Relationships between earliness of head formation and developmental characteristics of cabbage (*Brassica oleracea* L.) in two different growing seasons, autumn and spring

Norifumi Tanaka^{*1)}, Satoshi Niikura¹⁾ and Kazuyoshi Takeda²⁾

¹⁾ Tohoku Seed Co., 1625 Nishihara, Himuro, Utsunomiya, Tochigi 321-3232, Japan

²⁾ Research Institute for Bioresources, Okayama University, 2-20-1 Chuo, Kurashiki, Okayama 710-0046, Japan

We investigated and compared the relationships between the earliness of head formation and developmental characteristics of cabbage cultivars grown in spring (sown in early spring, harvested in early summer) and autumn (sown in summer, harvested in late autumn). In both seasons, earliness of head formation, namely the duration of the period to attain the target head weight from transplanting, was highly correlated with the leaf position at which head formation started (LPH): the lower the LPH value, the earlier head formation. This result suggests that a low LPH value is necessary for early-head-forming cultivars. However, the LPH value in some cultivars varied with the growing season, showing a significant genotype (G) $\times$ environment (E) interaction. To determine whether this G $\times$ E interaction might influence the use of LPH as a selection criterion, we analyzed the developmental pattern of the leaf shape. In cultivars with LPH values that largely differed between the two seasons, the leaves were longer up to a higher leaf position and widened later in the spring than in autumn, mainly because of delayed shortening of the petiole. We thus characterized the complex nature of early head-forming in spring, and suggested that LPH was a useful selection criterion for the development of early head-forming spring cultivars.

Key Words: cabbage, head formation habit, leaf shape, petiole length, genotype-environment interaction.

Introduction

Presently, cabbage is cultivated all the year round in Japan. Cultivars with early head formation (hereafter referred to as “Early-head-forming cultivars”) are utilized at the beginning of autumn and spring, soon after the end of the summer or winter conditions that are suboptimal for cabbage growth. Autumn temperature falls and spring temperature rises along with decreasing and increasing day length, respectively, and this obviously creates completely opposite conditions for cabbage growth. Cabbage is known to be a green vernalization plant, in which reproductive growth is induced by low temperature after growth to a certain size (Shinohara 1959). Development of early-head-forming cultivars in autumn is facilitated by a yearly cycle in which the parents are directly selected in autumn, then vernalized in winter, and produce their offspring seeds in spring. In contrast, the development of early-head-forming spring cultivars is a slow process, because it takes two years to obtain seeds from parents directly selected in spring. In addition, we empirically know that the use of autumn early-head-forming cultivars in spring is not always successful. Regis-

tration of new autumn cultivars is frequent, while that of new spring cultivars is rare (Ashizawa 2003). During a long period of time, the objective of cabbage breeders had been to raise a larger number of early-head-forming spring cultivars with a high quality. However, it remains to be determined whether the earliness of head formation in spring is governed by factors similar to those in autumn. In addition, we wondered whether the autumn selection step could be utilized for the raising of early-head-forming spring cultivars.

A cabbage forms its head during the vegetative growth period. The number and size of head leaves increase until the head acquires a weight, size and tightness suitable for harvest (Tanaka and Niikura 2003). Accordingly, we defined earliness of head formation in F_1 hybrid cultivars as the number of days after transplanting required for the head to attain a target weight of 1250 g (duration of head-maturation period to attain 1250 g, HMP_{1250}), the optimum marketable weight in Japan (Tanaka and Niikura 2003). Analysis in the autumn growing season has revealed that early-head-forming cultivars exhibit larger primary wrapper leaves, earlier leaf widening with the increase of the leaf position, and a lower LPH value than later-head-forming cultivars (Tanaka and Niikura 2003). The inheritance of earliness of head formation is largely influenced by heterosis (Swarup *et al.* 1963, Morgan 1969, Moore and Wallace 1987). Additionally, since head weight is a dominant character, with a

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*Corresponding author (e-mail: breeding@tohokuseed.co.jp)

low narrow-sense heritability, selecting parents based on head weight is not suitable for the development of early-head-forming cultivars (Tanaka and Niikura 2006). In contrast, the inheritance of LPH is additive, with a high narrow-sense heritability, suggesting that LPH is a suitable criterion for selecting parents with a good combining ability for early head formation in autumn (Tanaka and Niikura 2006).

We examined the relationships between the earliness of head formation and developmental characteristics in spring and compared them with the same relationships in autumn. Based on the strong correlation between earliness of head formation and LPH in spring, we considered the possibility of using LPH as a selection criterion for raising early-head-forming cultivars in spring, taking into account of the relationship between LPH and leaf developmental patterns in two growing seasons.

Materials and Methods

Materials

We used nine F_1 hybrid cultivars, consisting of six commercial cultivars—‘YR-Seishun’ (Watanabe Seed Co., Ltd., Miyagi, Japan); ‘YR-Aoba’ and ‘YR-Kinshu-kyoryoku 152’ (Masuda Seeds, Shizuoka, Japan); ‘Wakamine’ and ‘Asashio’ (Takii & Co., Ltd., Kyoto, Japan); and ‘Uji No. 1’ (Marutane Co., Ltd., Kyoto, Japan)—and three crosses of inbred lines—‘Yoshin $\times$ Early Summer’ (C-009 $\times$ C-341), ‘Yoshin $\times$ Black Leaf Succession’ (C-009 $\times$ C-324), and ‘Early Summer $\times$ Black Leaf Succession’ (C-341 $\times$ C-324).

The ‘Early Summer $\times$ Black Leaf Succession’ cross was used for observing leaf development by dissection, since its earliness of head formation was intermediate and its leaf developmental pattern was typical (Fig. 1).

Growing seasons and investigation of developmental characteristics

For autumn growing, seeds were sown on July 18, 2003 and the seedlings were transplanted on August 19, 2003. For spring growing, seeds were sown on February 6, 2004 and the seedlings were transplanted on March 26, 2004. The seedlings were grown in a greenhouse in 39 cm $\times$ 49 cm plug trays with 80 holes and transplanted to an Andosol field at Utsunomiya, Tochigi Prefecture, Japan (36°31'N, 139°59'E), at a spacing of 35 cm $\times$ 60 cm and using a completely randomized design with two replications. The composition of the fertilizer was 15 : 23 : 14 and 13 : 19 : 13 kg/1000 m² for N : P : K in autumn and spring, respectively. The minimum temperature in the nursery in spring was kept at above 5°C. The LPH and leaf characteristics of six plants in each plot were continuously investigated in a nondestructive manner. LPH was recorded when the cultivars had completed head formation and the head leaves (rolled leaves) could be distinguished from the wrapper leaves (unrolled leaves). The first leaf of the head was defined as the leaf attached to the next head leaf within 1 cm (Tanaka and Niikura 2003). The width, total (i.e., leaf + petiole) length and petiole length

of each wrapper leaf were measured at their maximum sizes, based on continuous observation. The border between the leaf blade and petiole was defined as the position where a clear constriction occurred, because this border was not clear and in some cultivars, the leaf blade seemed to have developed on the side of the petiole (Fig. 1). In the absence of a clear constriction, the petiole length was considered to be zero. The position of the first leaf without a petiole was referred to as the “non-petiole leaf position”. Leaf characteristics were determined on September 3 (5th leaf), September 26 (10th), October 1 (13th), October 6 (15th and 16th), October 9 (18th and 20th), October 21 (22nd) and November 5 (24th) in autumn, and on May 12 (5th), May 18 (10th), May 26 (13th), June 2 (15th and 16th), June 9 (18th and 20th), June 16 (22nd and 24th) and June 22 (>26th) in spring. Leaf shape index (LSI, width/total length), leaf blade shape index (LBSI, width/[total length – petiole length]), and leaf size (width $\times$ total length) were calculated. Four plants per plot were harvested each time to measure the head weight on days 56, 62, 69 and 79 after transplanting in autumn and on days 74, 80 and 88 in spring. We defined earliness of head formation in F_1 hybrid cultivars as the number of days after transplanting required for the head to attain a target weight of 1250 g (duration of head-maturation period to attain 1250 g, HMP_{1250}), the optimum marketable weight in Japan. HMP_{1250} was calculated by interpolation or extrapolation of the head weight data at harvest (Tanaka and Niikura 2003).

Statistical analyses

In the analysis of HMP_{1250} , the phenotypic value from each plot was calculated by interpolation or extrapolation of the mean values of the head weight data from four plants. In the analysis of LPH, non-petiole leaf position and leaf characteristics, the phenotypic value from each plot was taken as the average of six plants from each cultivar. Correlation analysis was performed using the Statistica software Ver. 6 (StatSoft Inc., USA). The correlation coefficient for the petiole length at the 20th leaf position in autumn was not calculated, since in most cultivars, the value of the petiole length was zero. Genotype $\times$ environment interaction for HMP_{1250} and LPH was examined by two-way ANOVA.

Results

Temperature and daylength during growing seasons

In autumn, the average temperature dropped from 24.7°C during the 5-day period following transplanting (August 19–23) to 16.0°C during the 5-day period preceding the last measurement (November 2–6). Conversely, in spring, it rose from 12.0°C during the 5-day period following transplanting (March 26–30) to 26.3°C during the 5-day period preceding the last measurement (June 18–22). The daylength from sunrise to sunset in autumn decreased from 13.5 to 10.7 h, and that in spring increased from 12.4 to 14.7 h, over the period of examination.

Comparison of genotypes and growing seasons in terms of HMP_{1250} and LPH

We compared the autumn and spring values of HMP_{1250} and LPH for each cultivar. HMP_{1250} ranged from 55.5 (YR-Seishun) to 72.4 days (Asashio) in autumn and from 65.1 (YR-Seishun) to 76.9 days (Asashio) in spring (Table 1). HMP_{1250} was positively correlated between the two growing seasons ($r=0.93$, $P<0.01$) (Table 2). According to two-way ANOVA, HMP_{1250} varied significantly for the genotype (G) and environment (E) at the 1% probability level, but did not vary significantly for $G \times E$ (Table 3). The variance of HMP_{1250} was larger in autumn (22.5) than in spring (11.5) (Table 1).

The LPH values ranged from 23.9 (YR-Seishun) to 29.5 (Early Summer $\times$ Black Leaf Succession) in autumn and from 22.8 (YR-Seishun) to 37.1 (Asashio) in spring (Table 1). The LPH value was positively correlated between the two growing seasons ($r=0.82$, $P<0.01$) (Table 2). The LPH value varied significantly for G, E, and $G \times E$ at the 1% probability level (Table 3). The variance of LPH was larger in spring (17.2) than in autumn (3.8), unlike that of HMP_{1250} (Table 1). 'Asashio' exhibited a marked difference in LPH between the two seasons (7.8) (Table 1). When 'Asashio' was excluded, the $G \times E$ interaction varied significantly but the variance decreased by half (data not shown), indicating that 'Asashio' specifically reacted to the growing seasons.

Relationship between HMP_{1250} and developmental characteristics in the two growing seasons

To determine whether the relationships between HMP_{1250} and the developmental characteristics were similar in the two growing seasons, we compared their correlation coefficients in autumn with those in spring (Table 4). In both seasons, HMP_{1250} was significantly and positively correlated with LPH, and it was significantly and negatively correlated with LSI at higher leaf positions. The petiole length tended

to show higher correlation coefficients at higher leaf positions, and the non-petiole leaf position was significantly and positively correlated with HMP_{1250} in both seasons. Leaf size at the lower leaf positions tended to display higher correlation coefficients in both seasons. In these characteristics, LPH in both seasons was strongly and significantly correlated with HMP_{1250} (Table 2 and Table 4).

Relationship between LPH and leaf developmental pattern

We had already demonstrated that LPH was negatively correlated with LSI in autumn (Tanaka and Niikura 2003). Therefore, we examined the correlation coefficients between the LPH value and leaf characteristics in both seasons to analyze the relationship between the LPH value and leaf characteristics, which might enable to rule out the possibility that the $G \times E$ interaction in LPH (Table 3) would influence the use of LPH as a selection criterion for the parents of early-head-forming cultivars (Table 5). LPH showed an increasingly and strongly negative correlation with LSI at higher leaf positions, especially in spring. It was significantly and positively correlated with the non-petiole leaf position in both seasons.

To determine why the correlation coefficient between LPH and LSI increased with the increase of the leaf position, we investigated the leaf developmental pattern in detail (Fig. 1). In the F_1 hybrid of the cross 'Early Summer $\times$ Black Leaf Succession' in autumn, the primary wrapper leaves showed relatively long petioles. At around the 23rd leaf position, the value of the petiole length had become zero. The LSI value increased with increasing leaf position, in accordance with the increase in LBSI and decrease of the petiole length, up to around the 23rd leaf position, and thereafter the value became stable.

We then examined the developmental patterns of LSI, LBSI and petiole length in 'YR-Seishun', in which the LPH value was the lowest and differed least between the two

Table 1. Duration of head-maturation period to attain 1250 g (HMP_{1250}) and leaf position at which head formation started (LPH) in nine F_1 hybrid cabbage cultivars

Cultivar	HMP_{1250} (days)			LPH		
	Autumn	Spring	Difference	Autumn	Spring	Difference
YR-Seishun	55.5	65.1	9.6	23.9	22.8	-1.1
Yoshin $\times$ Black Leaf Succession (C-009 $\times$ C-324)	59.1	67.3	8.2	25.0	26.2	1.2
Yoshin $\times$ Early Summer (C-009 $\times$ C-341)	61.3	68.4	7.1	25.8	28.9	3.1
YR-Aoba	64.5	68.5	4.0	25.3	23.7	-1.6
Wakamine	65.3	68.7	3.4	27.9	27.4	-0.5
Uji No. 1	66.6	72.0	5.4	26.9	31.1	4.2
Early Summer $\times$ Black Leaf Succession (C-341 $\times$ C-324)	68.2	72.6	4.4	29.5	31.3	1.8
YR-Kinshu-kyoryoku 152	65.7	72.9	7.2	29.0	30.6	1.6
Asashio	72.4	76.9	4.5	29.3	37.1	7.8
Average	64.3	70.3		27.0	28.8	
Variance	22.5	11.5		3.8	17.2	
MS	53.8	25.7		32.4	223	
F	4.6*	28.8**		45.1**	45.9**	

** and *: significantly different at 1% and 5% provability levels, respectively.

Table 2. Correlation coefficients between HMP₁₂₅₀ and LPH in different growing seasons, and correlation coefficients of each parameter between different growing seasons in nine F₁ hybrid cabbage cultivars

		Spring	
		HMP ₁₂₅₀	LPH
Autumn	HMP ₁₂₅₀	.93**	.84**
	LPH	.87**	.82**

** : Significant at 1% level.

Table 3. Two-way ANOVA of the effect of genotype, growing season, and their interaction on the duration of head-maturation period to attain 1250 g (HMP₁₂₅₀) and leaf position at which head formation started (LPH) in nine F₁ hybrid cabbage cultivars

Source	df	MS	
		HMP ₁₂₅₀	LPH
Genotype (G)	8	74.678**	38.213**
Growing season (E)	1	337.947**	30.311**
G × E	8	5.140	8.798**
Error	18	6.235	0.197

** : Significant at the 1% probability level.

seasons, and in ‘Asashio’, in which the LPH value was the second-highest (autumn) or highest (spring) and differed most between the two seasons (Fig. 2). The LSI value in ‘YR-Seishun’ increased earlier than that in ‘Asashio’ in both seasons (Fig. 2A). In ‘YR-Seishun’, the LSI value increased slightly earlier in spring up to around the 15th leaf position, but similarly thereafter in both seasons. In contrast, in ‘Asashio’ the increase in LSI occurred much later above the 15th leaf position in spring than in autumn. LBSI in both cultivars revealed that the developmental patterns were mostly similar between the two seasons, although the LBSI value in ‘YR-Seishun’ was temporarily higher between the 10th and 15th leaf positions in spring than in autumn (Fig. 2B). The petiole length showed markedly different developmental

patterns between the two cultivars (Fig. 2C). The value of the petiole length in ‘YR-Seishun’ decreased to zero at the 18th leaf position in both seasons, whereas that in ‘Asashio’ increased up to a higher leaf position in spring, compared to autumn.

Discussion

We demonstrated that the developmental pattern of early-head-forming cultivars in spring was similar to that in autumn. That is, a low LPH value was necessary for early-head-forming cultivars, indicating that LPH could be a useful selection criterion for the development of early-head-forming spring cultivars. However, it was important to consider the selection season due to the significant G × E interaction for LPH.

HMP₁₂₅₀ showed a strong correlation between the two growing seasons and failed to exhibit a G × E interaction (Table 2 and Table 3). In addition, the patterns of the correlation between HMP₁₂₅₀ and developmental characteristics were similar between the two seasons (Table 4). These results indicated that the developmental pattern of the early-head-forming cultivars in spring was similar to that in autumn as follows: larger primary wrapper leaves, broader leaves at a lower leaf position, and lower LPH value. We previously reported that both head weight and leaf size are significant dominant factors with a low narrow-sense heritability, but that LPH and LSI are additive factors with a high narrow-sense heritability (Tanaka and Niikura 2006). Since we performed the experiments just once in each growing season, the results may not be universal. However, due to the inheritance of LPH, and its strong correlation with HMP₁₂₅₀, LPH could be come an ideal criterion for selecting early-head-forming parents for the breeding of early-head-forming F₁ hybrid cultivars in spring. However, LPH showed a significant G × E interaction between the two growing seasons (Table 3). Therefore, it may not always be possible to develop early-head-forming cultivars in spring

Table 4. Correlation coefficients of the duration of the head-maturation period to attain 1250 g (HMP₁₂₅₀) with developmental characteristics in two growing seasons for nine F₁ hybrid cabbage cultivars

Characteristic	Season	LPH	LSI (width/total length)				LBSI (width/[total length – petiole length])			
			5th ^a	10th	15th	20th	5th	10th	15th	20th
HMP ₁₂₅₀	Autumn	.87**	–.31	–.25	–.59	–.71*	–.22	–.17	.00	.23
	Spring	.94**	–.28	–.59	–.70*	–.70*	–.15	–.46	–.52	–.44

Characteristic	Season	Non-petiole ^b leaf position	Petiole length				Leaf size (width × total length)			
			5th	10th	15th	20th	5th	10th	15th	20th
HMP ₁₂₅₀	Autumn	.69*	–.09	.51	.55	– ^c	–.69*	–.42	–.37	.17
	Spring	.91**	.02	.32	.49	.63	–.41	–.66	–.24	.30

^a Leaf position.

^b Position of first leaf without a petiole.

^c The correlation coefficient for the petiole length at the 20th leaf position in autumn was not calculated, since in most cultivars the value of the length was zero.

** and * : Significant at 1% and 5% levels, respectively.

Table 5. Correlation coefficients of leaf position at which head formation started (LPH) with leaf characteristics in two growing seasons for nine F₁ hybrid cabbage cultivars

Characteristic	Season	LSI (width/total length)				LBSI (width/[total length–petiole length])			
		5th ^a	10th	15th	20th	5th	10th	15th	20th
LPH	Autumn	–.26	–.03	–.49	–.60	–.38	–.36	–.44	–.31
	Spring	–.28	–.68*	–.74*	–.83**	–.12	–.53	–.58	–.56

Characteristic	Season	Non-petiole ^b leaf position	Petiole length				Leaf size (width×total length)			
			5th	10th	15th	20th	5th	10th	15th	20th
LPH	Autumn	.67*	–.15	.32	.35	— ^c	–.74*	–.57	–.65	–.02
	Spring	.83**	.12	.39	.53	.66	–.33	–.54	.04	.56

^a Leaf position.^b Position of first leaf without a petiole.^c The correlation coefficient for the petiole length at the 20th leaf position in autumn was not calculated, since in most cultivars the value of the length was zero.

** and *: Significant at 1% and 5% levels, respectively.

Fig. 1. Leaf developmental pattern of the F₁ hybrid Early Summer × Black Leaf Succession in autumn at 23 days (A) and 85 days (B) after transplanting. Wrapper leaves are arranged in the order of leaf position from top left to bottom right. Bottom right: remainder of the cabbage plant (head, stem, and roots). Scale=40 cm. In (A), the 10th to the 16th wrapper leaves and their petioles are shown before full expansion and elongation. In (B), wrapper leaves below the 18th leaf had withered and dropped off.

simply by using selection based on LPH in autumn. To utilize the efficient autumn selection, we determined whether the G × E interaction in LPH would influence the use of LPH as a selection criterion in plants with a low LPH value in autumn for application to plants in spring as follows.

The G × E interaction was not significant for HMP₁₂₅₀, while it was significant for LPH (Table 3). Meanwhile, the correlation between HMP₁₂₅₀ and LPH was high in both seasons (Table 4). These results may appear to contradict one another. The effect of the temperature may be one of the factors accounting for this discrepancy. LPH is determined in the middle of the growth period, while HMP₁₂₅₀ is determined after a certain time until the head weight reaches 1250 g. Since temperature decreased in autumn (see Results), it is possible that the delay of LPH resulted in the considerable

delay in HMP₁₂₅₀ in autumn due to gradual deceleration of growth. On the other hand, in spring, since the temperature changes were opposite to those in autumn, the delay of LPH may have induced a short delay in HMP₁₂₅₀ due to the gradual acceleration of growth. The late variety ‘Asashio’ showed a large (i.e., 7.8) difference in LPH between spring and autumn, which was the main reason for the G × E interaction. In spring, the delay in the initiation of head formation (i.e., high LPH) in Asashio, however, may not have affected significantly HMP₁₂₅₀, because the period after the initiation of head formation corresponded to the environment of conditions suitable for growth. Comparison of the early variety ‘YR-Seishun’ and late variety ‘Asashio’ showed that the difference in LPH was larger in spring than in autumn (i.e., 14.3 vs. 5.4), while the difference in HMP₁₂₅₀ was

Fig. 2. Developmental pattern of leaves. (A) leaf shape index (width/total length, LSI), (B) leaf blade shape index (width/[total length – petiole length], LBSI), and (C) petiole length in two F_1 hybrids in autumn (solid lines) and spring (dotted lines). The total length is represented by the sum of the leaf blade and petiole lengths. Points and bars denote means and standard deviation of two replications.

smaller in spring than in autumn (i.e., 11.8 vs. 16.9). This opposite trend of the LPH and HMP_{1250} values may account for the discrepancy in the results between the ANOVA and the correlation analysis.

Comparison of the developmental pattern in the LSI between autumn and spring seasons, based on the correlation between LPH and LSI (Tanaka and Niikura 2003; Table 5), showed that the pattern was different between the two seasons below the 15th leaf position in ‘YR-Seishun’ and largely above the 15th leaf position in ‘Asashio’ (Fig. 2). The LPH value in ‘YR-Seishun’ and ‘Asashio’ was at least 22.8 (Table 1), and the correlation between LPH and LSI was stronger at higher leaf positions (Table 5). Thus, the main

factor responsible for the $G \times E$ interaction in LPH was considered to be the seasonal difference in the developmental pattern above the 15th leaf position. Above that leaf position, the developmental pattern of LBSI was not different, while the developmental pattern of the petiole length was clearly different between cultivars and growing seasons (Fig. 2B, C). In addition, LPH was strongly correlated with the non-petiole leaf position in both seasons (Table 5). The value of the petiole length of ‘YR-Seishun’ decreased to zero at almost the same leaf position in each growing season, in the same way as the LPH value remained almost similar between the two seasons. In contrast, since the petiole in ‘Asashio’ was longer at higher leaf positions in spring than

in autumn, the LPH value was markedly different between the two seasons. Thus, the difference in the developmental pattern of the petiole length at higher leaf positions was the main factor for the difference in the developmental pattern of LSI between the two seasons. That is, the varietal difference in the developmental pattern between the LSI and the petiole length may result in a significant $G \times E$ interaction for LPH.

Based on these results, the following method could be used to select parents of spring early-head-forming cultivars. We can utilize LPH as a selection criterion due to the strong correlation between LPH and HMP_{1250} (Table 2 and Table 4), but we need to be aware that the $G \times E$ interaction for LPH might influence that for HMP_{1250} (Table 3). Therefore, it is preferable to select plants with a low LPH value directly in spring than in autumn. However, selection in spring is inefficient, because, due to the seed production conditions, it takes two years from plant selection to the sowing of seeds of offsprings. As previously reported, the narrow-sense heritability of LPH was high (Tanaka and Niikura 2006). In addition, HMP_{1250} in spring was strongly correlated with LPH in autumn (Table 2). Accordingly, it would be most efficient to select plants with a low LPH value in autumn in some generations, and afterwards, select lines based on evaluation in the next spring. Parents developed by the above method might be stable plants with a low LPH value in either environment. Therefore, based on the characterization of the complex nature of early head formation in spring, we suggest that LPH could be a useful selection criterion for the development of early-head-forming spring cultivars. This information should contribute to our understanding of the process in other head-forming vegetables such as lettuce and Chinese cabbage, which show similar developmental patterns of the leaf shape, with leaves becoming wider with increasing leaf position (Bensink 1961, Kato 1964).

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