Seasonal variation in agronomic characteristics and sugar content of cabbage genotypes

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ABSTRACT

Cabbage is one of the most popular vegetables that is rich in sugars contributing to flavor and consumer accept ance; however, little information is available on the effect of genotypes and growing conditions on sugar accumulation. We assessed the seasonal variation in agronomic characteristics and free sugar content in cabbage (Brassica oleracea L. var. capitata L.) grown under open field conditions. Seventy-five cabbage genotypes were grown in the spring and autumn 2019, and their morphological characteristics and sugar concentrations were evaluated. Six cabbage types produced predominantly round-shaped heads (64 genotypes). Bright green and green were the dominant colors depending on the outer and inner leaves of the cabbage head. The most variable quantitative trait was head weight in both spring (36.9%) and autumn (49.2%). Glucose was the predominant sugar in most genotypes in both seasons. Mean glucose content in spring and autumn was 209.3 and 214.9 mg g⁻¹ with 14.8% and 14.6% variation, respectively. Most genotypes produced higher fructose concentrations in fall than in spring. Sucrose levels showed the highest variation in both spring (36.0%) and autumn (60.5%), followed by fructose and glucose levels. Most agronomic parameters exhibited nonsignificant or negative correlations with sugar content, except the correlation of head height and width with glucose content. Fructose and glucose were positively correlated with total sugar content, while there was nonsignificant correlation with sucrose. Genotypes 160330 and 183701 produced comparably high and stable total sugar content in both seasons and can therefore be used as commercial breeding materials. We revealed a significant effect of genotype and season on cabbage agronomic characteristics and sugar content.

Key words: Agronomic characteristics, Brassica oleracea var. capitata, fructose, genetic variation, glucose, growing season.

INTRODUCTION

Cabbage (Brassica oleracea L. var. capitata L.) is one of the most important brassicaceous crops and it is grown worldwide. The cultivated area and annual production of cabbage in South Korea is 7906 ha and 371 651 t, respectively (Korean Statistical Information Service, 2018). Cabbage is commonly consumed as salad, boiled leaves, juice, fermented products, and stir-fry. This plant shows substantial variability in its genetics and morphological characteristics (Balkaya et al., 2005; Kibar et al., 2016), which is important to genetically improve any particular characteristic. Many epidemiological studies have reported that the consumption of Brassica crops, including cabbage, is associated with reducing the risk of chronic diseases and cancer incidence (Terry et al., 2001; Wu et al., 2013). Cabbage exhibits antioxidant, chemo-preventive, and anti-obesity properties (Williams et al., 2013; Samec et al., 2017; Koss-Mikolajczyk et al., 2019), and it is also used
in traditional medicine (Samec et al., 2017). Cabbage is also a good source of dietary fiber. Such beneficial effects of cabbage have been mainly attributed to its glucosinolates, phenols, flavonoids, anthocyanins, carotenoids, vitamins, and carbohydrates (Park et al., 2014; Koss-Mikolajczyk et al., 2019; Bhandari et al., 2020; Zhao et al., 2020).

Carbohydrates are primary compounds of the metabolism of plants that can be used as energy sources for vegetative growth and development. These compounds can be immediately transported or temporarily stored and are precursors in the biosynthesis of different compounds, including proteins, lipids, and polysaccharides (Rosa et al., 2001; Eveland and Jackson, 2012; Ciereszko, 2018). Carbohydrates serve as signaling molecules that affect enzyme activity and gene expression and help to regulate plant growth and development (Eveland and Jackson, 2012). Free sugars, specifically sucrose, serve as anti-oxidative agents under abiotic stress conditions (Keunen et al., 2013). Sweetness is determined by differential concentrations of fructose, glucose, and sucrose in which fructose contributes the most to sweetness, followed by sucrose and glucose (Joesten et al., 2007). They also may alter flavor and palatability of vegetables in various ways (VandenLangenberg et al., 2012) and help to perceive flavors associated with other organic compounds (Auerswald et al., 1999). Furthermore, higher sugar concentrations can mask the bitter taste of S compounds such as glucosinolates, which increase palatability (Schonhof et al., 2004). The accumulation and relative concentration of sugars depends on several factors such as genotype, tissue type, plant developmental stages, and growing season (Rosa et al., 2001; Aires et al., 2011; VandenLangenberg et al., 2012; Bhandari and Kwak, 2015a; Zhao et al., 2020).

Several studies have been conducted to assess the effects of genotype, growing season, postharvest conditions, and plant parts on a range of bioactive compounds in cabbage, including glucosinolates, vitamins, phenols, and flavonoids (Banerjee et al., 2014; Choi et al., 2014; Ciska et al., 2016; Pessoa et al., 2016; Bhandari et al., 2020; Zhao et al., 2020). However, information regarding sugar composition is limited to a few genotypes (Rosa et al., 2001). The effect of the growing season on sugar content in cabbage heads has not been examined in detail. Genotype and growing conditions are important parameters for phytochemical accumulation, so that genotypes producing high and stable free sugar concentrations under various environmental conditions should be identified. Variability in agronomic characteristics between several cabbage genotypes was previously studied (Singh et al., 2010; Kibar et al., 2016), but the effects of origin and season on changes in such agronomic parameters are yet unclear.

We examined genotypic and seasonal variation in agronomic characteristics and free sugar content of 75 cabbage genotypes grown under open field conditions in spring and autumn to identify genotypes with high sugar content and favorable agronomic parameters, which can be used for commercial breeding.

**MATERIALS AND METHODS**

**Plant material and cultivation**

Seeds of 75 cabbage (*Brassica oleracea* L. var. *capitata* L.) genotypes were obtained from the National Agrobiodiversity Center, Jeonju, South Korea. Common names, accession numbers, and source details are shown in Table 1. Plants were grown at the Breeding Research Institute of the Koregon Co. (Gimje, South Korea) in two seasons. Seeds were sown in 72-cell trays on 10 March and 31 July 2019 for the spring and autumn growing periods, respectively. Approximately 30 d after sowing, seedlings were transplanted to an experimental field (Breeding Research Institute of the Koregon Co.) where they were planted in rows with 30 cm spacing between plants and 100 cm spacing between rows. Base fertilizer had been applied to the experimental field according to the study by Bhandari et al. (2020). Compost fertilizer (3700 kg ha⁻¹) was applied during the experiment. Plants were irrigated with sprinklers every day in the morning. Cabbage heads were first harvested 40 d after transplanting, depending on the genotype. Meteorological data were collected from a weather station close to the experimental field from the date of transplanting to harvesting in both seasons (Figure 1). Leaf length was measured during harvest. Three cabbage heads of each genotype were used for sampling. Once harvested, cabbage heads were immediately taken to the laboratory and two to three outer leaves were removed to account for contamination with dust particles. The shape and color of the outer and inner leaves were evaluated. Head weight, height, width, and core length were measured. Each cabbage head was vertically cut into four parts with a knife and one part of each head was then cut into small pieces that were freeze-dried at -54 °C, ground into a fine powder, and stored at -20 °C until sugar analysis. Cabbage head shape and outer and inner leaf color were only evaluated in spring and all other measurements were recorded in both seasons. The leaf color was visually determined at harvest.
Table 1. Seasonal variation in agronomic characteristics of cabbage genotypes.

| Number | Origin | Head shape | Outer color | Inner leaf color | Leaf length | Head weight | Head height | Head width | Core length |
|--------|--------|------------|-------------|------------------|-------------|-------------|-------------|------------|-------------|
| 1      | CHN    | Flat       | BRG         | BRG              | 34.0        | 12.0        | 20.0        | 5.5        | 6.3         |
| 2      | ITA    | Round      | G           | G                | 31.1        | 17.0        | 16.5        | 5.2        | 7.0         |
| 3      | UKR    | Round      | BRG         | BRG              | 44.2        | 12.4        | 17.5        | 6.5        | 4.9         |
| 4      | KAZ    | Round      | G           | G                | 66.0        | 13.0        | 18.0        | 8.0        | 4.8         |
| 5      | KOR    | Round      | BRG         | BRG              | 40.3        | 13.8        | 14.3        | 5.1        | 3.9         |
| 6      | UNK    | Round      | G           | G                | 33.0        | 13.0        | 18.0        | 6.5        | 7.8         |
| 7      | KOR    | Flat       | BRG         | BRG              | 29.0        | 12.5        | 12.0        | 4.5        | 6.5         |
| 8      | MNG    | Round      | BRG         | LG               | 40.0        | 13.2        | 16.2        | 6.2        | 4.6         |
| 9      | MNG    | Round      | BRG         | G                | 44.0        | 13.8        | 16.8        | 5.7        | 6.5         |
| 10     | MNG    | Round      | BRG         | G                | 39.0        | 13.5        | 16.7        | 6.2        | 5.5         |
| 11     | MNG    | Round      | BRG         | G                | 48.0        | 14.0        | 17.2        | 5.1        | 4.8         |
| 12     | MNG    | Round      | BRG         | G                | 43.0        | 13.0        | 16.8        | 6.3        | 4.8         |
| 13     | MNG    | Round      | BRG         | G                | 43.0        | 14.0        | 17.3        | 6.5        | 4.8         |
| 14     | MNG    | Round      | BRG         | G                | 30.0        | 14.0        | 17.0        | 6.0        | 5.2         |
| 15     | KOR    | Round      | BRG         | BRG              | 46.0        | 12.5        | 16.8        | 4.4        | 5.0         |
| 16     | CHN    | Round      | BRG         | BRG              | 27.0        | 12.5        | 16.8        | 4.4        | 5.0         |
| 17     | KOR    | Round      | BRG         | BRG              | 43.0        | 13.5        | 17.3        | 6.8        | 4.4         |
| 18     | KOR    | Flat       | BRG         | BRG              | 43.0        | 12.5        | 16.8        | 4.4        | 5.0         |
| 19     | UZB    | Round      | LG           | LG               | 50.0        | 13.5        | 17.3        | 6.5        | 6.0         |
| 20     | RUS    | Round      | BRG         | BRG              | 23.0        | 12.5        | 17.3        | 6.0        | 5.2         |
| 21     | RUS    | Round      | BRG         | BRG              | 30.0        | 14.0        | 17.0        | 6.0        | 5.5         |
| 22     | RUS    | Round      | BRG         | BRG              | 32.0        | 13.5        | 17.3        | 6.5        | 5.5         |
| 23     | RUS    | Round      | BRG         | BRG              | 32.0        | 13.5        | 17.3        | 6.5        | 6.0         |
| 24     | RUS    | Round      | BRG         | BRG              | 40.0        | 13.5        | 17.3        | 6.0        | 6.0         |
| 25     | RUS    | Round      | BRG         | BRG              | 29.0        | 13.5        | 17.3        | 6.0        | 6.0         |
| 26     | RUS    | Round      | BRG         | BRG              | 43.0        | 13.5        | 17.3        | 6.5        | 6.0         |
| 27     | RUS    | Round      | BRG         | BRG              | 32.0        | 13.5        | 17.3        | 6.5        | 6.0         |
| 28     | RUS    | Round      | BRG         | BRG              | 43.0        | 13.5        | 17.3        | 6.5        | 6.0         |
| 29     | RUS    | Round      | BRG         | BRG              | 32.0        | 13.5        | 17.3        | 6.5        | 6.0         |
| 30     | RUS    | Round      | BRG         | BRG              | 43.0        | 13.5        | 17.3        | 6.5        | 6.0         |
| 31     | RUS    | Round      | BRG         | BRG              | 43.0        | 13.5        | 17.3        | 6.5        | 6.0         |
| 32     | RUS    | Round      | BRG         | BRG              | 43.0        | 13.5        | 17.3        | 6.5        | 6.0         |
| 33     | RUS    | Round      | BRG         | BRG              | 43.0        | 13.5        | 17.3        | 6.5        | 6.0         |
| 34     | RUS    | Round      | BRG         | BRG              | 43.0        | 13.5        | 17.3        | 6.5        | 6.0         |
| 35     | RUS    | Round      | BRG         | BRG              | 43.0        | 13.5        | 17.3        | 6.5        | 6.0         |
| 36     | RUS    | Round      | BRG         | BRG              | 43.0        | 13.5        | 17.3        | 6.5        | 6.0         |
| 37     | RUS    | Round      | BRG         | BRG              | 43.0        | 13.5        | 17.3        | 6.5        | 6.0         |

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Continuation Table 1.

| SN  | Number  | Resource name  | Origin¹ | Head shape | Leaf length | Head weight | Head height | Head width | Core length |
|-----|---------|----------------|---------|------------|-------------|-------------|-------------|------------|-------------|
|     |         |                |         |            | Spring Autumn | Spring Autumn | Spring Autumn | Spring Autumn | Spring Autumn |
| 57  | K166240 | Red Drumhead 2 | SWE     | Round PG   | 43.0         | 22.9        | 12.5        | 7.4        | 4.4         |
|     |         |                |         |            | 490         | 128         | 15.5        | 12.8       | 14.0        |
| 58  | K175584 | 213 KOR        | G       | Round G    | 33.5         | 21.6        | 1260        | 1028       | 17.0        |
|     |         |                |         |            | 2160        | 1560        | 20.0        | 16.5       | 17.0        |
| 59  | K176590 | Da shanghai xin zheng chin ganlan | CHN | Round G | 41.0         | 25.6        | 2160        | 1560        | 17.0        |
|     |         |                |         |            | 210          | 1500        | 20.0        | 16.5       | 17.0        |
| 60  | K176592 | Qing Feng      | CHN     | Round BRG  | 40.2         | 29.8        | 2330        | 1150        | 19.0        |
|     |         |                |         |            | 210          | 1240        | 15.0        | 14.0       | 16.0        |
| 61  | K176593 | Zhong Gan 21   | CHN     | Round G    | 29.0         | 24.5        | 2430        | 624         | 17.5        |
|     |         |                |         |            | 1240        | 644         | 18.0        | 12.2       | 17.5        |
| 62  | K176594 | Zhao Hong      | CHN     | Round P P  | 30.5         | 20.1        | 2430        | 624         | 17.5        |
|     |         |                |         |            | 1240        | 644         | 18.0        | 12.2       | 17.5        |
| 63  | K176595 | Zhong Gan 11   | CHN     | Round G    | 32.0         | 28.5        | 924         | 15.0        | 14.0        |
|     |         |                |         |            | 1250        | 924         | 15.0        | 14.0       | 16.0        |
| 64  | K195951 | Golden Acre Imp | IND | Round G | 30.0         | 16.0        | 710         | 248         | 12.0        |
|     |         |                |         |            | 248         | 710         | 12.0        | 9.5        | 14.0        |
| 65  | K204466 | CT-260         | KOR     | Round G G  | 22.1         | 21.7        | 750         | 554         | 12.5        |
|     |         |                |         |            | 750         | 554         | 12.5        | 12.1       | 12.0        |
| 66  | K222934 | CH 83          | KOR     | Round BRG  | 32.0         | 29.1        | 980         | 428         | 14.5        |
|     |         |                |         |            | 428         | 980         | 14.5        | 11.1       | 13.1        |
| 67  | K243819 | Miya Bi        | THA     | Round G G  | 42.0         | 29.2        | 1865        | 1116        | 14.4        |
|     |         |                |         |            | 1865        | 1116        | 14.4        | 11.3       | 19.2        |
| 68  | K246353 | 90ms           | KOR     | Round BRG  | 34.0         | 26.9        | 1140        | 668         | 15.8        |
|     |         |                |         |            | 1140        | 668         | 15.8        | 13.6       | 13.6        |
| 69  | K246359 | P15-41         | KOR     | Round G G  | 29.9         | 18.7        | 1265        | 354         | 14.5        |
|     |         |                |         |            | 354         | 1265        | 14.5        | 18.1       | 15.7        |
| 70  | K246894 | Succession Green Leaved | ARM | Flat BRG | 45.0         | 30.0        | 750         | 502         | 10.3        |
|     |         |                |         |            | 502         | 750         | 10.3        | 10.3       | 16.8        |
| 71  | K246912 | A5-7           | TWN     | Round BRG  | 46.1         | 35.0        | 1380        | 658         | 14.0        |
|     |         |                |         |            | 1380        | 658         | 14.0        | 12.4       | 16.0        |
| 72  | K247130 | N 127          | NA      | Round G G  | 39.0         | 29.0        | 830         | 676         | 14.0        |
|     |         |                |         |            | 830         | 676         | 14.0        | 13.5       | 13.5        |
| 73  | K247132 | Mihnevskaia    | RUS     | Round PG PG| 34.0         | 29.5        | 1750        | 544         | 14.2        |
|     |         |                |         |            | 1750        | 544         | 14.2        | 12.2       | 13.1        |
| 74  | K247741 | TJK-PHJ-2014-6-8 | TJK | Round BRG | 43.0         | 28.8        | 1125        | 606         | 14.9        |
|     |         |                |         |            | 1125        | 606         | 14.9        | 11.2       | 15.6        |
| 75  | K247794 | Apsheronskaya  | TJK     | Round G G  | 47.3         | 35.6        | 910         | 680         | 17.2        |
|     |         |                |         |            | 910         | 680         | 17.2        | 15.2       | 13.8        |

¹Alpha-3 country code.
Bold numbers are official introductory numbers, and the other numbers are temporary accession numbers; NA: no information available; R-P: round and pointed; Semi-F: semi-flat; Semi-R: semi-round; BRG: bright green; G: green; DG: dark green; LG: light green; PG: purple green, P: purple.

Figure 1. Changes in air temperature, air humidity, cumulative radiation, and rainfall at the experimental field in spring (A and C) and autumn (B and D). Horizontal dotted lines indicate average values.
Sugar content and sweetness analysis
Sugar content was analyzed according to the method described by Bhandari and Kwak (2015a) with some modifications. Sugar was extracted from powdered cabbage samples (0.2 g) with distilled water (5.0 mL) in a water bath at 80 °C under shaking at 150 rpm for 20 min. The samples were immediately cooled, centrifuged at 3500 rpm for 10 min, and filtered through a 0.22 μm syringe filter. The filtrate was analyzed with a 1260 HPLC system (Agilent Technologies, Santa Clara, California, USA) equipped with a quaternary HPLC pump, an auto-sampler, and a refractive index detector. The separation of sugars was performed with a carbohydrate analysis column (4.6 × 250 mm, 5 μm; ZORBAX, Agilent Technologies) protected by a guard column and at a column oven temperature of 30 °C. Acetonitrile/distilled water (75/25, v/v) at a flow rate of 1.4 mL min⁻¹ was used as the mobile phase. Individual sugar peaks were identified and quantified based on retention times and peak areas compared with authentic standards. Authentic standards of glucose, fructose, and sucrose were obtained from Sigma-Aldrich (St. Louis, Missouri, USA). All analyses were performed in triplicate and results were expressed as mg g⁻¹ dry weight (DW).

The total sweetness index (TSI) was calculated using concentration and the sweetness coefficient of each sugar according to Magwaza and Opara (2015).

Statistical analyses
Means of three replicates were used for statistical analyses. Data were analyzed with SPSS Statistics 20.0 (IBM, Armonk, New York, USA). Effects of cultivar, growing season, and their interaction were analyzed by fitting a mixed model one-way ANOVA. Correlations were tested using Pearson’s correlation coefficient (r) at p ≤ 0.05. All the figures were computed with SigmaPlot 12.0 (Systat Software Inc., San Jose, California, USA).

RESULTS AND DISCUSSION

Variation in agronomic characteristics
Qualitative and quantitative agronomic parameters were measured during and after harvest. Qualitative parameters such as head shape and outer and inner leaf color were only recorded in spring, while the quantitative agronomic parameters were recorded in both seasons. Six categories of head shapes were identified as round, flat, semi-flat, pointed, semi-round, and round-pointed; most genotypes (n = 64) showed a round head shape (Table 1). Similar cabbage head shapes were observed in previous studies (Cervenski et al., 2010; De Mortel, 2018). Cabbage genotypes also showed considerable variability in outer and inner leaf color, which was classified in six categories of bright green, green, dark green, light green, purple green, and purple. Outer leaves were bright green in 31 genotypes and green in 25 genotypes (Figure 2). In contrast, inner leaves were green in most genotypes (n = 38), followed by bright green (n = 17). Eight genotypes belonged to the red cabbage category because they had purple/purple green outer and inner leaves, depending on genotype. Detailed information on agronomic characteristics of each genotype is displayed in Table 1. The quantitative parameters evaluated in the present study included leaf length, head weight, head height, head width, and core length, which also exhibited variability across genotypes. All of these parameters showed higher mean values in spring than in autumn, and variation expressed as coefficients of variation was higher in autumn than in spring (Table 2). Mean leaf length, head height, head width, and core length were 39.4, 15.1, 15.8, and 6.4 cm, respectively, in spring and 28.7, 14.5, 16.7, and 25.3 cm in autumn with a coefficient of variation of 23.7%, 17.0%, 24.3%, and 27.6%, respectively.

Among the quantitative agronomic parameters, head weight exhibited the largest variation in spring (36.9%) and autumn (49.2%). Substantial genotypic variation associated with quantitative parameters was previously observed in different crops, including cabbage (Balkaya et al., 2005; Weerakoon and Somaratne, 2011; El-Esawi et al., 2012; Kibar et al., 2016; Garcia-Diaz et al., 2018; Ribeiro et al., 2019). However, this is the first report describing seasonal variation in morphological characteristics of different cabbage genotypes from different origins. Our results suggest that overall fluctuations in agronomic parameters are mostly due to plant genotypes and different climatic conditions between spring and autumn.
Variation in free sugar concentrations and total sweetness index (TSI)
The concentrations of the three sugars, glucose, fructose, and sucrose, in cabbage head germplasm during spring and autumn 2019 are shown in Figure 3. Fructose and glucose were the predominant sugars in cabbage germplasm, which concurred with findings from previous studies on cabbage (Rosa et al., 2001; Zhao et al., 2020) and other brassicaceous vegetables such as broccoli and cauliflower (Bhandari and Kwak, 2015a; 2015b). In most cases, the germplasm content of glucose was the highest, followed by fructose and sucrose in both growing seasons.

The mean glucose content in spring was 209.3 mg g\(^{-1}\), which varied between 126.5 and 276.7 mg g\(^{-1}\) dry weight, whereas it ranged from 115.8 to 272.1 mg g\(^{-1}\) in autumn with a mean of 214.9 mg g\(^{-1}\). However, genotypic variation as measured by the coefficient of variation was similar across seasons (approximately 15%, Table 3). The proportion of glucose in the total free sugar content was higher in spring (55.0%) than in autumn (48.6%, Figure 4). Glucose represented the highest sugar proportion in spring in all genotypes, but only in approximately 75% of all genotypes in autumn. Approximately 33% of the genotypes showed higher glucose content in spring than in autumn, whereas the other genotypes showed either higher or similar glucose content in autumn. Bhandari and Kwak (2015a) found higher glucose content in spring than in autumn in 12 broccoli cultivars. Similarly, Rosa et al. (2001) observed higher glucose content in cabbage grown in spring than in autumn. Effects of genotype and growing season on other bioactive compounds have been previously observed (Cartea et al., 2008; Choi et al., 2014; Bhandari et al., 2020), suggesting that the accumulation of phytochemicals in vegetables depends on plant species and on the nature of phytochemicals. Furthermore, we found a differential accumulation of glucose content that depended on the genotype. Further studies on molecular genetics are required to elucidate genotype-dependent seasonal variation in sugar content. Five genotypes (183701, K176592, K246359, K154726, and 906763) showed higher glucose concentrations (> 250.0 mg g\(^{-1}\) DW) in spring, whereas genotypes 160330, K044570, K004538, K176595, K176593, K121377, and K176592 showed higher glucose concentrations (> 250 mg g\(^{-1}\) DW) in autumn (Figure 3).
Figure 3. Seasonal variation in fructose (A), glucose (B), and sucrose (C) concentrations in 75 cabbage genotypes. Refer to Table 1 for detailed information on genotypes.

Bars indicate the mean ± standard deviation of three replicates.
Fructose, which was also abundant, showed significant variations among genotypes in both seasons with some reverse accumulation between seasons when compared to glucose. Most genotypes showed higher fructose content in autumn than in spring (Figure 3) ranging from 69.5 to 197.6 mg g⁻¹ in spring and from 93.2 to 253.3 mg g⁻¹ in autumn. Mean fructose concentrations were higher in autumn (202.1 mg g⁻¹) than in spring (155.3 mg g⁻¹, Table 3). The concentrations observed in the present study were higher than those previously reported (Rosa et al., 2001); this could be due to differences in genotypes and environmental conditions. The proportion of fructose was higher in autumn (45.6%) than in spring (40.6%, Figure 4), but genotypic variation was slightly lower in autumn than in spring. Higher fructose concentrations in autumn increased the sweetness of cabbage because fructose is the predominant contributor to sweetness and can mask bitter taste, thereby increasing palatability (Schonhof et al., 2004; Joesten et al., 2007).

In some genotypes (n = 18), fructose was higher in autumn. The proportions of glucose were typically lower in autumn than in spring; however, these proportions were higher in both seasons compared to fructose. Our results are consistent with the results reported by Rosa et al. (2001), who found higher fructose concentrations in autumn than in spring. Seven genotypes showed higher fructose concentrations (> 190 mg g⁻¹ DW) in spring, whereas 50 genotypes produced higher fructose concentrations (> 190 mg g⁻¹ DW) in autumn. Three genotypes (K222934, K176593, and 906763) produced relatively high and stable fructose concentrations in both seasons.

Sucrose content showed substantial changes and produced considerable genotypic variation (Figure 3). In spring, sucrose showed more than six-fold variation, ranging from 6.0 to 37.2 mg g⁻¹ with a mean concentration of 16.0 mg g⁻¹. This range was wider in autumn than in spring, with about 18-fold variation between highest and lowest values. The average sucrose content in autumn was 24.7 mg g⁻¹ which was higher than that observed during spring. The variation as measured by the coefficient of variation was higher in autumn (60.5%) than in spring (36.0%; Table 3). The proportion of sucrose was higher in autumn (5.8%) than in spring (4.4%; Figure 4), which was probably due to higher fluctuation in climatic factors (Figure 1) as sucrose is a compatible solute that accumulates during stress conditions (Serraj and Sinclair, 2002). Furthermore, acid invertase activity may be lower in autumn than in spring which would cause an increase in the

### Table 3. Free sugar content and total sweetness index (TSI) in cabbage genotypes (n = 75) grown in two seasons.

| Season | Sugar | Average | Range | CV  |
|--------|-------|---------|-------|-----|
|        | mg g⁻¹ | mg g⁻¹  | %     |     |
| Spring | Fructose | 155.3 | 69.5-197.6 | 17.8 |
|        | Glucose  | 209.3 | 126.5-276.7 | 14.8 |
|        | Sucrose  | 16.0  | 6.0-37.2 | 36.0 |
|        | Total sugar | 380.5 | 233.1-475.3 | 14.0 |
|        | TSI      | 407.9 | 237.5-510.5 | 14.6 |
| Autumn | Fructose | 202.1 | 93.2-253.0 | 15.4 |
|        | Glucose  | 214.9 | 115.8-272.1 | 14.6 |
|        | Sucrose  | 24.7  | 4.2-77.9 | 60.5 |
|        | Total sugar | 441.7 | 286.9-354.8 | 12.3 |
|        | TSI      | 491.2 | 297.1-599.7 | 12.7 |

CV: Coefficient of variation.

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**Figure 4. Average proportions of fructose, glucose, and sucrose in total sugar content in spring (A) and autumn (B).**

Fructose, which was also abundant, showed significant variations among genotypes in both seasons with some reverse accumulation between seasons when compared to glucose. Most genotypes showed higher fructose content in autumn than in spring (Figure 3) ranging from 69.5 to 197.6 mg g⁻¹ in spring and from 93.2 to 253.3 mg g⁻¹ in autumn. Mean fructose concentrations were higher in autumn (202.1 mg g⁻¹) than in spring (155.3 mg g⁻¹, Table 3). The concentrations observed in the present study were higher than those previously reported (Rosa et al., 2001); this could be due to differences in genotypes and environmental conditions. The proportion of fructose was higher in autumn (45.6%) than in spring (40.6%, Figure 4), but genotypic variation was slightly lower in autumn than in spring. Higher fructose concentrations in autumn increased the sweetness of cabbage because fructose is the predominant contributor to sweetness and can mask bitter taste, thereby increasing palatability (Schonhof et al., 2004; Joesten et al., 2007).

In some genotypes (n = 18), fructose was higher in autumn. The proportions of glucose were typically lower in autumn than in spring; however, these proportions were higher in both seasons compared to fructose. Our results are consistent with the results reported by Rosa et al. (2001), who found higher fructose concentrations in autumn than in spring. Seven genotypes showed higher fructose concentrations (> 190 mg g⁻¹ DW) in spring, whereas 50 genotypes produced higher fructose concentrations (> 190 mg g⁻¹ DW) in autumn. Three genotypes (K222934, K176593, and 906763) produced relatively high and stable fructose concentrations in both seasons.

Sucrose content showed substantial changes and produced considerable genotypic variation (Figure 3). In spring, sucrose showed more than six-fold variation, ranging from 6.0 to 37.2 mg g⁻¹ with a mean concentration of 16.0 mg g⁻¹. This range was wider in autumn than in spring, with about 18-fold variation between highest and lowest values. The average sucrose content in autumn was 24.7 mg g⁻¹ which was higher than that observed during spring. The variation as measured by the coefficient of variation was higher in autumn (60.5%) than in spring (36.0%; Table 3). The proportion of sucrose was higher in autumn (5.8%) than in spring (4.4%; Figure 4), which was probably due to higher fluctuation in climatic factors (Figure 1) as sucrose is a compatible solute that accumulates during stress conditions (Serraj and Sinclair, 2002). Furthermore, acid invertase activity may be lower in autumn than in spring which would cause an increase in the
proportion of sucrose (Sung et al., 1994). Seven genotypes produced higher sucrose concentrations (> 25.0 mg g⁻¹) in spring and 31 genotypes in autumn.

Total sugar concentrations in spring ranged from 233.1 to 475.3 mg g⁻¹ with a mean concentration of 380.5 mg g⁻¹. Total sugar concentrations were higher in autumn (286.9-534.8 mg g⁻¹), with an average value of 441.7 mg g⁻¹ (Figure 5, Table 3). Lower sugar content in spring was probably due to increased photorespiration under higher temperatures which likely reduced photosynthetic efficiency (Nilsen and Orcutt, 1996). Overall variation was lower in autumn (12.3%) than in spring (14.0%). Genotypes namely 160330 (Nr 1), 183701 (Nr 2), 906763 (Nr 15), K154726 (Nr 48), K176592 (Nr 60), K222937 (Nr 66), K246359 (Nr 69), and K247794 (Nr 75) belonged to upper 10% of the total genotypes with higher total sugar concentrations (> 445.0 mg g⁻¹) in spring, while the upper 10% of the total genotypes exhibited total sugar concentration higher than 510.0 mg g⁻¹ in autumn. Only two genotypes; 160330 and 183701 exhibited relatively high and stable total sugar content belonging to the upper 10% of the genotypes in both seasons.

One of the commonly used sweetness indexes to indicate the sweetness of horticultural crops, TSI, exhibited different values depending upon the genotypes and seasons (Figure 5). Average TSI was about 25% higher in autumn compared to spring although quite similar genotypic variation was found in both the seasons (Table 3). Similar to the fructose and total sugar concentration, almost of the genotypes showed higher TSI in autumn than in spring (Figure 5). Similar genotypes as in the total sugar concentration also belonged to the upper 10% of the total genotypes with the higher TSI in both spring and autumn as a result only two genotypes 160330 and 183701 showed relatively stable and higher TSI in both seasons. As TSI has been considered more suitable parameter compared to the other sweetness indices for the prediction of overall acceptability in vegetables (Magwaza and Opara, 2015), the results along with total sugar concentration might be useful for the selection of high sweetness cabbage genotypes.

Figure 5. Seasonal variation in total free sugar content (A) and total sweetness index (B) in 75 cabbage genotypes. Refer to Table 1 for detailed information on genotypes.
Taken together, our study showed significant effects of cabbage genotypes and environmental conditions on the composition of sugars. We also found significant genotypic variation in glucosinolate concentrations in a different study (Bhandari et al., 2020). To the best of our knowledge, this is the first report on variation in sugar content in a large number of cabbage genotypes from diverse origins grown in two different seasons, as most previous studies used fewer genotypes and were limited to one season. Our results may be of use for selecting candidate cabbage genotypes for future breeding programs.

Our results also showed that free sugar content in cabbage heads is affected by genotype, growing season, and their interaction (Table 4), suggesting that free sugar in cabbage is markedly influenced by genetic and environmental factors. Similar results were previously reported by Rosa et al. (2001). Furthermore, genotype- and season-dependent variation have been reported in other phytochemicals of many brassicaceous vegetables (Aires et al., 2011; Bhandari and Kwak, 2014). However, the current study is the first to examine variation sugar concentrations in a large number of cabbage genotypes from different origins grown in different seasons. Production of high concentrations of sugars in selected genotypes may be of interest for selecting cabbage breeding material.

**Correlation analyses**

To test direction and magnitude of correlations between parameters, correlation analyses of quantitative agronomic characters and sugar content were performed. We observed significant positive correlations among quantitative agronomic parameters (Table 5) with the strongest positive correlation between cabbage head weight and head height ($r = 0.727; p < 0.01$) and weakest positive correlation between leaf length and core length ($r = 0.347; p < 0.01$), which is in line with results of previous studies (Cervenski et al., 2010; Singh et al., 2010; Adzic et al., 2012). Thus, selection based on these parameters either in combination or individually may help identify genotypes with potential for higher yields. Head height and width were strongly positively correlated with glucose content, whereas all other combinations of agronomic characters and individual sugar content produced either significantly negative or nonsignificant correlations, suggesting weak association of yield and sweetness. Only fructose and glucose showed a significant positive correlation with the strongest correlation between total sugar content and fructose ($r = 0.947; p < 0.01$). Furthermore, fructose was significantly correlated with glucose ($r = 0.684; p < 0.01$). In contrast, sucrose concentration produced either significantly negative or nonsignificant correlations with other sugar and total sugar concentrations. However, sucrose showed significant negative correlations with concentrations of other sugars and total sugar content in spring and autumn (data not shown) suggesting general conversion of sucrose to glucose and fructose in spring.

| Variables | Fructose | Glucose | Sucrose | Total sugar | TSI |
|-----------|----------|---------|---------|-------------|-----|
| Genotype (G) | 47.9 *** | 46.7 *** | 113.7 *** | 41.9 *** | 45.2 *** |
| Season (S) | 2980.8 *** | 35.5 *** | 2295.8 *** | 1355.9 *** | 2096.0 *** |
| G × S | 15.1 *** | 13.5 *** | 91.2 *** | 13.9 *** | 14.9 *** |

***Significance at $p < 0.001$.  

| Parameters | Leaf length | Head height | Head width | Core length | Fructose | Glucose | Sucrose | Total sugar | TSI |
|-----------|-------------|-------------|------------|-------------|----------|---------|---------|-------------|-----|
| Head weight | 0.407** | 0.727** | 0.723** | 0.590** | -0.095 | 0.270** | -0.253** | 0.028 | 0.153 |
| Leaf height | 0.356** | 0.458** | 0.478** | 0.347** | -0.511** | -0.250** | -0.017 | -0.440** | -0.351** |
| Head height | 0.470** | 0.593** | -0.081 | 0.283** | -0.324** | 0.303 | 0.151 |
| Head width | 0.420** | 0.079 | 0.079 | 0.247** | -0.135 | 0.147 | 0.221** |
| Core length | -0.247** | -0.039 | 0.039 | -0.168** | -0.164* | -0.069 |
| Fructose | 0.684** | -0.039 | 0.947** | 0.892** | 0.891** |
| Glucose | -0.382** | 0.846** | 0.891** |
| Sucrose | -0.020 | 0.969** |
| Total sugar | 0.969** |

*, **Significant at $p < 0.05$ and $p < 0.01$, respectively.  
TSI: Total sweetness index.
CONCLUSIONS

The cabbage genotypes showed variation in agronomic characteristics and sugar content. Information on variation in agronomic characteristics is useful for identifying candidate genotypes for breeding programs. Furthermore, we also found significant differences in the levels of individual and total free sugars in cabbage in relation to genotype and growing season. Most genotypes produced higher fructose concentrations in autumn than in spring. Sucrose showed the highest genotypic and seasonal variation among the free sugars. The genotypes 160330 and 183701 produced higher free sugar concentrations in both growing seasons, suggesting their superiority in terms of sugar content. The findings of this study may be of use for developing novel cabbage breeding lines with desirable agronomic characteristics and high free sugar concentrations.

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