Temporal Changes in Quercetin Accumulation and Composition in Onion (Allium cepa L.) Bulbs and Leaf Blades

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Bulb onion (Allium cepa L.) contains several functional components such as quercetin glycosides, a type of flavonoid. The quercetin content of bulb onion has been determined at harvest and storage; however, little is known about the changes in quercetin accumulation during development. In this study, two yellow onion varieties, ‘Momiji No. 3’ and ‘Quergold’, which differ in quercetin content at harvest, were grown on lowland soil following spring sowing in 2018 and 2019. Then, the changes in quercetin accumulation and composition in the bulbs and leaf blades from the seedling stage to harvest were evaluated. In both years, quercetin accumulation in the bulbs followed a similar trend, with ‘Quergold’ tending to have a higher quercetin content than ‘Momiji No. 3’, except for two weeks following transplanting. Significant differences between the quercetin contents in the two varieties were observed at harvest. The content of quercetin-4’-glucoside (Q-4’-G) was the same or higher than that of quercetin-3,4’-diglucoside (Q-34’-DG) throughout development, except on October 6, 2018, and July 29, 2019, in both varieties. Meanwhile, the quercetin content per bulb increased with bulb formation in both varieties. In contrast, quercetin accumulation in the leaf blades was lower than that in the bulbs throughout development in both years. An increase was observed from July, with accumulation of Q-34’-DG dominating until early July, whereafter accumulation of both Q-34’-DG and Q-4’-G was observed until harvest. Overall, these findings suggest that accumulation of quercetin glucoside content varies dramatically with growth, differing between onion bulbs and leaf blades.

Key Words: bulb development, flavonoid, quercetin distribution, varietal difference.

Introduction

Onion (Allium cepa L.) is a biennial plant in the subfamily Allioideae, family Amaryllidaceae. Thought to have originated in central Asia, onions are one of the oldest and most widely consumed vegetables worldwide, and the third highest in terms of domestic production, according to the Japanese Ministry of Agriculture, Forestry and Fisheries (2020). Onion bulbs accumulate flavonoids, fructan (fructo-oligosaccharides), and sulfur-containing compounds, all of which are recognized for their positive health benefits (Jaime et al., 2000; Platel and Srinivasan, 2016; Tsushida and Suzuki, 1995; Vågen and Slimestad, 2008). Flavonoids, a type of polyphenol, possess antioxidant properties, and have also been shown to reduce visceral fat area, blood pressure, and the risk of cancer, heart disease, and lifestyle diseases (Arts and Hollman, 2005; Hertog et al., 1993; Larson et al., 2012; Nishimura et al., 2020). Moreover, in both onions and other plants, flavonoids are utilized to attract insects via expression in brightly colored flowers and to prevent tissue damage from pathogens and ultraviolet light (Cook and Samman, 1996). Onions contain two main types of glycosides, quercetin glycosides and anthocyanidin glycosides, with yellow onion bulbs tending to accumulate quercetin-3,4’-diglucoside (Q-34’-DG) and quercetin-4’-glucoside (Q-4’-G), while red onion bulbs also accumulate cyanidin glycosides (Fossen et al., 1996; Zhang et al., 2016).

Previous analyses of quercetins in onions tended to focus on the content of onion bulbs at harvest and during storage (Lachman et al., 2003; Pérez-Gregorio et al., 2010). For example, Okamoto et al. (2006) compared the quercetin content of 105 onion varieties at both harvest and five months after harvest. Based on the
findings, various onion varieties with a high quercetin content were then developed (Muro et al., 2010, 2015). Meanwhile, Oku et al. (2018) reported varietal differences in the quercetin content of eight onion varieties in Aomori prefecture, Japan, while Tsukazaki et al. (2021) obtained trait data, including quercetin content, from 95 genetically diverse varieties. A study in Slovakia also reported changes in quercetin formation during the vegetative stage (Bystricka et al., 2015), although no information on the cultivation conditions and timing was provided. Reports on quercetin accumulation and its dynamics in *A. cepa* are limited, and it remains unclear how quercetin accumulation and distribution differ with growth. It is important to clarify when quercetin content increases to help produce quercetin-rich onions. Since an onion bulb is an organ formed by overlapping leaves, leaf blades also accumulate quercetin. However, there are no reports of quercetin accumulation in onion leaf blades. We thus tried to understand the quercetin accumulation differences between bulbs and leaf blades. In this study, varietal differences in quercetin accumulation were examined in two onion varieties that differ in their quercetin content at harvest. Quercetin accumulation and composition in the bulbs and leaf blades were determined from the seedling to harvest stage, providing an overall understanding of the changes that occur throughout bulb onion development.

**Materials and Methods**

**Plant materials and cultivation conditions**

Two varieties of bulb onion, ‘Momiji No. 3’ (Shippo, Mitoyo, Japan) and ‘Quergold’ (National Agriculture and Food Research Organization [NARO], Tsukuba, Japan), were used in this study. Their characteristic features are as follows: ‘Momiji No. 3’, color: yellow, photoperiod: long-day, bulb shape: globe, cultivation area: mainly Honshu, Shikoku, and Kyushu (autumn-sown), quercetin content at harvest: normal (Ikeda et al., 2019; Iwata, 1988); ‘Quergold’, color: yellow, photoperiod: long-day, bulb shape: flat globe, cultivation area: mainly Hokkaido (spring-sown), quercetin content at harvest: high (Muro et al., 2015). Seeds were sown on February 14, 2018 and February 13, 2019 in 288-cell (20 × 20 × 40 mm) plug trays filled with nursery soil (K-200; Yanmar, Osaka, Japan) and 2% fertilizer (Micro Long Total 280-100; Jcaim Agri Co., Ltd., Tokyo, Japan). They were then placed in a greenhouse at Tohoku Agricultural Research Center, NARO (Morioka, Japan, 39.21°N, 141.60°E) and raised without heating until transplanting.

Before transplanting, fertilizer (N:P₂O₅:K₂O = 15:30:15 kg/10 a) was applied to an open field (Tohoku Agricultural Research Center, NARO) of lowland soil. Two-month-old seedlings were then transplanted on April 17, 2018, and April 22, 2019, at 20,800 plants/10 a. Six to twelve plants (6 to 10 in 2018 and 8 to 12 in 2019) were collected every two weeks from transplanting to harvest. Day length from transplanting to harvest was 13 to 15 hours (data from the National Astronomical Observatory of Japan <https://eco.mtk.nao.ac.jp/koyomi/>, and the daily mean temperature (average minimum/maximum) was −1.0°C/8.7°C to 24.5°C/34.8°C in 2018 and −0.4°C/6.0°C to 24.9°C/33.2°C in 2019 (data from meteorological observation data of Tohoku Agricultural Research Center, NARO).

**Growth characteristics survey**

Samples were collected from transplanting to harvest and were measured for plant height (cm), total leaf number, bulb diameter (mm), leaf sheath diameter (mm), and plant weight (g). The start of bulb enlargement was determined by a bulbing ratio (bulb diameter/leaf sheath diameter) of more than 2.0. Collected samples were separated into leaf blades and edible bulb components then stored at −80°C until quercetin analysis.

**Quercetin glycoside analysis**

Two major quercetin glycosides were examined, Q-3′-DG and Q-4′-G, both of which are the main quercetins found in yellow onion bulbs (Rhodes and Price, 1996). Frozen bulb peeled outer protective skins and leaf blade samples were dried by lyophilization and then ground to a fine powder using a mill mixer. Two bulbs or leaf blades derived from each sampling date were used for one extraction sample of quercetin glycosides to reduce individual differences and used for quercetin analysis. Quercetin glycoside extraction and analysis were conducted according to Watanabe et al. (2012) with slight modifications. Briefly, lyophilized tissue powder (50 mg) and 5 mL of 80% methanol were placed in a 15-mL tube and centrifuged at 15,000 rpm for 10 min at 5°C. Equal amounts of supernatant and 1 mg/100 mL of quercetin dihydrate (Fujifilm Wako Pure Chemical Corporation, Osaka, Japan) as an internal standard were mixed together. Then, 10 μL of the mixed sample was injected into a high-performance liquid chromatography apparatus (HPLC) equipped with a UV detector. The HPLC equipment consisted of a Mightryt RP-18 GP Aqua column (4.6 × 150 mm; Kanto Chemical Co., Inc., Tokyo, Japan), an SCL-10A HPLC system (Shimadzu Corporation, Kyoto, Japan) equipped with an SPD-10AV UV detector (360 nm; Shimadzu), a LC-10AD pump (Shimadzu), and a CTO-10A column oven (Shimadzu). Sample components were separated using a 17-min linear gradient of 20% to 88% solvent B (methanol with 2% acetic acid) in solvent A (Milli-Q water with 2% acetic acid), followed by equilibration with 20% solvent B in solvent A for 10 min at a flow rate of 1.0 mL min⁻¹ at 30°C. Q-3′-DG and Q-4′-G were calculated and quantified using a calibration curve for quercetin dihydrate. Sample extractions and HPLC analyses were conducted in triplicate.
**Statistical analysis**

The statistical significance of the results was analyzed using the Student’s $t$-test at the 0.05 and 0.01 levels using the application software JMP 12.0 (SAS Institute Inc., Cary, NC, USA).

**Results**

**Growth and harvest characteristics**

The growth of both varieties from the seedling to the harvest stage is shown in Figure 1. Bulb development occurred earlier in ‘Momiji No. 3’ than ‘Quergold’, with harvest dates of July 18 and Aug 2, respectively. The growth characteristics at each sampling date are shown in Figure 2 and Supplemental Figure S1.

In 2019, the plant height and total number of leaves were similar in both varieties up to June 17 (Fig. 2A, B). However, from July 1, plant height was significantly higher in ‘Quergold’ than ‘Momiji No. 3’, as was the total number of leaves (Fig. 2B). From April 22 to July 1, excluding May 19, bulb diameter increased with...
growth in both varieties, and bulb diameter was significantly greater in 'Momiji No. 3' (Fig. 2C). However, at harvest, bulb diameter was greater in 'Quergold' (harvest date: July 29) than 'Momiji No. 3' (July 16) (Fig. 2C). The date of bulbing, as determined by a bulbing ratio greater than 2.0, was June 17 for 'Momiji No. 3' and July 1 for 'Quergold' (Fig. 2D). The plant weights of both varieties increased rapidly after June 17 (Fig. 2E).

In 2018, plant height was lower in 'Quergold' than 'Momiji No. 3' from May to June (Supplemental Fig. S1A). Meanwhile, the plant weights of both cultivars increased in a similar manner to the 2019 trial, but was smaller in 2018 (Supplemental Fig. S1D).

Quercetin accumulation in the onion bulbs during development

Quercetin accumulation in the onion bulbs during development is shown in Figure 3. In 2019, the total quercetin glucoside content ranged from 2.8 to 10.4 mg·g\(^{-1}\) dry weight (DW) in 'Momiji No. 3' and 4.6 to 21.8 mg·g\(^{-1}\)DW in 'Quergold' (Fig. 3A). Significant differences between the two varieties were observed after June 17, which represented the beginning of bulbing. The quercetin content at transplanting was 8.2 mg·g\(^{-1}\)DW in 'Momiji No. 3' and 21.8 mg·g\(^{-1}\)DW in 'Quergold'. The quercetin content of 'Quergold' at transplanting was the highest during development, whereas in 'Momiji No. 3', the quercetin content increased slightly for four weeks after transplanting, reaching its highest value of 10.4 mg·g\(^{-1}\)DW. Although this was followed by a decrease until July 1 (2.8 mg·g\(^{-1}\)DW), a further increase was observed in line with bulb enlargement and lodging (6.7 mg·g\(^{-1}\)DW). In contrast, in 'Quergold', the quercetin content decreased abruptly on May 6 to its lowest value of 4.6 mg·g\(^{-1}\)DW. A temporary increase was observed on May 19 followed by a decrease until June 17, followed by a sub-

![Fig. 3.](image_url)

*Fig. 3. The quercetin content of the bulbs during development in 'Momiji No. 3' and 'Quergold' in 2019. (A) The total quercetin glucoside content (quercetin-3,4′-diglucoside (Q-3,4′-DG) + quercetin-4′-glucoside (Q-4′-G)) at each developmental stage (the content at harvest in 'Momiji No. 3' represents samples taken on July 29). The quercetin composition of (B) 'Momiji No. 3' and (C) 'Quergold'. The quercetin glucoside content per bulb in (D) 'Momiji No. 3' and (E) 'Quergold'. Data represent the Q-4′-G/Q-3,4′-DG ratio. Error bars indicate standard errors of three biological repeats. Differences in means between varieties were evaluated using Student’s t-test; one asterisk (*) and two asterisks (**) indicate significant difference at the 0.05 and 0.01 levels, respectively.*
sequent increase with bulb enlargement and lodging.

In terms of quercetin composition, Q-4'-G tended to be higher than Q-34'-DG throughout development, with a Q-4'-G/Q-34'-DG ratio of 0.8 to 1.6 in ‘Momiji No. 3’ and 1.0 to 3.4 in ‘Quergold’ (Fig. 3B, C). The quercetin content per bulb ranged from 0.6 to 196.6 mg/bulb in ‘Momiji No. 3’ and 1.5 to 476.6 mg/bulb in ‘Quergold’ (Fig. 3D, E). The quercetin content per bulb increased from July 16 in ‘Quergold’ and from July 29 it was higher in ‘Quergold’ than ‘Momiji No. 3’.

In 2018, the total quercetin glucoside content ranged from 0.6 to 23.9 mg·g⁻¹ DW in ‘Momiji No. 3’ and 1.7 to 53.7 mg·g⁻¹ DW in ‘Quergold’ (Supplemental Fig. S2A). Quercetin accumulation in the bulbs differed between 2018 and 2019, but the general trends were similar, except for two weeks after planting in ‘Momiji No. 3’ (May 7, 2018 and May 6, 2019), when quercetin accumulation tended to be higher in ‘Quergold’ than ‘Momiji No. 3’. A significant difference between the two varieties was also observed at harvest. The ratio of Q-4'-G/Q-34'-DG ranged from 0.8 to 1.6 in ‘Momiji No. 3’ and 1.1 to 1.5 in ‘Quergold’ (Supplemental Fig. S2B, C), and the Q-4'-G content was also higher than that of Q-34'-DG throughout development, except on October 6, 2018, similar to the 2019 findings. The quercetin content per bulb ranged from 1.4 to 109.9 mg/bulb in ‘Momiji No. 3’ and 0.4 to 324.4 mg/bulb in ‘Quergold’ (Supplemental Fig. S2D, E), increasing from July 17 in both varieties, similar to the 2019 trial.

**Quercetin accumulation in the leaf blades during development**

Quercetin accumulation in the leaf blades during development is shown in Figure 4. Temporal changes in total quercetin glucoside ranged from 0.5 to 1.5 mg·g⁻¹ DW in ‘Momiji No. 3’ and 0.9 to 2.6 mg·g⁻¹ DW in ‘Quergold’ (Fig. 4A). Significant differences between the two varieties were observed on May 6 and June 3, 2019. The quercetin content at transplanting was similar (1.5 mg·g⁻¹ DW) in both cultivars. In ‘Momiji No. 3’, little change in quercetin content was observed from transplanting to May 19 (1.4 to 1.5 mg·g⁻¹ DW). However, after May 19, the quercetin content remained low until July 1 (0.6 mg·g⁻¹ DW) before increasing once again (1.4 mg·g⁻¹ DW), similar to the bulb findings. In contrast, in ‘Quergold’, the quercetin content increased on May 6 (2.5 mg·g⁻¹ DW), different from the bulbs, and then decreased from May 6 to July 1 before increasing again (2.6 mg·g⁻¹ DW), the same as in the bulbs. Overall, the quercetin content of the leaf blades tended to be higher in ‘Quergold’ than ‘Momiji No. 3’ throughout development, although the content was much lower than that of the bulbs. In terms of quercetin composition, the Q-34'-DG content was much higher than that of Q-4'-G throughout development in both varieties (Fig. 4B, C), with the ratio of

Fig. 4. The quercetin content and composition of the leaf blades during development in ‘Momiji No. 3’ and ‘Quergold’ in 2019. (A) The total quercetin glucoside content (Q-34'-DG + Q-4'-G) at each developmental stage. The quercetin composition of (B) ‘Momiji No. 3’ and (C) ‘Quergold’. Data show the Q-4'-G/Q-34'-DG ratio. Error bars indicate standard errors of four or five biological replicates.
Quercetin accumulation in the leaf blades of ‘Momiji No. 3’ sharply as the bulbs enlarged, becoming almost as high as that of Q-34'-DG. These patterns differed from those of the bulbs.

The quercetin content of the leaf blades of both varieties in 2018 is shown in Supplemental Figure S3. The total quercetin glucoside content ranged from 0.3 to 5.0 mg·g⁻¹DW in ‘Momiji No. 3’ and 0.4 to 8.3 mg·g⁻¹DW in ‘Quergold’ (Supplemental Fig. S3A). Quercetin accumulation in the leaf blades of ‘Quergold’ differed between 2018 and 2019, but the changes showed a similar tendency from transplanting to early July, with a decrease followed by an increase. Meanwhile, the changes in quercetin accumulation in the leaf blades of ‘Momiji No. 3’ differed between 2018 and 2019 from transplanting to early July, although the increase from July onwards was consistent. The ratio of Q-4'-G to Q-34'-DG in the bulbs was similar throughout development, while, in the leaf blades, the quercetin content was much higher than that of Q-4'-G from transplanting to July 1, after which an increase in Q-4'-G was observed, similar to that in 2019.

Discussion

Onion bulbs contain a wealth of functional ingredients such as flavonoids, sulfur-containing compounds, and fructan. Most studies to date have tended to focus on the contents of these functional ingredients at harvest and during storage. Presently, little is known about quercetin accumulation and its dynamics in onions and shallots (Bystricka et al., 2015; Yaguchi et al., 2009), and thus the changes with development have yet to be determined. In this study, we investigated the temporal changes in quercetin accumulation in onion bulbs and leaf blades during development and found that quercetin glucosides are synthesized not only in the bulbs, but also in the leaf blades throughout growth (Figs. 3 and 4; Supplemental Figs. S2 and S3). From July onwards, following spring sowing, quercetin accumulation was observed in both sets of tissue samples, different from fructan, which accumulates in the bulbs only at this stage (Oku et al., 2019).

Plant height and the total number of leaves were greater in ‘Quergold’ than ‘Momiji No. 3’ before harvest (Fig. 2A, B; Supplemental Fig. S1A, B), although bulb diameter was greater in ‘Momiji No. 3’ (Fig. 2; Supplemental Fig. S1C). These differences were the result of their different growth characteristics, with the daylength response of the autumn-sown ‘Momiji No. 3’ occurring earlier than that of the spring-sown ‘Quergold’. Similar results were also reported by Ikeda et al. (2020) and Tsukazaki et al. (2021).

The quercetin content of the bulbs at transplanting was 23.9 mg·g⁻¹DW in 2018 and 8.2 mg·g⁻¹DW in 2019 in ‘Momiji No. 3’, and 53.7 mg·g⁻¹DW in 2018 and 21.8 mg·g⁻¹DW in 2019 in ‘Quergold’ (Fig. 3; Supplemental Fig. S2A). Although the quercetin content of ‘Quergold’ at transplanting was the highest throughout development in both years, the content in 2018 was approximately three times greater than that in 2019. Meanwhile, the quercetin content of ‘Momiji No. 3’ was also high at transplanting compared with other sampling dates in both 2018 and 2019. To clarify why quercetin contents were high at the transplanting stage, we investigated them at one week before transplanting in 2020. In a 2020 trial, the quercetin content of both varieties was lowest at this stage (data not shown). Onion seedlings are usually exposed to the outside air four to five days before transplanting to improve root conditions after transplanting. These findings are thought to be related to the effects of cold and/or moisture stress on onion seedlings during cold acclimation before transplanting, which results in a dramatic temporary increase. However, as shown in Figure 3D, E and Supplemental Figure S2D, E, the quercetin content (mg/bulb) of bulbs did not affect the overall content, regardless of the high values (mg·g⁻¹DW) at transplanting (Fig. 3A; Supplemental Fig. S2A). This is probably because the bulb weight was low at this time.

After transplanting, the quercetin contents of the bulbs decreased in both varieties until June or early July, after which another increase was observed in line with bulb development. Varietal differences in quercetin content were observed after June 17 in 2019 and after August 14 in 2018, respectively (Fig. 3; Supplemental Fig. S2A).

Meanwhile, in the leaf blades, the quercetin content tended to be higher in April and May compared with June and July (Fig. 4; Supplemental Fig. S3A). The sharp increase in April to May followed by a decrease was similar to the changes in polyphenol accumulation in shallots, as well as the accumulation of fructan in both onions and shallots (Hang et al., 2004; Oku et al., 2019; Yaguchi et al., 2008, 2009). These findings suggest that the polyphenol and sugar content of Allium species decreases with growth. Analyses of quercetin accumulation in onion seedlings from germination to pre-transplantation, as well as the genetic characteristics of these two varieties are now needed.

Quercetin in onion is composed mainly of Q-34'-DG and Q-4'-G. In this study, the ratio of Q-4'-G to Q-34'-DG in the bulbs was similar throughout development, ranging from 0.8 to 1.8 in 2019 (Fig. 3B) and 0.8 to 1.6 in 2018 (Supplemental Fig. S2B) in ‘Momiji No. 3’, and from 1.0 to 3.4 in 2019 (Fig. 3C) and 1.1 to 1.5 in 2018 (Supplemental Fig. S2C) in ‘Quergold’. Meanwhile, in the leaf blades, the quercetin composition consisted mainly of Q-34'-DG until June or early July, after which a dramatic increase in Q-4'-G close to the Q-34'-DG content was observed (Fig. 4; Supplemental
Fig. S3). These results suggest that quercetin metabolism in the bulbs differs from that in the leaf blades.

The quercetin content per bulb was correlated with bulb formation ($r = 0.82^{**}$ for bulb diameter in 2019, $r = 0.66^{**}$ in 2018) (Figs. 2C and 3C, D; Supplemental Fig. S2C, D). Lee et al. (2013) previously reported that bulb formation is regulated by two antagonistic FLOWERING LOCUS T (FT)-like genes, AcFT1 and AcFT4, with downregulation of AcFT4 during a long-day photoperiod and upregulation of AcFT1 leading to bulb formation. They also reported that the expression of sucrose: 1-fructosyltransferase (1-SST) increased with bulb formation. Similarly, Oka et al. (2019) reported 1-SST-induced synthesis of fructan, resulting in an increase in the fructan content of the onion bulbs with development. Taken together, these results suggest that bulb formation and quercetin accumulation in the bulbs are related because the quercetin content increased with bulb formation.

Q-4′-G accumulation in the leaf blades was also observed with bulb enlargement at harvest in July (Fig. 3; Supplemental Fig. S3). Tsushida and Suzuki (1996) reported that onion bulbs contain two enzymes responsible for degradation of quercetin glucosides, quercetin-3-O-β-glucosidase and quercetin-4′-O-β-glucosidase, as well as two enzymes responsible for synthesis of quercetin aglycon or quercetin glycosides: quercetin-3-O-β-glucosyltransferase and quercetin-4′-O-β-glucosyltransferase (Supplemental Fig. S4). They also suggested that onion bulbs accumulate Q-4′-G and Q-34′-DG, but rarely quercetin-3-glucoside because enzymatic activity of quercetin-3-O-β-glucosidase was found to be higher than that of quercetin-3-O-β-glucosyltransferase. Furthermore, Q-4-G was found to be readily synthesized in onion bulbs because the enzymatic activity of quercetin-4′-O-β-glucosyltransferase was higher than that of quercetin-4′-O-β-glucosidase. Thus, as shown here, the Q-34′-DG content of the leaf blades does not change dramatically during development, with accumulation in July thought to be the result of quercetin-4′-O-β-glucosyltransferase synthesis via quercetin aglycon. Despite our findings, the enzymatic mechanism of Q-34′-DG and Q-4′-G accumulation in the leaf blades was not clarified. Further analyses of quercetin accumulation and metabolism as well as other functional ingredients are therefore needed to fully elucidate the roles of quercetin glycosides in onion bulbs and leaf blades.

In conclusion, our results suggest that quercetin accumulation and its distribution in onion bulbs and leaf blades differs according to growth, with ‘Quergold’ having a greater potential for quercetin accumulation in the bulbs compared with ‘Momiji No. 3’. The quercetin content of the bulbs increased at transplanting and with bulb enlargement, and is therefore thought to be an important component of bulb formation prior to harvest given that the quercetin content per bulb increased dramatically at this stage. The findings also suggest that quercetin metabolism in the bulbs differs from that in the leaf blades because the composition of Q-4′-G and Q-34′-DG was found to differ. Further analyses are needed to determine the underlying genes affecting quercetin accumulation in onion bulbs and leaf blades.

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Literature Cited

Arts, I. C. W. and P. C. H. Hollman. 2005. Polyphenols and disease risk in epidemiologic studies. Am. J. Clin. Nutr. 81 (Suppl.): 317–325.

Bystricka, J., J. Musilova, J. Tomas, J. Noskovic, E. Dadakova and P. Kavalcová. 2015. Dynamics of quercetin formation in onion (Allium cepa L.) during vegetation. Acta Aliment. 44: 383–389.

Cook, N. C. and S. Samman. 1996. Flavonoids-chemistry, metabolism, cardioprotective effects, and dietary sources. J. Nutr. Biochem. 7: 66–76.

Fossen, T., O. M. Andersen, D. O. Øvstedal, A. T. Pedersen and A. Raknes. 1996. Characteristic anthocyanin pattern from onions and other Allium spp. J. Food Sci. 61: 703–706.

Hang, T. T., M. Shigyo, S. Yaguchi, N. Yamauchi and Y. Tashiro. 2004. Effect of single alien chromosome from shallot (Allium cepa L. Aggregatum group) on carbohydrate production in leaf blade of bunching onion (A. fistulosum L.). Genes Genet. Syst. 79: 345–350.

Hertog, M. G. I., E. J. M. Feskens, P. C. H. Hollman, M. B. Katan and D. Kromhout. 1993. Dietary antioxidant flavonoids and risk of coronary heart disease: the Zutphen elderly study. Lancet 342: 1007–1011.

Ikeda, H., T. Kinoshita, T. Yamamoto and A. Yamasaki. 2019. Sowing time and temperature influence bulb development in spring-sown onion (Allium cepa L.). Sci. Hortic. 244: 242–248.

Ikeda, H., T. Yamamoto, T. Kinoshita, H. Tsukazaki and A. Yamasaki. 2020. A comparative study on the growth and bulb development of several onion (Allium cepa L.) cultivars sown in spring in the northeast region of Japan. Hort. J. 89: 589–592.

Iwata, T. 1988. Momiji No. 3. p. 177. In: Nihon engei seisan Iwata, T. 1988. Momiji No. 3. p. 177. In: Nihon engei seisan 589–592.

Jaime, L., F. Martínez, M. A. Martín-Cabrejas, E. Mollá, F. J. López-Andréu, K. W. Waldron and R. M. Esteban. 2000. Study of total fructan and fructooligosaccharides content in different onion tissues. J. Sci. Food Agric. 81: 177–182.

Lachman, J., D. Pronek, A. Hejtmanková, J. Dudjak, V. Pivec and K. Faitová. 2003. Total polyphenol and main flavonoid antioxidants in different onion (Allium cepa L.) varieties. Hort. Sci. (Prague) 30: 142–147.
Larson, A. J., J. D. Symons and T. Jalili. 2012. Therapeutic potential of quercetin to decrease blood pressure: review of efficacy and mechanisms. Adv. Nutr. 3: 39–46.

Lee, R., S. Baldwin, F. Kenel, J. McCallum and R. Macknight. 2013. Flowering locus T genes control onion bulb formation and flowering. Nat. Commun. 4: 2884. DOI: 10.1038/ncomms3884.

Ministry of Agriculture, Forestry and Fisheries. 2020. Crop statistics survey (In Japanese). <https://www.e-stat.go.jp/stat-search/files?page=1&layout=datalist&toukei=00500215&tstat=000001013427&cycle=7&year=20190&month=0&tclass1=000001032286&tclass2=000001032933&tclass3=000001147186>.

Muro, T., D. Kami and K. Sugiyama. 2015. ‘Quergold’, a new cultivar of hybrid onion with high quercetin glycoside contents. Hort. Res. (Japan) 14: 305–311 (In Japanese with English abstract).

Muro, T., Y. Noguchi, M. Morishita, K. Ito, K. Sugiyama, T. Kondo, Y. Kurenuma and T. Ono. 2010. ‘Quer-rich’, a new variety of hybrid red onion with high quercetin content. Res. Bull. Natl. Agric. Res. Cent. Hokkaido Reg. 192: 25–32 (In Japanese with English abstract).

Nishimura, M., T. Muro, M. Kobori and J. Nishihira. 2020. Effect of daily ingestion of quercetin-rich onion powder for 12 weeks on visceral fat: A randomised, double-blind, placebo-controlled, parallel-group study. Nutrients 12: 91. DOI: 10.3390/nu12010091.

Okamoto, D., Y. Noguchi, T. Muro and M. Morishita. 2006. Genetic variation of quercetin glucoside content in onion (Allium cepa L.). J. Japan. Soc. Hort. Sci. 75: 100–108 (In Japanese with English abstract).

Oku, S., T. Maeda, N. Hirakawa, A. Hirano, Y. Sasaki, M. Muraki, D. Z. Wambrauw, S. Osanai, K. Honda, T. Suzuki and A. Yamashita. 2018. Evaluation of onion varieties using spring-sowing method in Aomori prefecture. Hort. Res. (Japan) 17: 359–367 (In Japanese with English abstract).

Oku, S., K. Ueno, Y. Tsuruta, Y. Jitsuyama, T. Suzuki, S. Onodera, T. Maeda and H. Shimura. 2019. Sugar accumulation and activities of enzymes involved in fructan dynamics from seedling to bulb formation in onion (Allium cepa L.). Sci. Hortic. 247: 147–155.

Pérez-Gregorio, R. M., M. S. García-Falcón, J. Simal-Gándara, A. S. Rodrigues and D. P. Almeida. 2010. Identification and quantification of flavonoids in traditional cultivars of red and white onions at harvest. J. Food Compost. Anal. 23: 592–598.

Platel, K. and K. Srinivasan. 2016. Bioavailability of micronutrients from plant foods: an update. Crit. Rev. Food Sci. Nutr. 56: 1608–1619.

Rhodes, M. J. C. and K. R. Price. 1996. Analytical problems in the study of flavonoid compounds in onions. Food Chem. 57: 113–117.

Tsukazaki, H., S. Oku, M. Honjo, A. Yamashita and T. Muro. 2021. Multivariate analysis based on agronomic traits of 95 bulb onion (Allium cepa L.) cultivars. Hort. Res. (Japan) 20: 39–47 (In Japanese with English abstract).

Tsushida, T. and M. Suzuki. 1995. Isolation of flavonoid-glycosides in onion and identification by chemical synthesis of the glycosides. Nippon Shokuhin Kagaku Kogaku Kaishi 42: 100–108 (In Japanese with English abstract).

Tsushida, T. and M. Suzuki. 1996. Content of flavonol glucosides and some properties of enzymes metabolizing the glucosides in onion. Nippon Shokuhin Kagaku Kogaku Kaishi 43: 642–649.

Vågen, I. M. and R. Slimestad. 2008. Amount of characteristic compounds in 15 cultivars of onion (Allium cepa L.) in controlled field trials. J. Sci. Food Agric. 88: 404–411.

Watanabe, J., J. Takebayashi, Y. Takano-Ishikawa and A. Yasui. 2012. Evaluation of a method to quantify quercetin aglycone in onion (Allium cepa) by single- and multi-laboratory validation studies. Anal. Sci. 28: 1179–1182.

Yaguchi, S., J. McCallum, M. Shaw, M. Pither-Joyce, S. Onodera, N. Shiomi, N. Yamauchi and M. Shigyo. 2008. Biochemical and genetic analysis of carbohydrate accumulation in Allium cepa L. Plant Cell Physiol. 49: 730–739.

Yaguchi, S., N. Yamauchi and M. Shigyo. 2009. Single alien chromosome additions from shallot (Allium cepa L. Aggregatum group) increase endogenous polyphenol contents in Japanese bunching onion. J. Japan. Soc. Hort. Sci. 78: 431–435.

Zhang, S., D. Peng, Y. Xu, S. Lü and J. Wang. 2016. Quantification and analysis of anthocyanin and flavonoids compositions, and antioxidant activities in onions with three different colors. J. Integr. Agric. 15: 2175–2181.