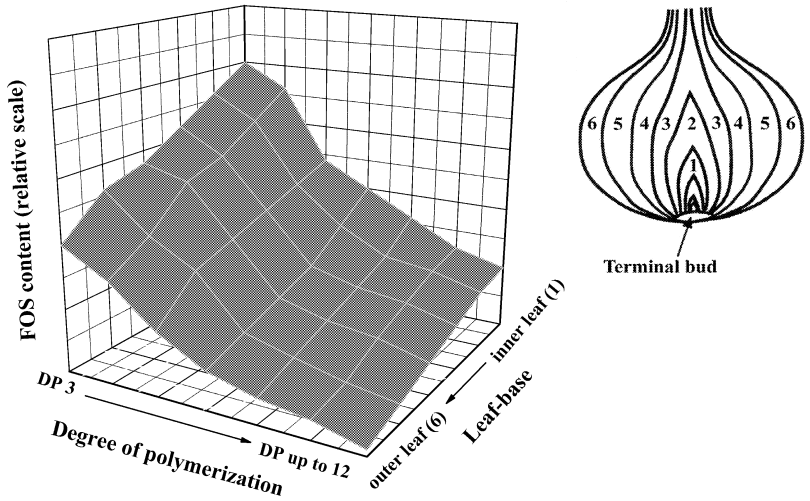

Fig. 2. The distribution of fructooligosaccharides in onion bulbs [adapted from Darbyshire and Henry[19]].

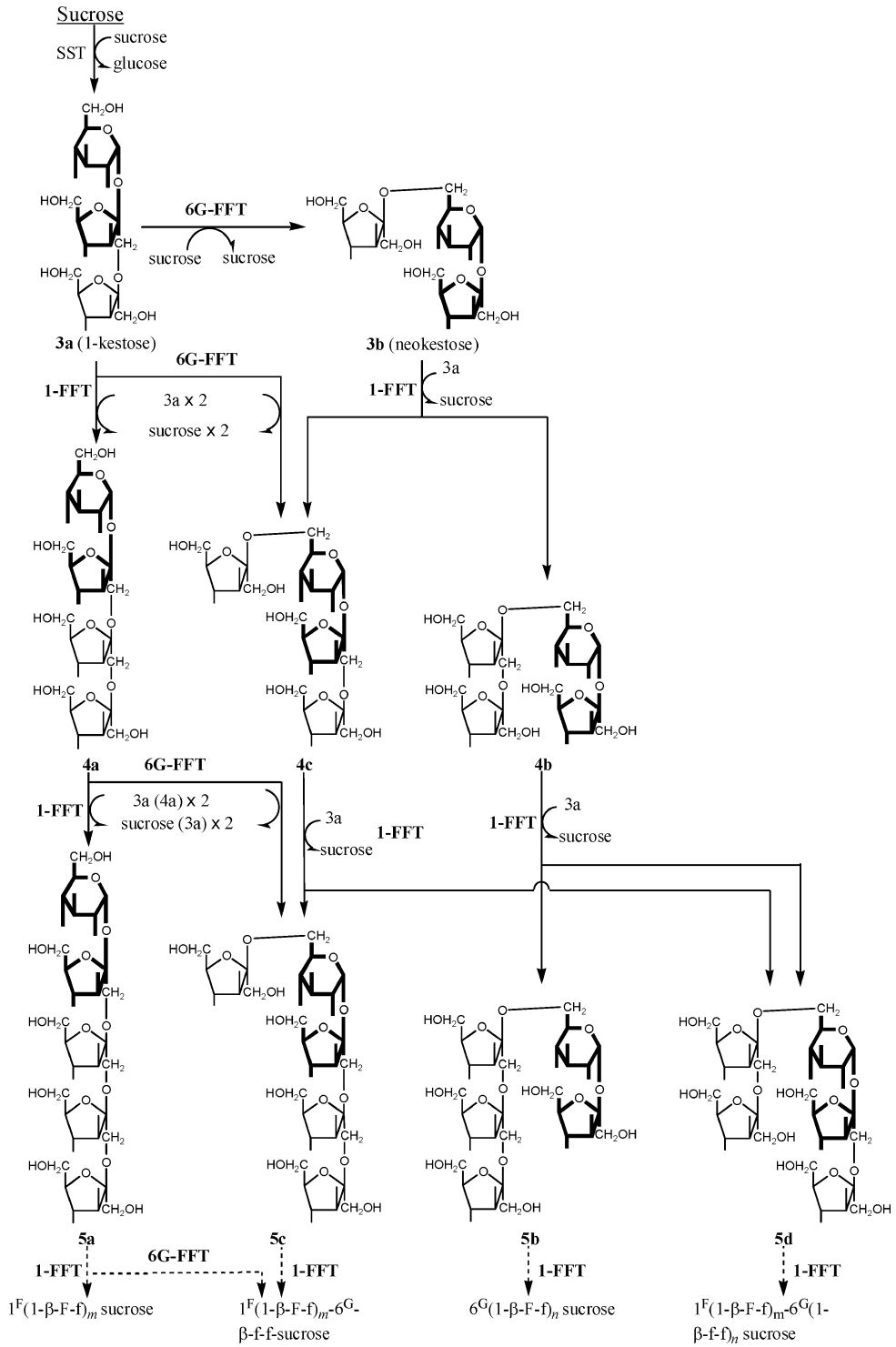

Fig. 3. Pathway of the enzymatic synthesis of the fructooligosaccharides in liliaceous plants.[31]

SST, sucrose: sucrose 1-fructosyltransferase; 1-FFT, fructan: fructan 1^F-fructosyltransferase; 6G-FFT, fructan: fructan 6^G-fructosyltransferase.

established in other vegetables, *i.e*. asparagus, recent proteomic and genomic studies carried out on 6G-FFT and 1-FFT activities have demonstrated that both activities in onion bulbs are assigned to a single and unique enzymatic protein,[33,34] and production of FOS was studied by their activity *in vitro* as shown in Fig. 4. The purified enzyme was classified as fructan: fructan 6^G fructosyltransferase (6G-FFT),[34] while 1-SST was purified and biochemically characterized from onion seeds[35] and bulb tissues.[36]

Nevertheless, despite this large amount of literature available on the synthesis of FOS in plants, especially artichoke, chicory, grass and barley, description of the biochemical process during the growth or pre-harvest period of onion is limited to that in the study of Shiomi *et al*.,[22] and a few descriptions of this process in other roots, rhizomes or bulbs.[37–39] In their investigation, Shiomi *et al*.[22] assessed the activities of the 1-SST, 6G-FFT and 1-FFT during the last three months of growth of three cultivars of onions. They noted that 1-SST showed regular and stable activity, while 6G-FFT and 1-FFT increased significantly two months before harvest and then decreased. This decrease indicates the end point of bulbing and com-

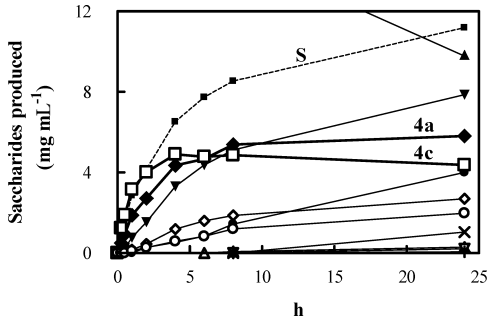

Fig. 4. Production of tetrasaccharides and other oligosaccharides from 1-kestose by onion fructosyltransferase[34]

■, sucrose; ▲, 1-kestose (3a); ▼, Neokestose (3b); ◆, nystose (4a); ●, (6^G(1-β-D-fructofuranosyl)$_2$ sucrose (4b); □, [1^F, 6^G-Di-β-D-fructofuranosyl sucrose] (4c); △, [1^F(1-β-D-fructofuranosyl)$_3$ sucrose] (5a); ▽, [6^G(1-β-D-fructofuranosyl)$_3$ sucrose] (5b); ◇, [1^F(1-β-D-fructofuranosyl)$_2$-6^G-β-D-fructofuranosyl sucrose] (5c); ○, [1^F-β-D-fructofuranosyl-6^G(1-β-D-fructofuranosyl)$_2$ sucrose](5d); ×, [6^G(1-β-D-fructofuranosyl)$_4$ sucrose] (6); +, [1^F(1-β-D-fructofuranosyl)$_m$-6^G(1-β-D-fructofuranosyl)$_n$ sucrose ($m+n=5$) (7).

plete maturity of the bulb which could be appreciated when 50 to 90% of the green tops have fallen.

Surprisingly, the activities of the synthesis enzymes during the post-harvest stage were also not investigated except in a work of Benkeblia *et al*.[40] These authors reported that the activities of the 6G-FFT and the 1-FFT in onion bulb tissues kept at 10 and 20°C showed similar patterns, although they were slightly higher at 10°C than at 20°C, particularly during the three last months.

However, it is pertinent to draw attention to the fact that pre-harvest and post-harvest anabolisms of FOS in onion bulb tissues are strictly different. The first one is mainly environmentally (day length and drought stress) dependent while the second is mainly physiologically (dormancy and sprouting) dependent. Furthermore, the few investigations providing some data on the activities of the enzymes involved in the synthesis of FOS, remain in fact insufficient and further studies are needed to further clarify the relation between the environmental and/or the physiological factors and the biosynthesis of FOS in onion bulb tissues, particularly during growth stage.

3. Catabolism FOS in onion bulb tissues.

When onion bulbs are harvested after complete maturity, FOS are no longer exported to meristematic cells and photosynthesis normally ceases.[41,42] Thus, harvesting may result in a change in the allocation of carbon with new sources (areas of carbohydrate supply) and sinks (areas of carbohydrate demand), resulting in redirection of metabolism.[41,43] Thus, dormancy in onion bulbs, as in other dormant organs, is a physiological stage that may be linked to the metabolic changes following this source-to-sink transition, when bulbs are preparing to sprout.[44] Physiologically, dormant bulbs are still metabolically active, although at greatly reduced levels. However, it is well established that the duration of dormancy varies among growing years and among cultivars, and depends on atmospheric and environmental conditions.[26,37,45,46] Thus, during storage of onion bulbs, as other plant tissues, FOS are hydrolyzed to low DP FOS, then disaccharides, and finally to monosaccharides. This hydrolysis usually takes place early in the first weeks following harvesting with little further change during the first few weeks of dormancy. However, after a prolonged period, and when sprouting starts, a considerable increase in the amount of reducing sugars (*i.e*. fructose and glucose) can occur.[47]

For the pre-harvest period, catabolism of the FOS in onion bulb tissues during growth has not been documented except by the work of Shiomi *et al*.[22] For post harvest life, numerous investigation were carried out on the variation of mono- and disaccharides,[7,8,48–50] and a few assessed the FOS.[8,20,21,47,49,51] Surprisingly, all of these investigation focused on the variation of these compounds, but little has been done on the variation of the different FOS isomers, and none have focused on the enzymatic processes behind this variation except for the studies of Fujishima *et al*.[34] and Benkeblia *et al*.[52]

Shiomi *et al*.[22] reported the activity of invertase in three onion cultivars during growth period and noted that activity decreased significantly during the last two months of growth when bulbs are ready for harvest. Thus, the enzyme activity could be a good indicator of bulb maturity, indicating that bulbs are about to "go in" the period of dormancy, reducing their metabolic activity.

The enzyme responsible for hydrolysis of fructans in plants is fructan exohydrolase (FEH, EC 3.2.1.80) and it is localized in vacuoles of the protoplasts.[53,54] A number of fructan-degrading enzymes have been identified from bacteria,[55,56] fungi[57–60] and higher plants;[61–67] however, the higher plants' FEHs which have been characterized exhibit a strong preference for either the β-2-1 or the β-2-6 linkage but were not completely specific for one type of linkage and many showed some ability to hydrolyze sucrose.[68,69] FEH hydrolyzes fructan molecules at the terminal, non-reducing fructosyl-residue (exolytic attack), thus releasing free fructose. Initially, two FEH activities (hydrolase A and B) were found in *Helianthus tuberosus* tubers.[70] Later, other FEHs were purified from oat[63] and Jerusalem artichoke,[64] while FEH from chicory has been purified,[65–67] cloned and well characterized.[71,72] However, the detection of FEH activity can be limited in crude or partially purified enzyme preparations by contaminating invertase (EC 3.2.1.26),[61] and very little is known about the regulation of its activity, which is of considerable interest because the vacuole is also the site of fructan synthesis and storage.

Nevertheless, in spite of these advances in FOS and enzymes involved in their hydrolysis, few or no investigations focused on the FEHs in onion bulbs during the post-harvest period except a study reported by Benkeblia *et al*.[52] These authors noted that 1-FEH showed low activity that peaked sharply for two weeks afterwards, then decreased to values observed during the first weeks, when bulbs are dormant. Thus, the activity of 1-FEH seems to be under strict control because of the evidence of seasonal variation. It was also reported that a degrading activity of 1-kestose which showed patterns closely reflecting 1-FEH activity, was independent of temperatures under which onion bulbs were kept during six months. Similar variation of 1-FEH activity in rhizophores of *Vermonia herbacea* was noted by Asega and Carvalho,[37] although this plant is biologically different from onion. Thus, the general pat-

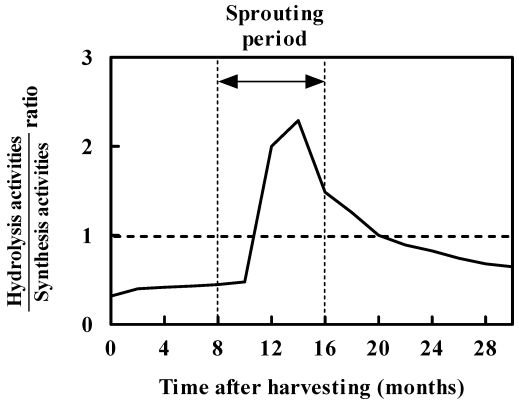

Fig. 5. Profile of the ratio of the enzyme activities of the hydrolysis to those of the synthesis in onion bulb tissues estimated under different temperatures.

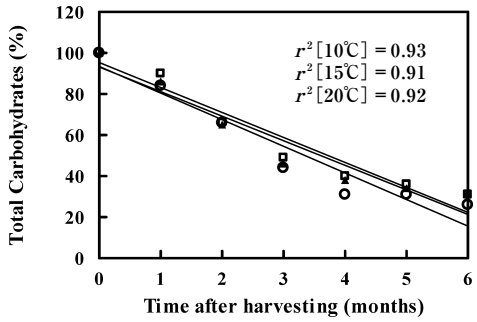

Fig. 6. Linear regression curves and coefficient of determination (r^2) of the total carbohydrates *versus* keeping time after harvesting at different temperatures.[3,73]

□, 10℃; ▲, 15℃; ○, 20℃.

tern of enzyme activities during the post-harvest life of bulbs was characterized by a peak where hydrolyzing activities are about three-fold higher, as shown in Fig. 5. This peak occurs after two months, indicating the break of dormancy and the onset of sprout regrowth, suggesting that hydrolyzing activities of FOS are higher during the regrowth of the sprout than that observed immediately after harvesting when onion bulbs are still in a dormant state. Furthermore, little researches have been done on the variation of different FOS of onion bulbs during post-harvest life. The total carbohydrates decrease progressively as they are consumed in sprout regrowth (sprouting),[3,8,20,73] However, the results showed that hydrolysis of FOS in onion tissues (*in vivo*) is temperature-independent, shown by a pseudo-linear regression in Fig. 6. The results also confirm the claim that saccharides and low DP FOS (DP 3−4) play a role in the balance of the catabolism of FOS in onion tissues during dormancy and sprouting. This balance maintains a specific level of monosacharides (glucose and fructose), avoiding their accumulation. They also probably exert a feedback effect by inducing the synthesis activities (1-FFT and 6G-FFT) which help to maintain this balance.

4. Conclusions and perspectives.

Despite increased attention in the past 10 years, FOS metabolism in onion bulbs has not yet been adequately explained in terms of biochemical and enzymological pathways. Undoubtedly, the pre- and post-harvest metabolism of FOS in onion tissues, such as in other roots and tubers, is unique both in terms of reaction products and the enzymes that catalyze their synthesis and degradation, but unfortunately this significance is not yet clear. Nevertheless, the results obtained to date show that pre-harvest metabolism of FOS in onion bulbs is primary under the influence of environmental factors, which act during the bulbing and maturation stages. On the other hand, post-harvest metabolism of FOS in onion bulb tissues evolves independently of the storage temperatures and is mainly associated with the dormancy and sprouting states of the bulbs. Indeed, the decrease and the peaks of the synthesizing or the degrading enzymes activities could be a strong signal of the complete maturity or the release from dormancy of the bulbs, respectively.

Besides providing some basic and essential information on FOS evolution during pre- and post-harvest life of onion bulbs, and variation of different enzymes involved in their metabolism, further experiments are needed in regard to: (i) the activity of a purified enzyme of 1-FEH of onion bulbs because its activity is not always highly present and seems to rise only during FOS mobilization, (ii) a better understanding of the 1-kestose hydrolyzing activity, and (iii) the relationship between the degradation rates of the different FOS isomers, *in vitro* and *in vivo*. It also seems appropriate that an immediate objective of future investigations must be the unambiguous purification of one or more relevant enzymes, especially 1-FEH. Ultimately, the best way to overcome these problems and produce a convincing enzyme model for onion FOS is to isolate the genes involved in these mechanisms.

REFERENCES

1) V.E. Rubatzky and M. Yamaguchi: World vegetables; principles, production and nutritive values. Chapman & Hall, New York (1997).
2) D.C.E. Wurr, D.W. Hand, R.N. Edmondson, J.R. Fellows, M. A. Hannah and D.M. Cribb: Climate change: a response surface study of the effects of CO_2 and temperature on the growth of beetroot, carrots and onions. *J. Agric. Sci*., **131**, 125−133 (1998).
3) N. Benkeblia, P. Varoquaux, N. Shiomi and H. Sakai: Storage technology of onion bulbs c.v. Rouge Amposta: effects of irradiation, maleic hydrazide and carbamate isopropyl, N-phenyl (CIP) on respiration rate and carbohydrates. *Int. J. Food Sci. Technol*., **37**, 169−175 (2002).
4) N. Benkeblia, P. Varoquaux, B. Gouble and G. Selselet-Attou: Respiratory parameters of onion bulbs (*Allium cepa*) during storage. Effects of ionising radiation and temperature. *J. Sci. Food Agric*., **80**, 1772−1778 (2000).
5) N. Benkeblia and G. Selselet-Attou: Effect of γ irradiation and storage time on the ascorbic acid concentration in onion bulbs (*Allium cepa* L.). *Int. Agrophysics*, **13**, 417−420 (1999).
6) J.L. Brewster: Onions and allied crops. in *Onions and Allied Crops, Vol. III Biochemistry, Food Science, and Minor Crops*, H.D. Rabinowitch and J.L. Brewster, eds., CRC Press, Boca Raton, pp. 63−102 (1990).
7) B. Darbyshire: Changes in the carbohydrate content of onion bulbs stored for various times at different temperatures. *J. Hortic. Sci*., **53**, 195−201 (1978).
8) M. Suzuki and J.A. Cutcliffe: Fructans in onion bulbs in relation to storage life. *Can. J. Plant Sci*., **69**, 1327−1333 (1989).
9) G.A.F. Hendry: Evolutionary origins and natural functions of fructans: a climatological, biogeographic and mechanistic appraisal. *New Phytol*., **123**, 3−14 (1993).
10) G.A.F. Hendry and R.K. Wallace: The origin, distribution, and

evolutionary significance of fructans. in *Science and Technology of Fructans*, M. Suzuki and N.J. Chatterton, eds., CRC Press, Boca Raton, pp. 119−139 (1993).
11) I. Vijn and S. Smeekens: Fructan: more than a reserve carbohydrates. *Plant Physiol*., **120**, 351−359 (1999).
12) D.P. Livingston III and C.A. Henson: Apoplastic sugars, fructans, fructan exohydrolase, and invertase in winter oat: responses to second-phase cold hardening. *Plant Physiol*., **116**, 403−408 (1998).
13) D.K. Hincha, E.M. Hellwege, A.G. Heyer and J.H. Crowe: Plant fructans stabilize phosphatidylcholine liposomes during freeze-drying. *Eur. J. Biochem*., **267**, 535−540 (2000).
14) M. Frehner, F. Keller and A. Wiemken: Localization of fructan metabolism in the vacuoles isolated from protoplasts of Jerusalem artichoke tubers (*Helianthus tuberosus* L). *J. Plant Physiol*., **116**, 197−208 (1984).
15) W. Wagner and A. Wiemken: Properties and subcellular localization of fructan hydrolase in the leaves of barley (*Hordeum vulgare* L. cv. Gerbel). *J. Plant Physiol*., **123**, 429−439 (1986).
16) H.K. Archbold: Fructosans in the monocotyledons. A review. *New Phytol*., **39**, 185−219 (1940).
17) J.S.D. Bacon: The trisaccharides fraction of some monocotyledons. *Biochem. J*., **73**, 507−514 (1959).
18) B. Darbyshire and R.J. Henry: Differences in fructan content and synthesis in some *Allium* species. *New Phytol*., **87**, 249−256 (1981).
19) B. Darbyshire and R.J. Henry: The distribution of fructans in onions. *New Phytol*., **81**, 29−34 (1978).
20) L. Jaime, M.A. Martín-Cabrejas, E. Mollá, F.J. López-Andréu and R.M. Esteban: Effect of storage on fructan and fructooligosaccharides of onion (*Allium cepa* L.). *J. Agric. Food Chem*., **49**, 982−988 (2001).
21) J.M. Campbell, L.L. Bauer, G.C. Fahey, A.J.C.L. Hogarth, B.W. Wolf and D.E. Hunter: Selected fructooligosaccharides (1-kestose, nystose, and 1^F-β-fructofuranosylnystose) composition of foods and feeds. *J. Agric. Food Chem*., **45**, 3076−3082 (1997).
22) N. Shiomi, S. Onodera and H. Sakai: Fructo-oligosaccharide content and fructosyltransferase activity during growth of onion bulbs. *New Phytol*., **136**, 105−113 (1997).
23) N. Shiomi: Structure of fructo-polysaccharide (asparagosin) from roots of asparagus (*Asparagus officinalis* L.). *New Phytol*., **123**, 263−270 (1993).
24) N. Shiomi, S. Onodera, N.J. Chatterton and P.A. Harrison: Separation of fructooligosaccharide isomers by anion-exchange chrommatography. *Agric. Biol. Chem*., **55**, 1427−1428 (1991).
25) B. Stahl, A. Linos, M. Karas, F. Hillenkamp and M. Steup: Analysis of fructans from higher plants by Matrix-Assisted Laser Desorption/Ionization Mass Spectrometry. *Anal. Biochem*., **246**, 195−204 (1997).
26) A.A. Mahmoud, B. Kalman and J. Farkas: A study of some chemicals in onion bulbs and their inner buds as affected by gamma radiation and storage. in *Food Preservation by Irradiation*, AIEA publications, Vienna, Vol. III, pp. 99−111 (1978).
27) J.L. Brewster: Onions and other vegetable *Alliums*. CAB International, Wallingford, UK, pp. 236 (1994).
28) B. Darbyshire and B.T. Steer: Carbohydrate biochemistry. in *Onions and Allied Crops, Vol. III Biochemistry, Food Science, and Minor Crops*, H.D. Rabinowitch and J.L. Brewster, eds., CRC Press, Boca Raton, pp. 1−16 (1990).
29) M.K. Ernst, N.J. Chatterton, P.A. Harrison and G. Matitschka: Characterization of fructan oligomers from species of the genus *Allium* L. *J. Plant Physiol*., **153**, 53−60 (1998).
30) C.J. Pollock and A.J. Cairns: Fructan metabolism in grasses and cereals. *Annu. Rev. Plant Physiol. Plant Mol. Biol*., **42**, 77−101 (1991).
31) N. Shiomi: Properties of fructosyltransferases involved in the synthesis of fructan in liliaceous plants. *J. Plant Physiol*., **134**, 151−155 (1989).
32) A. Wiemken, N. Sprenger and T. Boller: Fructan- an extension of sucrose by sucrose. in *International Symposium on Sucrose Metabolism*, H.G. Pontis, G.L. Salerno and E.J. Echeverria, eds., American Society of Plant Physiologist, Rockville, pp. 179−189 (1995).
33) T. Ritsema, J. Joling and S. Smeekens: Patterns of fructan synthesized by onion fructan: fructan 6^G-fructosyltransferase expressed in tobacco BY2 cells-is fructan: fructan 1-fructosyltrasferase needed in onion? *New Phytol*., **160**, 61−67 (2003).
34) M. Fujishima, H. Sakai, K. Ueno, N. Takahashi, S. Onodera, N. Benkeblia and N. Shiomi: Purification and characterization of a fructosyltransferase from onion bulbs and its key role in the synthesis of fructo-oligosaccharides *in vivo*. *New Phytol*., **165**, 513−524 (2005).
35) N. Shiomi, H. Kido and S. Kiriyama: Purification and properties of sucrose : sucrose 1^F-β-D-fructosyltransferase in onion seeds. *Phytochemistry*., **24**, 695−698 (1985).
36) R.J. Henry and B. Darbyshire: Sucrose : sucrose fructosyltransferase, and fructan : fructan fructosyltransferase from *Allium cepa*. *Phytochemistry*, **19**, 1017−1020 (1980).
37) A.F. Asega and M.A.M. Carvalho: Fructan metabolising enzymes in rhizophores of *Vernonia herbacea* upon excision of aerial organs. *Plant Physiol. Biochem*., **42**, 313−319 (2004).
38) N.M. Itaya, M.A.M. Carvalho and R.C.L. Figueiredo-Ribeiro: Fructosyl transferase and hydrolase activities in the rhizophores and tuberous roots upon growth of *Polymnia sonchifolia* (Asteraceae). *Physiol. Plant*., **116**, 451−459 (2002).
39) B. Orthen: Sprouting of the fructan- and starch-storing geophyte *Lachenalia minima*: Effects on carbohydrate and water content within the bulbs. *Physiol. Plant*., **113**, 308−314 (2001).
40) N. Benkeblia, S. Onodera and N. Shiomi: Effect of temperature and storage time on fructosyltransferase activities (1-FFT and 6G-FFT) in onion bulb tissues. *Acta Agric. Scand*., **53**, 211−214 (2003).
41) G.A. Lang: *Plant dormancy: Physiology, biochemistry and molecular biology*. CAB International, Wallingford, p. 386 (1996).
42) T. Nilsson: Postharvest handling and storage of vegetables. in *Fruit and Vegetable Quality* (*An Integrated View*), R.L. Shewfelt and B. Brückner, eds., Technomic Publishing Inc, Lancaster, pp. 96−121 (2000).
43) H. Mohr and P. Schopfer: *Plant Physiology*. 4th Ed., Springer-Verlag, Berlin (1995).
44) L. Espen, S. Morgutti, A. Abruzzese, N. Negrini, A. Rivetta, M.M. Quattrini, M. Cocucci and S.M. Cocucci: Changes in the potato (*Solanum tuberosum* L.) tuber at the onset of dormancy and during storage at 23°C and 3°C. I. Biochemical and physiological parameters. *Potato Res*., **42**, 189−201 (1999).
45) G.A. Lang: Dormancy: a new universal terminology. *HortScience*, **22**, 817−820 (1987).
46) M. Le Nard and A.A. De Hertogh: Bulb growth and development and flowering. in *The Physiology of Flower Bulbs*, A.A. De Hertogh and M. Le Nard, eds., Elsevier, Amsterdam, pp. 29−42 (1993).
47) P.P. Rutherford: Some biochemical changes in vegetables during storage. *Ann. Appl. Biol*., **98**, 538−541 (1981).
48) H. Böttcher: Qualitätsveränder-ungen während der lagerun von speisezwiebeln (*Allium cepa* L.). I: Mitt. Ernährungsphysiologische qualitätsmerkmale. *Die Nahrung*, **34**, 346−356 (1992).
49) N. Gorin and S. Börcsök: Chemical composition of stored onions, cultivar hyduro, as a criterion of freshness. *Lebensm. Wiss. Technol*., **13**, 164−166 (1980).
50) P.P. Rutherford and R. Whittle: The carbohydrates composition of onions during long term cold storage. *J. Hortic. Sci*., **57**, 349−356 (1982).
51) C.A. Croci, S.A. Banek and O.A. Curzio: Effect of gamma-irradiation and extended storage on chemical quality in onion (*Allium cepa* L.). *Food Chem*., **54**, 151−154 (1995).
52) N. Benkeblia, S. Onodera and N. Shiomi: Variation in 1-fructo-exohydrolase (1-FEH) and 1-kestose-hydrolysing (1-KH) activities and fructo-oligosaccharide (FOS) status in onion bulbs. Influence of temperature and storage time. *J. Sci. Food Agric*., **85**, 227−324 (2005).
53) W. Wagner, A. Wiemken and P. Matile: Regulation of fructan metabolism in leaves of barley (*Hordeum vulagare* L. cv. Gerbel). *Plant Physiol*., **81**, 444−447 (1986).
54) C.W.E. Darwen and P. John: Localization of the enzyme of fructan metabolism in vacuoles isolated by a mechanical method from tubers of Jerusalem artichoke (*Helianthus tubero-*

sus L). *Plant Physiol*., **89**, 658–663 (1989).
55) K. Muramatsu, S. Onodera, M. Kikuchi and N. Shiomi: Purification and some properties of β-fructofuranosidase from *Bifidobacterium adolescentis* G1. *Biosci. Biotechnol. Biochem*., **57**, 1681–1685 (1993).
56) K. Muramatsu, S. Onodera, M. Kikuchi and N. Shiomi: Substrate specificity and subsite affinities of β-fructofuranosidase from *Bifidobacterium adolescentis* G1. *Biosci. Biotechnol. Biochem*., **58**, 1642–1645 (1994).
57) S. Onodera and N. Shiomi: Purification and substrate specificity of *endo*-type inulinase from *Penicillium purpurogenum*. *Agric. Biol. Chem*., **52**, 2569–2576 (1988).
58) S. Onodera and N. Shiomi: Purification and subsite affinities of *exo*-inulinase from *Penicillium trzebinskii*. *Biosci. Biotechnol. Biochem*., **56**, 1443–1447 (1992).
59) S. Onodera, T. Murakami, H. Ito, M. Mori, H. Matsui, M. Honma, S. Chiba and N. Shiomi: Molecular cloning and nucleotide sequences of cDNA and gene encoding *endo*-inulinase from *Penicillium purpurogenum*. *Biosci. Biotechnol. Biochem*., **60**, 1780–1785 (1996).
60) K. Ohta, H. Akimoto and S. Moriyama: Fungal inulinases: Enzymology, molecular biology and biotechnology. *J. Appl. Glycosci*., **51**, 247–254 (2004).
61) R.J. Simpson, R.P. Walker and C.J. Pollock: Fructan exohydrolase activity from leaves of *Lolium temulentum* L. *New Phytol*., **119**, 499–507 (1991).
62) R.J. Simpson and G.D. Bonnet: Fructan exohydrolase from grasses. *New Phytol*., **123**, 453–469 (1993).
63) C.A. Henson and D.P. Livingston III: Purification and characterization of an oat fructan exohydrolase that preferentially hydrolases β-2,6-fructans. *Plant Physiol*., **110**, 639–644 (1996).
64) S.P. Marx, J. Nösberger and M. Frehner: Seasonal variation of fructo-β-fructosidase (FEH) activity and characterization of a β-(2-1)-linkage specific FEH from tubers of Jerusalem artichoke (*Helianthus tuberosus*). *New Phytol*., **135**, 267–277 (1997).
65) G. Claessens, A. Van Laere and M. De Proft: Purification and properties of an inulinase from chicory roots (*Cichorium intybus* L.). *J. Plant Physiol*., **136**, 35–39 (1990).
66) J. De Roover, A. Van Laere, M. De Winter, J.W. Timmermans and W. Van den Ende: Purification and properties of a second fructan exohydrolase from the roots of *Cichorium intybus*. *Physiol. Plant*., **106**, 28–34 (1999).
67) W. Van den Ende, A. Michiels, J. De Roover and A. Van Laere: Fructan biosynthetic and breakdown enzymes in dicots evolved from different invertases. Expression of fructan genes throughout chicory development. *The Scientif. World J*., **2**, 1273–1287 (2002).
68) C.A. Henson: Purification and properties of barley stem fructan exohydrolase. *J. Plant Physiol*., **134**, 186–191 (1989).
69) G.D. Bonnett and R.J. Simpson: Fructan hydrolyzing activities from *Lolium rigidum* Gaudin. *New Phytol*., **123**, 443–451 (1993).
70) J. Edelman and T.G. Jefford: The metabolism of fructose polymers in plants. 4. β-fructofuranosidases of tubers of *Helianthus tuberosus*. *Biochem. J*., **93**, 148–161 (1964).
71) W. Van den Ende, A. Michiels, D. Van Wonterghem, S.P. Clerens, J. De Roover and A.J. Van Laere: Defoliation induces fructan 1-exohydrolase II in witloof chicory roots. Cloning and purification of two isoforms, fructan 1-exohydrolase IIa and fructan 1-exohydrolase IIb. Mass fingerprint of the fructan 1-exohydrolase II enzymes. *Plant Physiol*., **126**, 1186–1195 (2001).
72) W. Van den Ende, A. Michiels, J. De Roover, P. Verhaert and A. Van Laere: Cloning and functional analysis of chicory root fructan 1-exohydrolase I (1-FEH I): a vacuolar enzyme derived from a cell-wall invertase ancestor? Mass fingerprint of the 1-FEH I enzyme. *Plant J*., **124**, 447–456 (2000).
73) N. Benkeblia, S. Onodera and N. Shiomi: Effect of gamma irradiation and temperature on fructans (fructo-oligosaccharides) of stored onion bulbs *Allium cepa* L. *Food Chem*., **87**, 377–382 (2004).

たまねぎ鱗茎におけるフルクトオリゴ糖代謝

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過去 20 年間に，高等植物におけるフルクトオリゴ糖（FOS）に関する研究は化学的，生物化学的および酵素化学的に大いに発展した．しかし，フルクタンの科学が急速に進歩したのにも拘わらずフルクタン代謝のメカニズムは十分に理解されていない．たまねぎの大きさや収量は品種によってまちまちで，乾物量やフルクトオリゴ糖含量がそれらに影響しさらに保存性にも影響を及ぼしている．たまねぎの生育中と貯蔵中における FOS の合成および分解のメカニズムに関する知見は非常に興味深い．タマネギ鱗茎の貯蔵炭水化物である FOS は発芽中に重要な役割を果たしており，鱗茎の生長，生体防御，貯蔵の際にも生理学的に関わっている．ここではたまねぎ鱗茎における FOS の代謝を理解するために最近の情報に基づき解説した．鱗茎収穫前と収穫後における FOS やその合成・分解に関わる酵素活性が鱗茎の品質や長期保存性と関係していること，そして FOS 関連糖が休眠打破の引き金となっていること，などのメカニズムについて，明解に説明するのには限度があるが，概説する．