Analysis of Successive Internode Growth in Sweet Sorghum Using Leaf Number as a Plant Age Indicator

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Abstract: In sweet sorghum, which is a potential biomass crop, the diameter of internode is an important component of stem yield. However, the thickening of successive internodes is poorly understood. The objective of this study was to clarify the relationship between the thickening of successive internodes using the age indicated by the leaf number on the main stem (AL) as a time scale. Furthermore, the relationship between the elongating and thickening period of successive internodes along the stem was analyzed. Internodes were collected from AL3, when the 3rd leaf had just expanded above the 2nd leaf sheath, to AL17, and at 9 weeks after heading as final harvest. Although the internode thickening patterns based on AL could not be combined into one or a few patterns, a significant correlation (P<0.001) was found between internode position and AL at which the internodes were thickening, suggesting that a regularity of internode thickening existed among successive internodes. The higher the internode position, the longer the first half of the thickening period (from 15% to 50% of thickening), whereas the period of the second half (50%–85% thickening) was constant irrespective of internode position. These results suggest that the degree of the elongation and thickening of successive internodes can be estimated by using AL.

Key words: Age in leaf number, Growth curve, Internode position, Internode thickening, Sorghum bicolor Moench, Stem growth, Sweet sorghum.

Sweet sorghum (Sorghum bicolor Moench) is a type of cultivated sorghum with a high sugar content in the juicy stems (Coleman, 1970). Although it is mainly used as a foliage crop for feeding livestock or as a sugar crop for making syrup (Coleman, 1970; Doggett, 1988), it is also a potential biomass energy crop (Monk et al., 1984; Smith and Buxton, 1993). Sugar extracted from its stem is convertible into ethanol for use as biofuel (Smith et al., 1987). A gasification method for efficiently converting the dry mass into methanol has been investigated (Nakagawa et al., 2007). Using this method, structural carbohydrates of the stem can also be used as biomass energy. A better understanding of the growth of stem would contribute to the establishment of a cultivation method for increasing stem yield.

Leaf emergence has been used as an indicator of the development and growth of some grasses. In rice (Oryza sativa L.), the intervals of leaf emergence (phyllochron) and leaf initiation (plastochron) always have the same duration; it takes 5 plastochrons for a leaf to reach full length after its initiation (Kaufman, 1959; Yamazaki, 1963a; Matsuba, 1991). The synchrony between plastochron and phyllochron is strong regardless of environmental factors such as temperature (Chonan, 1967), nutrition (Yamazaki, 1963b), or plant density (Yamazaki, 1963b). Thus, the phyllochron is a good index of the plastochron in vegetative rice shoots (Nemoto et al., 1995). Furthermore, the leaf number of initiated leaves at the shoot apex can be accurately estimated without dissection from the leaf number of emerging leaf during vegetative stage in rice. In rice, the plant age in leaf number on the main stem is used as an indicator and as a time scale of the growth. The plant age is expressed by the number of emerged leaves and the ratio of the visible length of an emerged leaf to its final length. For example, a plant age of 6.5 means that 6 leaves are fully emerged and the seventh leaf has emerged to half of its final length. The decimal fraction of the plant age changes continuously because there is only one emerging leaf in the rice plant. In maize (Zea mays L.), which has several emerging leaves, V (vegetative) stages are used to describe the growth stage during the vegetative period (Hicks and Thomison, 2004). The V stage is defined by the
number of leaves that are developed or extend from the whorl; in other words, the V stage is described only by the number of emerged leaves (collar visible leaves) on the main stem. For example, a V6-stage plant has 6 collared leaves, indicating that the V6 stage refers to the period from the appearance of the sixth leaf collar to that immediately before the appearance of the seventh. Unlike plant age used in rice, the V stage does not have a time scale that expresses the time between the emergence of 2 successive leaves—this is why the V stage is insufficient for analyzing the growth process of organs such as internodes in detail.

Sweet sorghum has several leaves emerging from a whorl like maize; therefore, the age of sweet sorghum is defined by the exact time the leaf collar on the main stem appears from the preceding leaf collar and is represented by the number of collared leaves (Goto et al., 1994). Using age as an indicator of the growth of sweet sorghum, a close relationship was obtained between age and the elongation of successive internodes (Goto et al., 1994). Furthermore, the same relationship was observed regardless of cultivar (i.e., early- or late-maturing cultivars) or planting density (Goto et al., 1994). These results indicate that it is possible to estimate the degree of internode elongation in sweet sorghum by using its age.

In sweet sorghum, the period of internode thickening is longer in the plants growing at a lower density (Goto et al., 1994). The difficulty in detecting very small changes in diameter compared with the lengths of internodes above ground has hindered the studies of internode thickening. The diameter of the internode is an important component of stem yield; the larger internod diameter contributes to increased stem yield and lodging tolerance.

In this study, we examined the relationship between the thickening of successive internodes, including basal short internodes, and the age shown by the collared leaf number in sweet sorghum and evaluated whether the extent of internode thickening can be predicted by using the plant age in leaf number. We also examined the relationship between internode elongation and age to confirm the results of our previous study and to understand the relationship between the elongating and thickening periods of successive internodes along the stem. To detect relatively small changes in internode thickening, we used a cultivar, ‘Wray’ (Broadhead et al., 1981), which has a high stem yield and high sugar contents; it also has smaller variations in stem characteristics, such as internode length and diameter than the other cultivars that we examined previously.

Materials and Methods

Sweet sorghum (Sorghum bicolor Moench) cultivar ‘Wray,’ a medium- to late-maturing variety, was grown in the experimental field of Tohoku University, Sendai, Japan (38°16′ N, 140°52′ E) in 2007. Wray is widely grown from cold regions (Nakamura et al., 2009) to tropical regions (Tsuzuki and Goto, 2004). Slow-release fertilizer with 12 g N m⁻², 10.6 g P₂O₅ m⁻², and 12 g K₂O m⁻² was applied. The seeds were sown on June 6, and the seedlings were thinned to one plant per hill with 0.85 and 0.15 m spacing between and within rows, respectively (about 78,400 plants ha⁻¹).

To analyze the elongation and thickening of individual internodes, we used the method reported by Nakamura et al. (1995) in which the age was indicated by the leaf number on the main stem. For example, the age in leaf number (AL) is represented by AL n at which the n-th leaf blade has just expanded. The leaves of plants grown in the field were labeled at every 3 or 5 leaf positions with a marking pen to determine the leaf and internodal positions of the plant at the time of sampling. The mean number of leaves on the main stems in 507 plants that we marked was 18.8. Plants with 19 leaves on the main stem accounted for 62% of the marked plants (Table 1). Plants with a large number of leaves on the main stem tend to have thick internodes (Nakamura et al., 1997). Accordingly, plants with 19 leaves were analyzed to minimize the variation of internode size caused by the difference in the number of leaves on the main stem. Among the samples, 15% and 100% of plants had young panicles at AL9 and AL10, respectively. Therefore, the transition to the reproductive phase would occur between AL9 and AL10.

Stem samples were collected from AL3 (13 d after seeding; 13DAS) to AL17 (66DAS). Ten to16 plants were collected at each AL and at 9 weeks after heading (final sampling). A significant correlation was found between AL and DAS (r=0.242X+0.262, where Y represents AL and X represents DAS; r=0.995, P<0.001), indicating that 1 AL corresponds to 4.1 d.

Samples plants were dissected to measure internode length, which was defined as the length between the two consecutive nodes with attached leaf sheaths, and the diameter, which was defined as the distance between the opposite sides with axillary buds in the middle of the internode segment.

The internode enclosed within the n-th leaf sheath was defined as the n-th internode (IN n); and the node with the n-th leaf sheath was defined as the n-th node (Nakamura et al., 1995; Nakamura and Goto, 1996). Fig. 1 shows a longitudinal section of the basal part of a sweet

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Table 1. Distribution of the total number of leaves on the main stem of sweet sorghum grown in the field.

| Total number of leaves | 17 | 18 | 19 | 20 | 21 |
|------------------------|----|----|----|----|----|
| %                      | 1.0| 28.6| 61.5| 8.5| 0.4|

Among the 507 marked plants, 62% had 19 leaves.
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sorghum stem. IN1–IN5 at the base of the stems were remarkably short, and designated as “non-elongated internodes” (non-EINs), whereas the longer internodes above the non-EINs were designated as “elongated internodes” (EINs) by Nakamura and Goto (1996).

The lengths and diameters of internodes in the apical region of the stem were measured using a stereoscopic microscope. The final lengths and diameters of IN5–IN19 were measured at the final harvest, whereas those of IN1–IN4 were measured during sampling when the size reached a plateau, because their accurate final lengths were not obtainable at the final harvest.

Results and Discussion

1. Internode length and diameter at final harvest

The final lengths and diameters of IN1–IN19 are presented in Fig. 2. IN1–IN3 were classified as non-elongated internodes (non-EIN) <1 cm long (Nakamura and Goto, 1996), and internodes IN6–IN19 were classified as elongated internodes (EIN) ≥1 cm long; the length of IN6 was slightly greater than 1 cm (1.25 cm). From IN7 to IN10, the internode length increased exponentially. The length of IN10–IN18 was between 20.6 (IN16) and 27.9 cm (IN18). The length of IN19, which was a neck internode of the panicle, was the longest (50.3 cm). This profile of internode length was similar to that measured by Goto et al. (1994). The internode diameter increased rapidly from IN1 to IN6; IN8 actually exhibited a peak in diameter (2.00 cm), and the diameter decreased gradually to IN19 above this internode position.

The plants used in this study were uniform in size; coefficients of variation (CV) of length and diameter of IN1–IN19 are shown in Table 2. The CV of the length was >20 in IN5 and IN7, but these values are much smaller than those reported by Nakamura and Goto (1996). The CV of diameter was <10 in all internodes (Table 2). The plants used were uniform in size probably because we used cultivar ‘Wray’ and plants with the same total leaf number.

2. Generalization of elongation pattern of internode

Fig. 3 shows the lengths of IN1–IN19 at AL3–AL17. The length of IN1 had already reached its final length at AL3, and the length of IN2 was in the early stage of elongation at AL3 (Fig. 3a), although the lengths of IN14–IN19 had not reached their final length at AL17 (Fig. 3b). In order to analyze the characteristics of elongation patterns in

| Internode position | Length (cm) | Diameter (cm) |
|--------------------|-------------|---------------|
| 1                  | 2           | 3             |
| 4                  | 5           | 6             |
| 7                  | 8           | 9             |
| 10                 | 11          | 12            |
| 13                 | 14          | 15            |
| 16                 | 17          | 18            |
| 19                 |             |               |

Table 2. Coefficient of variation of length and diameter of IN1 to IN19 in sweet sorghum.

Fig. 1. Photograph of a longitudinal section of a sweet sorghum stem. At the base, the stem consists of short internodes (IN1–IN5) <1 cm long called non-elongated internodes (non-EINs). The internode enclosed within the n-th leaf sheath that is attached to the n-th node is defined as the n-th internode.

Fig. 2. Length and diameter of IN1–IN19 in sweet sorghum. Data of IN1–IN4 and IN5–IN19 were collected from plants that had achieved their final size and from plants at harvest, respectively. Vertical bars represent the standard error of the mean.
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detail, we generalized the elongation pattern of internodes IN3–IN13, which showed a sigmoidal curve using the value of $A_{\text{L}n}$, which represents the age at which the $n$-th leaf enclosing the $n$-th internode has just expanded. Fig. 4a shows the internode length shown in Fig. 3 as a function of $A_{\text{L}n}$. For example, the lengths of IN10 at $A_{\text{L}10}$ and $A_{\text{L}13}$ were regarded as those at $A_{\text{L}n}$ and $A_{\text{L}(n+3)}$, respectively, and the length of IN8 at $A_{\text{L}8}$ and $A_{\text{L}11}$ were also regarded as $A_{\text{L}n}$ and $A_{\text{L}(n+3)}$. Next, the ratio of the internode length to final length at each $A_{\text{L}}$ was calculated using the maximum lengths of the internodes in the elongation curve as the final length (Fig. 4b). The elongation curves in this figure were classified into 2 patterns: one for IN3–IN6 and the other for IN7–IN13.

IN3–IN6 elongated rapidly from $A_{\text{L}(n+1)}$ to $A_{\text{L}(n+2)}$ and IN7–IN13 from $A_{\text{L}(n+1)}$ to $A_{\text{L}(n+3)}$; the former and the latter patterns respectively resemble the non-EIN and EIN elongation patterns in our previous report (Nakamura and Goto, 1996) using early- and late-maturing varieties. However, IN6, which was classified into EIN in the present experiment, showed the same elongation pattern as that of non-EINs in the previous study. Further studies including observations of the intercalary meristem are needed to distinguish non-EINs from EINs.

The pattern of internode elongation on the basis of $A_{\text{L}}$ supports the idea that the elongation pattern of internodes is almost identical irrespective of variety; except the internodes near the non-EIN threshold (Nakamura and Goto, 1996). Regarding maize, Fournier and Andrieu (2000) reported that the emergence of the sheath attached to the internode appeared to be a trigger for the transition from phase I, during which elongation was exponential, to phase II, which was short and during which elongation occurs rapidly. This time of leaf sheath emergence corresponds to $A_{\text{L}(n+1)}$ in this study. The $A_{\text{L}(n+1)}$ is the time when IN $n$ is at the beginning of the linear elongation corresponding to phase III in maize, during which the elongation rate is nearly constant and the internode length increases linearly (Morrison et al., 1994). In sugarcane, Ono (1990) reported that the internode length reached 20% of the maximum length at the time when the leaf emerged. Therefore, leaf emergence is a useful time scale for understanding the internode elongation of poaceous crops that have many elongated internodes such as maize, sugarcane, and sweet sorghum.
This is supported by the observation that the number of unexpanded leaves >1 mm in the whorl tends to increase as the plant ages (Nakamura et al., 1996).

The slope of the thickening curve in the first half of the thickening period of an internode tended to be more gradual than that in the second half (Fig. 6b). It seems likely that extension of cell size would preferentially occur rather than increase in cell number during the second half of the thickening period.

4. Comparison of internode thickening periods

In order to estimate the thickening periods of each internode (IN4-IN15), the ALs at which the thickening ratio of each internode was 15% (early), 50% (middle), and 85% (final stages of internode thickening) were obtained from the point of the intersection each individual thickening curve with each ratio of thickening (15, 50, and 85%) shown in Fig. 6b. The ratios of thickening of IN14 and IN15 were calculated by using data of their maximum diameter at the final harvest and are shown in Fig. 7. The longitudinal distance in Fig. 7 indicates the period based on AL.

The shortest thickening period (from the early to final stage) was 3.54 AL (15% at AL4.06, and 85% at AL7.60) in IN4, whereas the longest thickening period was 5.86 AL.
(15% at AL11.01 and 85% at AL16.87) in IN15. The higher the internode position, the longer tended to be the thickening period. IN7 through IN15, which account for most of the stem yield, exhibited a significant correlation ($P<0.001$) between internode position and the AL at which the thickening ratio was 15%, 50%, and 85% in sweet sorghum. The thickening ratio is the ratio of the diameter of the internode at AL (shown by $n$). Successive internodes on the basis of AL is helpful for identifying the cause of the difference in the thickening rates between the first half and second half, and between internode positions.

To study the thickening period of internode in detail, we divided the thickening period into the first half and second half, which were defined as the periods with thickening ratios of 15–50% and 50–85%, respectively (Fig. 8). The first half of the thickening period was the shortest in IN4 (1.78 AL) and longest in IN13 (3.52 AL). A significant correlation was found between internode position and the period of the first half based on AL. ($Y=0.195X+0.88$, $r=0.993$, $P<0.001$, where $Y$ is the period of the first half based on AL and $X$ is the internode position). In contrast, the period of the second half of the thickening period was almost constant in all internodes (average 1.86 AL). These results suggest that the increase in the thickening period from the early to final stages was mainly due to the increase in the first half of the thickening period.

The final diameter (Fig. 2) and the period of the first and second halves based on AL were used to calculate the thickening rate per 1 AL (corresponding to 1 phyllochron) in the first and second halves for IN7 (19.2 mm in final diameter) and IN11 (18.9 mm), which had similar diameters; the estimated thickening rates of IN7 in the first and second halves were 3.00 and 3.61 mm in diameter per AL, respectively, while those of IN11 were 1.72 and 3.16 mm per AL, respectively. Further study is needed to identify the cause of the difference in the thickening rates between the first half and second half, and between internode positions.

### 5. Relationship between stem growth and the age in leaf number

The relationship between the age in leaf number (AL) and the growth of IN4–IN13 is summarized in Fig. 9. The elongation period of IN4–IN6 is represented by the period from AL $n$ to AL ($n+2$); and that of IN7–IN13, by the period from AL ($n+1$) to AL ($n+3$), where $n$ represents the internode position. The thickening period of IN4–IN6 was calculated using the data shown in Fig. 7; and that of IN7–IN13, using the formulas shown in Fig. 7.

Generalizing the elongation and thickening patterns of successive internodes on the basis of AL is helpful for understanding the stem growth in sweet sorghum (Fig. 9). For example, in IN5 (a non-EIN), elongation and thickening start at around AL5; rapid elongation ceases at around AL7. Its thickening subsequently continues until around AL8.5. In IN10 (an EIN), the internode rapidly...
elongates from about AL11 when the internode is about 50% of its final diameter; both elongation and thickening cease at around AL13.

Furthermore, the age in leaf number (AL) helps to estimate stem growth as shown in Fig. 9. For example, if the 12th leaf collar has just appeared from the 11th leaf sheath (AL12), the internode length and diameter of IN8 and lower internodes would already be determined and the elongation and thickening of IN9 would have almost ceased. At that time, IN10 would rapidly elongate and be in the second half of the thickening period.

This study shows that the synchrony between the beginning of internode elongation and the appearance of the leaf collar is strong, whereas the beginning of internode thickening appears to be related to leaf initiation. Kawahara et al. (1968) stated that in rice the duration and activity of residual meristems near the periphery of shoot apex play an important role in determining internode diameter prior to the differentiation of intercalary meristems, which is closely related to the marked elongation of the internode. After the differentiation of the intercalary meristems, the periclinal division does not greatly affect the diameter of internode due to its localization near the epidermis. However, in sweet sorghum, internode thickening continues after the beginning of internode elongation. This is considered to be related to the existence of parenchyma at the center of internode, although rice plants have an internodal lacuna in elongated internodes. In maize, which has parenchyma in the center of its internodes, Nemoto and Baba (1995) observed primary thickening meristems outside the small vascular bundles in the peripheral region of elongated internodes as in sweet sorghum. The final diameter is one of the determinants of stem yield in sweet sorghum, and it also plays an important role in increasing lodging tolerance. Further morphological studies are needed to clarify the mechanism of internode thickening after the formation of the intercalary meristem.

The patterns of elongation and thickening of internodes (excluding the upper internodes) could be successfully described by using the age in leaf number (AL), and these findings suggested that the degree of the elongation and thickening of successive internodes could be estimated by using AL. The elongation and thickening patterns of internode obtained here using cultivar ‘Wray’ can be basically regarded as the normal stem growth of sweet sorghum. Analyses of the differences in stem yield among varieties and the effects of fertilizer application on stem growth according to the age in leaf number are required to establish a cultivation method for increasing stem yield.
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