Relation between Stem Growth Processes and Internode Length Patterns in Sorghum Cultivar ‘Kazetachi’

Akihiro Fujii¹, Satoshi Nakamura² and Yusuke Goto¹

¹Graduate School of Agricultural Science, Tohoku University, Sendai 981-8555, Japan;
²School of Food, Agricultural and Environmental Sciences, Miyagi University, Sendai 982-0215, Japan

Abstract: Sorghum cultivar ‘Kazetachi’ has a unique internode length pattern, with a wavy shape that changes depending on the cultivation environment. It is regarded as a suitable material for analyzing the environmental factors affecting internode elongation. This study was conducted to clarify the relation between the final internode length at harvest and the increment of stem growth to establish a method to elucidate stem growth during the growing season. To confirm the internode elongation pattern, we sampled plants when each leaf had just expanded. The leaf number, plant length, and collar height of plants in the field were measured during the growing season. The internode elongation pattern of ‘Kazetachi’ resembled that reported in sweet sorghum, indicating that the elongation period of each internode can be estimated by recording the leaf number during the growing period. By measuring the plant length and the collar height as an index of stem growth, we can easily estimate the rapid elongation period of internode, which can be a peak or a trough in the internode length pattern during the growing period. The collar height during the growing period can be estimated by measuring the leaf number in the growth stage and recording the length of internodes and leaf sheaths at harvest. Even the plant length can be estimated by adding the leaf blade length to these traits. However, the collar height seemed to be a better index of stem growth than the plant length.

Key words: Collar height, Internode length, Internode length pattern, ‘Kazetachi’, Sorghum bicolor, Stem growth.

In recent years, sweet sorghum (Sorghum bicolor Moench), which accumulates sugar in its stem, has gained much attention as a bioenergy crop. Its sugar yield is closely related to the stem biomass yield (Tsuchihashi and Goto, 2004; Sato et al., 2008; Nakamura et al., 2009). In sorghum cultivated as a foliage crop, the stem is a major organ for harvest. The stem yield is closely related to the stem volume (Nakamura et al., 1997). Therefore, enlargement of the stem volume can engender the increase of the sugar yield and stem dry weight. The stem shape of sorghum affects the stem volume and tolerance for lodging. Factors determining the stem shape include the length and thickness of elongated internode with 1.0 cm or more in final length and the number of internodes, and the arrangement of long and short internodes in a stem.

The internode length pattern, which has been used to express the arrangement of internodes in sorghum (Ayyangar et al., 1938; Nakamura et al., 2010), is defined as the pattern drawn by arranging the internode length from the base to the top, plotting the internode position against the X-axis and the internode length against the Y-axis. Ayyangar et al. (1938) classified the internode length pattern into three types. Recently, the internode length pattern in sorghum cultivar ‘Kazetachi’ was confirmed to have more peaks than that in three types of sorghum (Nakamura et al., 2010).

The internode length pattern of ‘Kazetachi’ has unique characteristics: the positions of peaks and troughs are nearby and the difference in the internode length between the peak and trough is extremely large. In addition, it was reported that the peaks and troughs and the numbers of peaks in the internode pattern were changed depending on the environmental conditions (Nakamura et al., 2010, 2011a). These results suggest that Kazetachi is a suitable cultivar to identify the environmental factors affecting internode elongation.

To analyze the environmental factors influencing internode elongation, we need to ascertain the internode length pattern at harvest first. Then, when and how the long and short internodes constituting the internode length pattern elongated during the growing period must be elucidated. However, the internode length can not be
measured directly because the internode is enclosed by leaf sheaths. In normal sweet sorghum cultivars, the relation between the leaf expansion and the internode elongation, namely the elongation pattern of internodes, was clarified (Goto et al., 1994; Nakamura et al., 1995). We can estimate how internodes are elongated using this relation. The internode length pattern of ‘Kazetachi’, however, is different from that of general sweet sorghum cultivars; the position of a long internode is near the position of the short internode. It is necessary to examine whether the elongation pattern of internodes in ‘Kazetachi’ is consistent with that reported by Goto et al. (1994). Furthermore, to analyze the influence of environmental factors on internode elongation, we need to confirm whether the elongation pattern estimated in ‘Kazetachi’ corresponds with that actually recorded in growth research. If we are able to know the final length of internodes during the plant growing period, it would be easy to find the factors influencing the internode elongation.

In this study, we examined the elongation pattern of internodes of ‘Kazetachi’ and confirmed that the elongation pattern of internodes in sweet sorghum can adapt to that of ‘Kazetachi’. Furthermore, based on these results, we estimated the time of each internode elongation in ‘Kazetachi’ and analyzed the correlation of the value shown by the collar height and the plant length in the process of stem elongation and the final length of the internodes elongated during a given period.

**Materials and Methods**

Sorghum cultivar ‘Kazetachi’ was used in this study. Seeds were sown on 19 May, 2010 in an experimental field of Miyagi University, Sendai, Japan (38°13’ N, 140°48’ E). The seedlings were thinned to 1 plant per hill with 0.85 and 0.15 m spacing between and within rows. Slow-release fertilizer with 12 g m⁻² nitrogen (N), 10.6 g m⁻² phosphate (P₂O₅), and 12 g m⁻² potash (K₂O) and quick-acting fertilizer with 4 g m⁻² N, 4 g m⁻² P₂O₅, and 4 g m⁻² K₂O were applied as basal fertilizer before sowing.

1. Growth research and measurement of the final internode length

   Plant length, collar height, and leaf number on the main stem were recorded from 17 June at about 7 day intervals. The leaf number was defined as the fully expanded leaf number, not including expanding leaves. Tsuchihashi and Goto (2005) measured the height from the soil surface to the collar of the youngest expanded leaf as one parameter of stem elongation. They designated it as the stem length. In this study, the collar height of the youngest expanded leaf was measured for the same purpose, but named it collar height because the height did not represent the stem length precisely.

   To obtain the final length of all elongated internodes, we sampled 20 plants measured during the growth period at harvest and recorded the lengths of each internode.

2. Internode position, peak and trough in internode length pattern, and plant age indicated by leaf number

   The node with the n-th leaf sheath was defined as the n-th node. The internode between the n-th node and (n + 1)-th node was defined as the n-th internode (INₙ). The internode position of the peak in the internode length pattern was defined as that with the internode longer than the adjacent higher or lower internode. The internode position with a trough in the pattern was defined as that with an internode shorter than the adjacent higher or lower internode. The length of leaf sheaths on the main stem was measured at harvest, whereas the length of leaf blades was measured during the growing period.

   To analyze the elongation pattern of internode, we used the method by which the plant age was indicated by the leaf number on the main stem (Goto et al., 1994; Nakamura et al., 1995). The age in leaf number (AL) is represented by ALₙ at which the n-th leaf blade has just expanded. The AL is represented as a natural number, but we used AL as a continuous numerical value.

3. Sampling of plants for analysis of ‘Kazetachi’ elongation patterns

   To examine the elongation pattern of internode in ‘Kazetachi’, 12 plants were sampled when the 10th, 13th, 16th, 19th, 22nd, 23rd, 24th and 25th leaf had just fully expanded. At each sampling, lengths of internodes were measured by removing leaf sheaths. Length of internodes in the apical region of a stem was measured using a stereoscopic microscope.

![Fig. 1. Internode length pattern based on internode positions IN 9 – IN 32, drawn by averaging the internode lengths of 20 plants. Four distinct peaks and 4 troughs were designated as pA through pD upward (enclosed by a solid line) and tA through tD (enclosed by a dotted line), respectively. Vertical bars represent the standard error.](image-url)
Results

1. Final lengths of internode, leaf sheath, and leaf blade

The lowest position of elongated internode, which was 1.0 cm or longer in final length, ranged from IN 7 – IN 9. The percentages of plants in the lowest elongated internode position were 25% in IN 7, 55% in IN 8, and 20% in IN 9. The position of the neck internode immediately below the panicle ranged from IN 33 to IN 38.

The average length of internodes from IN 9 – IN 32, not including the internode less than 1.0 cm at the base and the neck internode, is presented in Fig. 1. The internode length pattern drawn by the average length at each internode position had four peaks (pA – pD) and four troughs (tA – tD).

Fig. 2 shows the lengths of leaf sheath and leaf blade of L 10 (the tenth leaf) to L 32, not including the leaf attached to the non-elongated internode and the flag leaf. Differences in length among positions were smaller in the leaf sheath than in the leaf blade. The leaf blade length increased as the leaf position rose to L 16, was slightly decreased in L 17 and L 18, increased again in L 21, and decreased gradually above this leaf position.

2. Plant growth

Changes in the expanded leaf number on the main stem from 21 June (33 days after seeding; 33 DAS) to 29 September (133 DAS) are depicted in Fig. 3a. Increase in leaf number can be approximated two straight lines: \( y = 0.27x - 1.72 \) (i) and \( y = 0.15x + 8.9 \) (ii) (y represents the leaf number and x represents DAS). The leaf number increased at a rate of 0.27 d\(^{-1}\). In other words, it expanded at a rate of 3.7 d per leaf expansion during the vigorous growth stage. The leaf number increased until mid-October, although the plant length almost stopped increasing in late September. The flag leaf number on the main stem in ‘Kazetachi’ was 33 – 38, with the average number of flag leaves as 36.1 ± 0.2.

Changes in plant length and collar height are depicted in Fig. 3b. Although the growth curves of plant length and collar height seemed to be sigmoidal, we approximated them to some straight lines in order to understand plant growth easily. Increase in plant length was approximated to two straight lines: \( y = 3.9x - 80.2 \) \( (R^2 = 0.996) \) (iii) and \( y = 0.9x - 216.6 \) \( (R^2 = 0.996) \) (iv). However, the increase in collar height was approximated to three straight lines: \( y = 1.4x - 38.5 \) \( (R^2 = 0.989) \) (v), \( y = 3.9x - 184.5 \) \( (R^2 = 0.989) \) (vi) and \( y = 1.3x + 67.9 \) \( (R^2 = 0.988) \) (vii). According to the approximate equations of (iii) and (vi) during vigorous growth from 19 July to 21 August, both the plant length and collar height increased at 3.9 cm d\(^{-1}\). During this period, 10 leaves from L 15 to L 24 expanded. These leaf blades were not so different in length (Fig. 2). The plant length and collar height at harvest were 333 ± 2 cm and 291 ± 4 cm, respectively.

The increase rates of plant length and collar height fluctuated during the growth period. The changes in the increase rate of leaf number, plant length and collar height
during July – September were depicted in Fig. 4a and Fig. 4b. The increase rate of leaf number was greatest during late July – early August. The increase rate of plant length remained nearly constant until 19 July, but it declined, thereafter and increased again from 28 July to 6 August. Subsequently it decreased with fluctuation. The increase rate of collar height increased gradually until 28 July to 6 August, and thereafter was almost identical to that of plant length. The increase rate of leaf number, plant length and collar height were the highest from 28 July to 6 August and the lowest from 31 August to 9 September. The large difference in increase rate between the plant length and the collar height up to 19 July may be attributed to the high increase rate of leaf blade length from L 10 to L 15 (Fig. 2). The maximum and minimum values of the increase rate were 0.32 d\(^{-1}\) and 0.1 d\(^{-1}\), respectively, in leaf number, 5.99 cm d\(^{-1}\) and 0.63 d\(^{-1}\) in plant length, and 5.55 cm d\(^{-1}\) and 0.82 d\(^{-1}\), respectively, in collar height. The ratio of the max/min increase rate was 3.2 in leaf number, 9.5 in plant length, and 6.7 in collar height. From 28 July to 6 August, the ratio of the max/min increase rate in leaf number was lower than that in plant length and collar height.

3. Elongation pattern of internode of ‘Kazetachi’

We investigated the elongation pattern of IN 11 to IN 25 by dissecting the sampled plants. To integrate the results of elongation pattern in each internode, we generalized the elongation pattern of internodes using the method reported by Nakamura et al. (2011b).

We describe here the generalization of the elongation pattern of internodes by using IN 11, IN 14, IN 17, and IN 20, which elongated in a stem at different time during growing period, as examples. First, the length of each internode was plotted against AL (age indicated by leaf number) as a time scale (Fig. 5a). Then, each internode position was regarded as \(n\) and each AL was expressed by \(n\) (Fig. 5b). For example, for the lengths of IN 11, AL 11 and AL 14 were denoted by AL \(n\) and AL \((n + 3)\), respectively, and for the lengths of IN 14, AL 14 and AL 17 were also denoted by AL \(n\) and AL \((n + 3)\), respectively. The expression of AL using \(n\) enabled us to compare elongation process of internodes at different internode positions (Fig. 5b). Next, the ratio of the internode length to the final length at harvest (elongation ratio of internode) was plotted against AL using \(n\) Fig. 5c. The ratio enabled us to compare
elaboration pattern of internodes with different final lengths. Such generalization of the internode elongation pattern permits us to compare the elongation pattern of each internode with different final lengths.

The elongation ratio of IN 11 through IN 25 was plotted against AL using $n$ (Fig. 6). The internode elongation curve of sweet sorghum reported by Goto et al. (1994) is also depicted in Fig. 6. This curve was coincident with the curve produced based on all elongated internodes except uppermost internodes, using in some different sweet sorghums grown in different years (Nakamura et al., 1995; Nakamura and Goto 1996). Variation in the elongation ratio of internode of ‘Kazetachi’ would be large at the internode position, which has large variation in final length. Then, the internodes with less than 20% and 20% or more in coefficient of variation of elongation ratio were denoted using black symbols and white symbols, respectively. Fig. 6 shows that these symbols of the elongation ratio were distributed near the internode elongation curve in ‘Kazetachi’.

**Discussion**

1. **Relation between leaf expansion and internode elongation (Internode elongation pattern)**

The internode elongation curve in ‘Kazetachi’ resembled that reported by Goto et al. (1994). The results obtained using AL as a time scale suggests that all internodes with different final lengths have the same internode elongation curve during the elongation period.

Fig. 7 shows the status of internode elongation wrapped with the sheath based on the internode elongation curve reported by Goto et al. (1994). Although elongating internodes enclosed by leaf sheaths are not visible from the outside, this diagram is depicted based on leaf expansion, which can be judged from the appearance. This schematic diagram represents the status at the time AL when the $p$-th leaf blade has just expanded. The internode between the $n$th and $(n+1)$-th node was defined as the $n$-th internode (IN $n$). The collar height was defined as height from ground surface to the collar of youngest expanded leaf.

Fig. 6. Relation between elongation ratio IN 11 – IN 25 to their final length and age indicated by leaf number (AL) in ‘Kazetachi’. The solid line represents the elongation pattern of internode reported for sweet sorghum (Goto et al., 1994).

Fig. 7. Schematic diagram showing the growth of stem, enclosed by leaf sheaths, consisting of elongating and elongated internodes when the $p$-th leaf blade has just expanded. The internode between the $n$th and $(n+1)$-th node was defined as the $n$-th internode (IN $n$). The collar height was defined as height from ground surface to the collar of youngest expanded leaf.

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### 2. Internode length pattern based on growth research

To examine the relation between internode elongation patterns and plant growth, it is necessary to ascertain when each internode elongates. For this purpose, the date of the rapid elongation of each internode, AL $(n+2)$ in Fig. 5,
was estimated from the number of leaves, which is the number of fully expanded leaves in this study. Therefore, the age of the plant with the number of leaves \( m \) is not younger than \( AL_\text{m} \), but less than \( AL_\text{m} + 1 \) in plant age, as indicated by the leaf number. Therefore, when the mean number of leaves is \( m \), the plant age is \( AL_\text{m} + 0.5 \). Based on this relation, the day on which the plant age is \( AL_\text{n} + 2 \) is regarded as the day when the number of leaves is \( n + 1.5 \). The date of the rapid elongation period was obtained. For example, the method to estimate the date of the rapid elongation period of IN 17 is presented in Fig. 8. The rapid elongation period of IN 17 is AL 19, and 18.5 by leaf number. It can be estimated as 31 July by the date according to the diagram of the leaf number change.

Fig. 9 shows the date of the rapid elongation period of IN 9 – IN 28, and the final internode length of each internode. It also shows the increase rate of plant length and that of the collar height shown in Fig. 4b. The date of rapid elongation of internode IN 17, which is at the highest peak \( pB \) in the internode length pattern (Fig. 1) was 31 July, which matched the time when the increase rate of plant length and that of collar height were at the maximum. In addition, the rapid elongation period of the second peak \( pC \) (IN 21) was 13 August – 21 August, when the rates of plant length increase and collar height increase were the second highest. Moreover, the rapid elongation period of at the large trough \( tC \) (IN 25) in the internode elongation pattern was 9 September, which matched the time when the rate of plant length increase and the rate of collar height increase were at the minimum. These results suggest that we can estimate the time when the elongating internode would be a peak or a trough in the internode length pattern by recording plant length and collar height. However the plant length includes the length of the upper leaf blade that increased with the rise in leaf position. During 1 – 12 July, the short internode of IN 9 to IN 11 at the basal stem elongated, but the rate of plant length increase was high because the expanded leaf blade length increased during this period. This result shows that the collar height is better than the plant length as a marker of the stem growth. Furthermore, it is easy to measure the collar height in a field compared with the plant length including the upper leaf blade length. Thus, the collar height may be a better index to ascertain the relation between the conditions of stem growth and the internode length pattern compared with the plant length.

Fig. 10 shows the collar height increase divided by the leaf number increase (increase rate of collar height per leaf), which is graded as the value to show how long the collar height elongates per leaf expansion. This ratio would correspond to the increase rate of stem on the time scale of plant age. In addition, the final lengths of IN 9 – IN 28 which were rapidly elongating on each date (Fig. 9) are also presented in Fig. 10. Stem elongation, which included two or three internode elongation, expressed by the increase rate of collar height per leaf expansion, overlapped with the final length of internodes in most periods. This graph roughly illustrates the internode length pattern, although we were unable to estimate the pattern of internode length accurately.
3. Estimating plant growth based on the internode length pattern

Here, we estimated the stem growth based on the internode length pattern, namely, the collar height and the plant length at each plant age were estimated using the length of internode and leaf sheaths at harvest and the elongation pattern of internodes. Then the estimated collar height and plant length were compared with those recorded in the field. The collar height at the time when \( L_p \) just expanded was the height from the soil surface to the collar of \( L_p \). This height corresponds to the total length of the leaf sheath of \( L_p \) and the lower internodes including from the lowest elongated internode to IN \((p-1)\) (Fig. 7). Each internode length was as shown in Fig. 7, and the length of leaf sheath of \( L_p \) was estimated as about 90% of the final length at AL \( p \) (Nakamura et al. 1995). Therefore, the collar height at AL \( p \) is calculated using the following equation: 
\[
\text{Length of IN } (p-1) \times 0.15 + \text{Length of IN } (p-2) \times 0.6 + \text{Length of IN } (p-3) \times 0.9 + \text{Total length of IN lower than IN } (p-3) \text{ except the non-elongated internodes underground} + \text{Length of leaf sheath of } L_p \times 0.9.
\]

To estimate the plant length, the relation between the lengths of leaf blade of \( L_p \) and \( L_{(p-1)} \) should be considered. The leaf blade length of \( L_p \) and that of lower leaves has already reached its final length at AL \( p \) (Nakamura et al., 1995). Therefore, when the leaf blade length of \( L_p \) is equal to or longer than that of \( L_{(p-1)} \), the plant length at AL \( p \) is calculated using the total length of the collar height at AL \( p \) and the length of leaf blade of \( L_p \). When the length of leaf blade of \( L_{(p-1)} \) is longer than that of \( L_p \), the plant length at AL \( p \) is calculated using the total length of the leaf blade and leaf sheath of \( L_{(p-1)} \) and the internode from the lowest elongated internode to IN \((p-2)\). When the length of the leaf blade lower than \( L_{(p-1)} \) is longer than that of \( L_p \), the plant length from the ground surface to the tip of the leaf lower than \( L_{(p-1)} \) and the length from the ground surface to the tip of leaf of \( L_p \) are calculated using the above method; then the plant length is determined as the longer length.

The date when the plant age became AL \( p \) is regarded as the date when the number of leaves was \( p - 0.5 \) using the relation between the plant age and the number of leaves described above (Fig. 3a).

Fig. 11a shows the estimated collar height depicted in Fig. 3b, overlaid on the recorded collar height. Fig. 11b shows the estimated plant length, depicted in Fig. 3b, overlaid on the recorded plant length. The estimated collar height and the estimated plant length were almost consistent with the recorded collar height and the recorded plant length, respectively. These results suggest that the measured leaf number can estimate the collar height during the growing period using the internode length pattern and the length of leaf sheaths at harvest. In addition, recording the length of leaf blades can estimate the total length of the leaf blade and leaf sheath of \( L_{(p-1)} \) and the internode from the lowest elongated internode to IN \((p-2)\).
We next examined whether the number of leaves can be estimated or not using the recorded data of the plant length and collar height during the growing period. Fig. 12 shows the leaf number changes estimated from the collar height and the plant length, overlaid on the recorded leaf number. The estimated leaf number was obtained using the following procedure: first, the plant length and the collar height at AL_p were estimated using the data of the lengths of internodes, leaf blade and leaf sheath. Next, the date when the estimated plant length and collar height reached its length was acquired in Fig. 3b based on the assumption that the plant length and collar height increased linearly between the adjacent dates recorded. The leaf number on the date was estimated from Fig. 3a similarly and the estimated leaf number at that time was regarded as L (p = 0.5). Fig. 12 shows that the leaf number estimated from plant length and collar height were almost consistent with the recorded leaf number.

4. Plant length and collar height

As described above, measuring the collar height as an index of stem growth allowed us to confirm the rapid elongation period of the internode, which would be at the peak or trough in the internode length pattern, at the time of measurement. In addition, the elongation period of each internode after harvest could be estimated by recording the number of leaves during the growing period and using the internode elongation pattern. Furthermore, the internode length pattern was roughly drawn by measuring the leaf number and the collar height. In contrast, the stem growth was estimated from the internode length pattern. In this case, when the data of the leaf sheath length were obtained, the collar height was estimated from the recorded leaf number. The leaf number also was estimated from data of the collar height recorded after we harvested the measured plants. Similarly, when the leaf blade length data were obtained, the leaf number was estimated from the recorded plant length. The plant length was estimated from the recorded leaf number.

Results show that this method of analyzing sorghum growth with coordination of growing and harvest surveys, which we described above, enables us to ascertain exactly when and how each internode elongated. Considering these results, the collar height represented the stem growth. It was easier to measure the plant length when plants were taller. Furthermore, results suggest that the collar height was more useful as the index of stem growth than the plant length because estimating the plant length required the measurement of leaf blade length, which was often damaged or lost because of events such as strong winds, insect infestation during the growing period, and also because leaf blade length measurements, require considerable labor and subject the plants to more stress due to handling.

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