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

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Onion (Allium cepa L.) is one of the most important vegetable crops worldwide. In Japan, it is grown using two different cultivation methods (spring-sowing and autumn-sowing). The traditional cultivation method for onion in the Tohoku region in northeast Japan has been autumn sowing; however, onion productivity has been low. Recently, spring sowing of onion has been established in this region to improve onion productivity in the off-crop season. To better understand the spring-sowing cultivation method, we examined the plant growth and bulb development of eight commercially-grown onion cultivars (‘Turbo’, ‘Aurora’, ‘Momiji No. 3’, ‘Marso’, ‘Okhotsk 222’, ‘Kitamomiji 2000’, ‘Super Kitamomiji’, and ‘Gunnison’) throughout the growth period. The results showed that this cultivation method enabled us to grow and compare relatively long-day and intermediate-day cultivars at the same time, under the same environmental conditions. Onion bulb development was induced and persisted during long day-lengths and was inhibited by short day-lengths which were longer or shorter than the critical day-lengths for bulb development of each cultivar. To elucidate this mechanism, expression analysis of AcFTs related to bulb development was conducted. Our expression analysis showed that AcFT1 was expressed in accordance with the maturity of the cultivars, and this gene expression can be used as an index for maturity types of the cultivars and bulb development. The results indicate that onion responds to a critical day-length for bulb development and starts bulb development before the bulbing ratio greatly exceeds 2. This metric can be used as an index of bulb development.

Key Words: AcFTs, bulbing ratio, spring-sowing cultivation.

Introduction

Onion (Allium cepa L.) is one of the most widely produced and consumed vegetable crops worldwide. Bulb size is an important factor in determining its productivity. According to data from the Food and Agriculture Organization of the United Nations (<http://faostat.fao.org/>), March 16, 2020), the total world production of dry bulb onion was about 96.8 million tons in 2018. In Japan, onion production was about 1.2 million tons in 2018 according to the statistical data of the Ministry of Agriculture, Forestry and Fisheries of Japan (<http://www.maff.go.jp/j/tokei/>), March 16, 2020), and these onions are primarily grown in two geographically isolated areas in Japan with two different cultivation methods (Maeda et al., 2017). In Hokkaido prefecture, the largest onion production area in Japan with a relatively cool climate, onions are sown in spring and harvested from late summer to autumn; these onions are stored and supplied until spring. In other regions, including Saga and Hyogo prefecture, the second and third largest onion production areas in Japan with a warmer climate, onions are sown in autumn and harvested from spring to early summer. In 2018, these major onion production areas, Hokkaido, Saga, and Hyogo prefecture, accounted for approximately 64.7%,
8.4%, and 10.5% of supply, respectively (<http://www.maff.go.jp/j/tokei/>, March 16, 2020). Recently, spring-sowing cultivation has been developed in the northeast region of Japan, in Tohoku (Aomori, Akita, Iwate, Miyagi, Yamagata, and Fukushima prefecture) where onion productivity is low and inferior to other growing regions. This spring-sowing cultivation in the Tohoku has been established to improve onion productivity in this region and produce onions in the off-season (Oku et al., 2018; Yamasaki et al., 2015), where it is also warmer compared to Hokkaido prefecture.

Several studies have been conducted to improve this cultivation method. Two of the most important factors in obtaining sufficient yield from onions are: (i) the selection of the cultivar; and (ii) selection of a sowing time appropriate for the climate and environment of the production area (Boyhan et al., 2009; Brewster et al., 1986; Caruso et al., 2014; Ikeda et al., 2019; Lancaster et al., 1996; Mondal et al., 1986). In the Tohoku region, previous studies have been attempted to find suitable cultivars and planting dates for spring-sowing cultivation in each prefecture (Ito and Ueda, 2012; Oku et al., 2018; Yamasaki et al., 2015). Bulb size is an important determinant of productivity in onions. Bulb development is induced by critical day-length, and progresses under an optimal temperature, which may differ among onion cultivars. Therefore, in order to achieve optimal onion production, studies of the characteristics and environmental responses of various cultivars were conducted. However, most of these studies on spring-sowing cultivation in the Tohoku region focused on plant growth and bulb development only at harvest time (Katayama and Yamasaki, 2015a, b; Oku et al., 2018; Yamasaki et al., 2015).

In this study, plant growth and bulb development of eight commercially-used onion cultivars were examined throughout the growing period to assess spring-sowing cultivation in the Tohoku region. The expression of AcFT1 and AcFT4 was also examined to elucidate the mechanism for critical day-length of cultivars for plant growth and bulb development. Previous studies demonstrated that flowering locus T (FT)-like genes play a key role in bulb development (Lee et al., 2013; Lyngkhoi et al., 2019; Manoharan et al., 2016; Rashid et al., 2019), but these expression patterns of onion cultivars during growth under field conditions are insufficient. It was hypothesized that the expression of AcFTs could be used as an index of maturity and bulb development for onion cultivars. Selection of optimal cultivars in each geographic zone could be facilitated with an appropriate metric to compare growth and seasonality of onions.

**Materials and Methods**

**Plant materials**

Experiments were conducted in 2016 and 2017 at the NARO Tohoku Agricultural Research Center in Iwate, Morioka, Japan (39.7°N, 141.1°E). In total, eight commercially-grown onion cultivars, ‘Turbo’ (Takii & Co., Ltd., Kyoto, Japan), ‘Aurora’ (Watanabe Seed Co., Ltd., Miyagi, Japan), ‘Momiji No. 3’, ‘Okhotsk 222’, ‘Kitamomiji 2000’, ‘Super Kitamomiji’ (Shippo Co., Ltd., Mitoyo, Japan), ‘Marso’ (Kaneko Seeds Co., Ltd., Maebashi, Japan), and ‘Gunnison’ (Bejo Seeds, Oceano, CA, USA) were used in this study. ‘Turbo’ was used only in 2017, and ‘Gunnison’ was used only in 2016. ‘Turbo’, ‘Aurora’, and ‘Momiji No. 3’ are relatively early maturing cultivars; ‘Marso’, ‘Okhotsk 222’, ‘Kitamomiji 2000’, ‘Super Kitamomiji’, and ‘Gunnison’ are relatively late maturing cultivars. Seeds were sown on February 17, 2016 and February 16, 2017 in plug trays with 288 cells (20 × 20 × 40 mm). Seedlings were transplanted by hand on April 15, 2016 and April 18, 2017 in replicate plots and cultivated as described in Ikeda et al. (2019).

**Plant growth surveys**

Plant growth surveys were conducted every week for five to ten plants per plot from about 30 days after transplanting to plant lodging (i.e., leaves had fallen to the ground). In this study, plant lodging was used as an indicator of bulb maturity and harvesting time. Total leaf number (i.e., the integrated number of leaf blades from emergence), plant height, leaf sheath and bulb diameter, and fresh and dry weights were measured for every plant beforeplant lodging. Plants of each cultivar were harvested within seven days after 50% of plants had lodged, and naturally dried more than a week in a dark greenhouse with a ventilator. Dried leaf blades and roots were removed, and bulbs were cured in a cool, dark room. After that, the final bulb size (diameter, fresh and dry weights, and dry matter content) was measured. Bulbs for dry weights and dry matter content analysis were cut and dried for more than a week at 70°C by using a ventilation dryer. The bulbing ratio was calculated as the ratio between the diameter of the bulb and leaf sheath of the onion (Brewster, 1982; Kedar et al., 1975; Mondal et al., 1986). Temperature and precipitation data were obtained from the meteorological observation system at the NARO Tohoku Agricultural Research Center. Day-length was calculated from the sunrise and sunset data for Morioka, Iwate, from the National Astronomical Observatory of Japan (<http://eco.mtk.nao.ac.jp/koyomi/dni/index.html.en>).

**Expression analysis of AcFT genes**

Expression analysis of AcFT1 and AcFT4 was conducted every two weeks for 10 plants per plot from 0 weeks after transplanting (0 WAT; April 18) to 12 WAT (July 11) in 2017 at the NARO Tohoku Agricultural Research Center laboratory. Leaf blades from 10 plants were sampled from triplicate plots at 10 a.m. on the sampling day. Samples in each plot were composited, homogenized, and stored at −80°C before use. Total
RNA was extracted from leaf blades using an RNeasy Plant Mini Kit (Qiagen, Venlo, Netherlands). Removal of genomic DNA from the RNA sample and reverse transcription were performed using a ReverTra Ace qPCR RT Kit (Toyobo, Co., Ltd., Osaka, Japan). Quantitative real-time PCR (qPCR) was performed using an Applied Biosystems 7500 Real-Time PCR System (Thermo Fisher Scientific, Waltham, MA, USA) with a THUNDERBIRD SYBR qPCR Mix (Toyobo). The following program was run: 95°C for 1 min; 40 cycles of 95°C for 15 s and 60°C for 1 min. A melting curve was used to confirm the presence of single products. The gene-specific primer sets of AcFT1, AcFT4, and Acβ-tubulin (which was used as a reference for normalization of gene expressions) were obtained from Lee et al. (2013) and Rashid et al. (2019). The fold changes in gene expression between three cultivars were determined by the ΔΔCt method of relative quantification.

Statistical analysis

Statistical analysis was performed using Excel (Microsoft, Redmond, WA, USA) and Bell Curve for Excel (Version 3.20; Social Survey Research Information Co., Ltd., Tokyo, Japan). The statistical significance of the results was analyzed with the Tukey–Kramer test at the 1% level with Bell Curve for Excel (Version 3.20) software.

Results

Ambient temperature and day-length during plant growth

Maximum, minimum, and average temperatures and day-length from transplanting (April 15 in 2016 and 2017) to the end of the experiment (August 12 in 2016 and August 1 in 2017) are shown in Figure 1. Monthly precipitation data are also shown in Figure 1. Environmental conditions for both years in the experimental fields were almost the same as the average year.

Plant growth and bulb size during development

Plant growth and bulb development of ‘Turbo’, ‘Aurora’, ‘Momiji No. 3’, ‘Marso’, ‘Okhotsk 222’, ‘Kitamomiji 2000’, ‘Super Kitamomiji’, and ‘Gunnison’ were observed from transplanting to lodging (Fig. 2). Fresh bulb weight and dry weight were investigated only in 2017. Total leaf number (Fig. 2A, B), plant height (Fig. 2C, D), bulb diameter (Fig. 2E, F), fresh bulb weight (Fig. 2G), and dry weight (Fig. 2H) were almost the same among cultivars in the middle phase of growth. About 10–11 WAT (June 23 to 30 in 2016, and June 27 to July 4 in 2017), most early maturing cultivars were lower than later maturing cultivars. While bulb diameter and fresh weight did not relate to the maturity of the cultivars, dry weight and dry matter content of early maturing cultivars were lower than later maturing cultivars.

Plant growth and bulb size at harvest time

Plant lodging, harvest and investigation date, plant growth (total leaf number, height) and bulb size (diameter, fresh, and dry weight, dry matter content) of eight cultivars are shown in Table 1. The same pattern of lodging was observed in both years; the eight commercially-used onion cultivars were lodged in the following order: ‘Turbo’ (used only in 2017), ‘Aurora’, ‘Momiji No. 3’, ‘Marso’, ‘Okhotsk 222’, ‘Kitamomiji 2000’, ‘Super Kitamomiji’, and ‘Gunnison’ (used only in 2016). The total leaf number of early maturing cultivars (‘Turbo’, ‘Aurora’, and ‘Momiji No. 3’) was lower than later maturing cultivars, and the order of plant lodging and total leaf number was identical apart from ‘Gunnison’. Plant height of early maturing cultivars was shorter than that of later maturing cultivars (‘Marso’, ‘Okhotsk 222’, ‘Kitamomiji 2000’, ‘Super Kitamomiji’, and ‘Gunnison’). While bulb diameter and...
Table 1. Plant growth and bulb size of eight cultivars.

| Year | Cultivar          | Lodging | Harvest and investigation | Total leaf number | Plant height (cm) | Bulb size |
|------|-------------------|---------|---------------------------|-------------------|------------------|-----------|
|      |                   |         |                           |                   |                  | Diameter (cm) | Fresh weight (g/bulb) | Dry weight (g/bulb) | Dry matter content (%) |
| 2016 | ‘Aurora’          | Jul. 11 | Jul. 14                   | 12.0 ± 0.2 a      | 82.1 ± 1.1 a     | 7.8 ± 0.1 a  | 225.7 ± 9.1 a          | 14.9 ± 0.5 a          | 6.7 ± 0.1 a            |
|      | ‘Momiji No. 3’    | Jul. 19 | Jul. 21                   | 12.6 ± 0.2 a      | 82.4 ± 1.1 a     | 7.7 ± 0.1 a  | 223.4 ± 7.5 a          | 19.1 ± 0.7 ab         | 8.6 ± 0.2 b            |
|      | ‘Marso’           | Jul. 25 | Jul. 29                   | 14.7 ± 0.2 b      | 92.9 ± 0.9 b     | 8.5 ± 0.1 bc | 296.7 ± 9.4 bc         | 23.2 ± 0.9 bc         | 7.8 ± 0.2 c            |
|      | ‘Okhotsk 222’     | Jul. 26 | Jul. 29                   | 17.0 ± 0.2 c      | 92.9 ± 0.8 b     | 8.2 ± 0.1 abc | 266.2 ± 10.9 abc       | 26.0 ± 1.0 ed          | 9.8 ± 0.1 de           |
|      | ‘Kitamomiji 2000’ | Jul. 29 | Jul. 29                   | 18.0 ± 0.2 cd     | 98.0 ± 1.2 b     | 8.1 ± 0.1 ab | 256.8 ± 8.9 ab         | 26.0 ± 0.9 cd         | 10.1 ± 0.1 e           |
|      | ‘Super Kitamomiji’| Aug. 1  | Aug. 5                    | 18.4 ± 0.2 d      | 94.0 ± 1.4 b     | 8.7 ± 0.1 cd  | 309.0 ± 9.2 cd         | 29.0 ± 1.0 d          | 9.4 ± 0.1 d            |
|      | ‘Gunnison’        | Aug. 8  | Aug. 12                   | 17.7 ± 0.4 cd     | 93.4 ± 1.5 b     | 9.0 ± 0.1 d  | 337.3 ± 12.7 d         | 34.4 ± 1.3 e          | 10.2 ± 0.1 e           |
| 2017 | ‘Turbo’           | Jul. 10 | Jul. 11                   | 12.8 ± 0.3 a      | 82.2 ± 1.7 a     | 8.0 ± 0.2 a   | 234.4 ± 12.7 a         | 17.5 ± 1.1 a          | 7.5 ± 0.3 a            |
|      | ‘Aurora’          | Jul. 13 | Jul. 18                   | 13.8 ± 0.2 ab     | 87.5 ± 1.9 a     | 9.5 ± 0.2 b   | 374.2 ± 22.3 b         | 24.3 ± 1.4 ab         | 6.5 ± 0.2 b            |
|      | ‘Momiji No. 3’    | Jul. 19 | Jul. 25                   | 14.5 ± 0.2 bc     | 87.2 ± 1.8 a     | 8.8 ± 0.2 abc | 322.1 ± 14.7 abc       | 25.9 ± 1.1 b          | 8.1 ± 0.2 a            |
|      | ‘Marso’           | Jul. 21 | Jul. 25                   | 15.6 ± 0.2 c      | 101.1 ± 2.2 b    | 9.0 ± 0.2 bc  | 346.9 ± 20.5 bc        | 27.0 ± 1.4 c          | 7.9 ± 0.2 a            |
|      | ‘Okhotsk 222’     | Jul. 24 | Jul. 25                   | 18.5 ± 0.1 d      | 102.5 ± 1.2 b    | 8.8 ± 0.2 abc | 312.1 ± 19.4 abc       | 24.7 ± 1.4 ab         | 8.0 ± 0.1 a            |
|      | ‘Kitamomiji 2000’ | Jul. 31 | Aug. 1                    | 18.7 ± 0.3 d      | 102.9 ± 1.2 b    | 8.8 ± 0.2 abc | 313.6 ± 21.7 abc       | 31.4 ± 2.1 b          | 10.1 ± 0.1 c           |
|      | ‘Super Kitamomiji’| Jul. 31 | Aug. 1                    | 18.8 ± 0.3 d      | 102.3 ± 1.8 b    | 8.1 ± 0.2 ac  | 273.3 ± 18.5 ac        | 28.1 ± 1.9 b          | 10.3 ± 0.1 c           |

* Lodging date is defined as when leaves have fallen on more than half of the plants in the experimental field of a cultivar.

† Plant growth was investigated within 7 days after lodging.

‡ The integrated number of leaf blades from emergence.

§ Values indicate means ± SE (n = 12–30), and values with the same letter were not significantly different at P < 0.01 (Tukey-Kramer test).

Changes in AcFT1 and AcFT4 expression during plant growth

AcFT1 and AcFT4 expression in leaf blades was determined in ‘Turbo’, ‘Momiji No. 3’, and ‘Okhotsk 222’ during plant growth in 2017 (Fig. 3). The expression of AcFT4 was higher than AcFT1 just after transplanting.
Therefore, the data reported agreed with previous studies that were conducted in spring-sowing cultivation and short-day cultivars are of all eight cultivars were over 5 cm in 2016 and 2017 (2019) used spring-sowing cultivation in Hokkaido prefecture and investigated bulb development during growth with multiple cultivars, but they used only two cultivars and did not focus on bulb development. Kato (1963) and Brewster (1982) investigated bulb development during growth using one or two cultivars and these onions were sown in autumn. Oku et al. (2019) used spring-sowing cultivation in Hokkaido prefecture and investigated bulb development during growth with multiple cultivars, but they used cultivars of the same maturity type (‘Kitamomiji 2000’ and ‘Pole Star’; Watanabe Seed). Therefore, in the present study, plant growth and bulb development of eight cultivars of different maturity types were investigated throughout the growing period to understand spring-sowing cultivation in the Tohoku region.

Plant lodging was as an indicator of bulb maturity and harvesting time in cultivars of different maturity types in 2016 and 2017 (Table 1). The same patterns were observed in both years, and the results for ‘Momiji No. 3’, ‘Marso’, ‘Okhotsk 222’, and ‘Kitamomiji 2000’ agreed with previous studies that were conducted in Aomori prefecture in the Tohoku region (Maeda et al., 2017; Oku et al., 2018). Therefore, the data reported previously can be reliably validated by this study. ‘Turbo’ and ‘Aurora’ were early maturing cultivars, and ‘Super Kitamomiji’ and ‘Gunnison’ were late maturing cultivars, compared to the other four cultivars in spring-sowing cultivation in the Tohoku region. In general, long-day onion cultivars are sown in cold regions for spring-sowing cultivation and short-day cultivars are sown in warm regions for autumn-sowing cultivation (Maeda et al., 2017); suitable cultivars are bred and sold by many vegetable seed breeding companies. A comparison of plant growth and bulb development between long-day and short-day or intermediate-day cultivars with the same cropping system has not previously been reported. In Japan, onions for sale are selected based on bulb diameter, and 5 cm is the lower limit in many production areas. In our study, the bulb diameters of all eight cultivars were over 5 cm in 2016 and 2017 (Table 1). Therefore, our study demonstrated that spring-sowing cultivation in the Tohoku region could enable producers to grow onions of sufficient bulb size for sale.

The number of total leaves and inner leaves that constitute the bulbs is lower in early maturing cultivars (‘Momiji No. 3’) than in later maturing cultivars (‘Okhotsk 222’ and ‘Kitamomiji 2000’) (Yamasaki et al., 2015). We did not investigate the number of inner leaves in this study, but the total leaf blades number of early maturing cultivars was lower than later maturing cultivars (Table 1), as shown by Yamasaki et al. (2015). The reason why dry weight and dry matter content of early maturing cultivars were lower than later maturing cultivars may therefore be related to the number of inner leaves. Total leaf number, plant height, and bulb size were observed every week from transplanting to lodging. Changes in the total leaf number, plant height, and bulb size were almost the same in the middle stage of plant growth (Fig. 2). Total leaf number and plant height reached a plateau in the early maturing cultivars, as depicted in Figure 2A–D. The final leaf number and plant height of early maturing cultivars at harvest were lower than late maturing cultivars in both 2016 and 2017 (Table 1). The onion stops leaf blade development and switches to make bulb scales when bulb development is induced (Brewster, 1982), and the number of leaf blades is closely related to the final bulb size (Ikeda et al., 2019). In this study, bulb size including diameter, fresh and dry weight increased rapidly in early maturing cultivars as depicted in Figure 2E–H.

A previous study reported that bulb development was controlled by day-length and temperature (Khokhar, 2017). Garner and Allard (1920) first reported that onion bulb development was induced under long day-length, and subsequent studies elucidated bulb development. Aoba (1964) reported that long-day treatments induced inner-leaf formation, and Brewster (2008) explained that short-day treatments or interruption during onion bulb development inhibited bulb formation, with the plant reinitiating leaf growth. These studies clearly demonstrated that onion bulb development was induced and persisted during long-day lengths, and that bulb development could be inhibited with short day-lengths longer or shorter than the critical day-length for the bulb development of each cultivar.

Lee et al. (2013) and Rashid et al. (2019) reported that the expression of AcFT1, which encodes an FT-like protein for bulb development, is upregulated under long day-lengths and downregulated under short day-lengths. Another AcFT gene, AcFT4, which regulates formation of leaf blades and suppression of bulb development, is upregulated under short day-lengths and downregulated under long day-lengths (Lee et al., 2013; Rashid et al., 2019). The expression of AcFT4 was higher than AcFT1 just after transplantation in the cultivars ‘Turbo’, ‘Momiji No. 3’, and ‘Okhotsk 222’ (Fig. 3). The expression of AcFT4 is regulated by day-length as described above, and Lee et al. (2013) suggested that AcFT4 prevents upregulation of AcFT1 that promotes
bulb formation. Therefore, high-level expression of AcFT4 is likely induced by relatively short day-lengths shorter than the critical day-length for bulb development, and persistent leaf initiation without bulb formation. As the plant grows, the AcFT4 expression level gradually decreases and AcFT1 expression gradually increases. Expression of AcFT1 in ‘Turbo’ reached a peak on June 13 (8 WAT) (Fig. 3A), in ‘Momiji No. 3’ it reached a peak on July 11 (12 WAT) (Fig. 3B), and in ‘Okhotsk 222’ it reached a peak on July 25 (14 WAT) (Fig. 3C). These results showed that AcFT1 is expressed in accordance with the maturity of the cultivars, and indicates that AcFT1 expression can be used as a metric of maturity types for cultivar and bulb development. In all three cultivars, the bulbing ratio did not greatly exceed 2 until AcFT1 expression became obvious and higher than AcFT4 expression (Fig. 3). These results indicate that onion responds to a critical day-length for bulb development and starts bulb development before the bulbing ratio greatly exceeds 2. Therefore, this can be used as an index of bulb development; the maturity of cultivars and initiation of bulb formation can be determined by AcFT1 expression.

In this study, we evaluated changes in plant growth and bulb development of eight onion cultivars with spring-sowing cultivation in the Tohoku region. Plant growth and bulb development of different early and late maturing cultivars were compared under the same environmental conditions. A comparison of the cultivars during growth revealed that changes in total leaf number, plant height, and bulb size were similar in the middle phase of growth, but reached a plateau depending on the cultivar’s maturity type. We also examined the AcFT1 and AcFT4 expression that regulate leaf initiation and bulb development in three cultivars (‘Turbo’, ‘Momiji No. 3’, and ‘Okhotsk 222’) grown in the field, and found that these genes were expressed in accordance with the maturity of the cultivars. The bulbing ratio is conventionally used as an indicator of bulb development, but our gene expression analysis indicated that the onions responded to day-length before the bulbing ratio greatly exceeded 2. Bulb development is controlled by photoperiod and temperature (Khokhar, 2017). The present study suggests that the expression of AcFTs is a useful metric of bulb development. Further study of environmental responses (not only day-length, but also temperature) together with this metric will be necessary to improve assessment of this cultivation method. We previously reported a relationship between temperature and bulb development using a single cultivar, ‘Momiji No. 3’, in a temperature gradient growth chamber (Ikeda et al., 2019). Growth chamber trials to investigate the effect of day-length are necessary to contribute to the knowledge base of onion growers and breeders.

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