Pseudostem Length as an Indicator of the Start of Internode Elongation in Wheat (*Triticum aestivum*)

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1. Introduction

The start of internode elongation is an important event in wheat cultivation. The application of excessive nitrogen fertilizer before this event promotes abundant tillering and causes lodging through extensive elongation of lower internodes (Eguchi 1983). Therefore, the application of nitrogen as a basal dressing followed by a topdressing after the start of internode elongation is the best way to increase yield and quality while reducing lodging, and is consistent with the ‘V-shaped rice cultivation’ theory (Matsushima 1980). To avoid preharvest sprouting in the rainy season and to allow the double cropping of wheat and rice, early heading and maturation are required. However, frost injury of young spikes in early spring is closely related to the earliness of internode elongation, since this is the process by which young spikes come out above the ground (Inamura et al. 1958). Therefore, to establish the optimum sowing time in areas subject to spring frosts, it is necessary to take account of the timings of the start of internode elongation and of heading and maturation.

The calendar date of the start of internode elongation differs among years, sowing times, and cultivars in the warmer regions of Japan (Fujita et al. 1995). To determine the date requires that the plants be dug out and dissected. This effort could be avoided if external characteristics that are closely related to the timing of internode elongation and that can be easily measured can be identified. Stem elongation was synchronized with apical development (Chinoy 1949, 1950; Tottman 1977; Hoshino and Tahir 1987; Fujita et al. 1992; Tanio and Kato 2007), and rapid stem elongation due to internode elongation started when floret initiation began (Baker and Gallagher 1983; Kirby et al. 1985; Craufurd and Cartwright 1989).

In the UK, ‘Growth stage 30’ (Zadoks et al. 1974) can be defined as the time when the stem length is $\geq 1$ cm, and gives a useful indication of the stage from beyond double ridges to floret initiation (Tottman et al. 1985; Tottman 1987). On the other hand, pseudostem length, measured from
the ground to the lamina joint of the uppermost unfolded leaf, was closely correlated with the apical development stage, without difference among varieties (Tottman 1977). Hay (1986) also reported that the pseudostem length at the double ridges stage differed little with changes in sowing time. These facts suggest the possibility of judging whether internodes have started to elongate from pseudostem length, irrespective of year, sowing time, or cultivar. However, in the warmer regions of Japan, the relationship between the start of internode elongation and the apical development stage is less clear (Suetsugu 1949; Noda and Ibaraki 1953; Hosoda and Iwasaki 1960), and that between pseudostem length and apical development stage remains to be investigated.

In this study, to develop a useful indicator of the start of internode elongation in the warmer regions of Japan, we analyzed the relationships between apical development stage, stem length, and pseudostem length in wheat (*Triticum aestivum*).

**2. Materials and Methods**

We grew wheat cultivar ‘Norin 61’, which is widely grown in the warmer regions of Japan. ‘Norin 61’ has a spring growth habit and shows medium heading and maturation times.

A total of 11 crops were sown in drained paddy fields (Ultisol, light clay) at Tsu (34° 46′ N, 136° 26′ E), in the warmer Tokai region of Japan, in 2009 following soybean and in 2010 and 2011 following rice (Table 1). Seeds were sown at 200 m⁻² in rows 0.24 m apart at a depth of about 2 cm by a shallow-tillage seeding machine (Watanabe et al. 2009) equipped with a drill seeder. N, P, and K were supplied as a basal dressing of a compound fertilizer at 5.0, 2.2, and 4.2 g m⁻², respectively, in 2009; at 7.0, 4.4, and 8.3 g m⁻² in 2010; and at 6.0, 2.6, and 5.0 g m⁻² in 2011. Topdressings were not applied until the heading time.

During the period from a few weeks before double ridges initiation (a mark of the transition from vegetative to reproductive development) to awn elongation, at least 10 randomly selected plants of each crop were dug out at about weekly intervals, and their main shoots were examined. The pseudostem length was measured from ground level (judged by the color change from white to green) to the lamina joint of the uppermost unfolded leaf (Fig. 1). Then the pseudostems were carefully dissected under a binocular microscope. The length from the base of the first leaf to the base of the young spike was recorded as the stem length. The apical development stages were determined according to the method of Inamura *et al.* (1955) and numbered from 2 to 10 for statistical analysis (see the footnote to Fig. 2 for details). The mean of 10 plants of each sample was calculated, unless otherwise noted. The emergence and heading dates of each crop were recorded. The crop sown on November 16 in 2010 was examined in more detail on March 9 and 22 in 2011 with a sample size of 92 and 62 plants, respectively. The pseudostem length, stem length, and apical development stage were recorded as above, the numbers of total leaves and unfolded leaves were counted, and the length of each internode was measured.

The daily mean temperature during the three cropping seasons was recorded 500 m away from the study fields. The monthly mean temperature and the monthly effective day length, which was calculated using the method of Gotoh (1977), are

![Fig. 1 Pseudostem length of the main shoot.](image-url)
shown in Fig. 2. The accumulated daily mean temperature above a base temperature of 0℃ was calculated as thermal time (℃・d).

3. Results

1) Calendar dates of apical development stages

There was great variation in the time course of apical development among the 11 sowing dates (crops) (Fig. 2). The apical development stage was significantly ($P<0.001$) correlated with thermal time in every crop; in each cropping season, the earlier the seeds were sown, the sooner the plants reached any stage of apical development (Table 1). Between years, however, the time course of apical development differed owing to differences in temperature; for example, the calendar date of stage 7 of the crop sown on November 4 in 2011 was 10 days earlier than that of the crop sown on November 4 in 2010. In particular, the calendar date of each stage differed widely among the five crops sown in 2011, with differences ranging from as high as 80 days at stage 3 to 36 days at stage 10. These results indicate that the time course of apical development differed with year and (greatly) with sowing time.

2) Relationship between stem length and apical development stage

Stem length increased markedly at stage 7 and then increased exponentially (Fig. 3A). This correspondence did not differ obviously with year or

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**Fig. 2** Time courses of apical development in wheat crops (cv. Norin 61) sown on 11 dates. Arrow indicates the range of sowing dates.

Apical development stages 2–10 equate to those of Inamura et al. (1955) as follows:

- Stage 2 = V (spikelet primordia cannot be observed)
- Stage 3 = VI (spikelet primordia, which can be seen as double ridges, initiate in the middle of the spike)
- Stage 4 = VII e (spikelet primordia initiate at the base of the spike)
- Stage 5 = VII l (double ridges become less distinct)
- Stage 6 = VIII (spikelet primordia begin to differentiate empty glumes, and the terminal spikelet initiates)
- Stage 7 = IX e (spikelet primordia differentiate into florets)
- Stage 8 = IX m (first florets differentiate into lemma, palea, stamen, and pistil)
- Stage 9 = IX l (differentiation into lemma, palea, stamen, and pistil goes on all over the florets)
- Stage 10 = X (empty glume and awn begin to elongate)
These results indicate that stem elongation was synchronized with apical development; the stems remained as crowns until stage 6, and the internodes probably started to elongate at stage 7 (which we refer to as the floret differentiation stage), irrespective of year or sowing time.

3) Relationship between pseudostem length and apical development stage

Pseudostem length increased exponentially with apical development stage (Fig. 3B). The regres-
sion was highly significant \( (P<0.001) \) in every crop. The overall regression for the 11 crops \( (y = \exp (0.238x + 0.061)) \), where \( y \) is the pseudostem length [cm] and \( x \) is the apical development stage was also highly significant \( (P<0.001, r^2 = 0.95) \). By this regression, the pseudostem length at stage 7 was 5.6 cm, with 95% confidence limits of 4.3 and 7.4 cm. In addition, the difference among the 11 crops in pseudostem length of the plants at stage 7 was not significant (Scheffé’s test), the overall mean being 5.5 cm. These results indicate that pseudostem length was closely correlated with the apical development stage, irrespective of year or sowing time.

4) Relationship between stem length and pseudostem length

Because of the close relationship of apical development stage with both stem length and pseudostem length, stem length increased markedly when the pseudostem length was around 5.5 cm in all years and at all sowing times (Fig. 3C). To investigate the relationship between the internode length and the pseudostem length after the start of internode elongation, we studied the crop sown on November 16 in 2010. There were differences among plants in the number of total leaves (9 or 10), the number of unfolded leaves (6 or 7), and the position of the lowermost elongated internode (N6 or N7). Therefore, we grouped the plants according to these characteristics for analysis (Table 2). As can be seen from the length of the internodes subtending the uppermost unfolded leaf (underlined in Table 2), the pseudostem length after the start of internode elongation was associated not only with the leaf sheath length of the uppermost unfolded leaf, but also with the length of elongated internodes. This explains why the pseudostem length was significantly \( (P<0.001) \) and linearly correlated with the stem length among the samples with a stem length of \( \geq 1.0 \) cm (Fig. 3C). The regression equation for these samples was \( y = 1.33x + 4.56 \) (where \( y \) is the pseudostem length [cm] and \( x \) is the stem length [cm]). These results indicated that internodes started to elongate when the pseudostem length was ca. 5 cm, irrespective of year and sowing time.

### 4. Discussion

Since the start of internode elongation is a critical event, it is important to reveal its physiological mechanisms. Among the organs that constitute a phytomer, the lamina starts to elon-

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**Table 2**  Means of internode length, stem length, pseudostem length, and apical development stage of plant types classified according to the numbers of total leaves and unfolded leaves, and the position of the lowermost elongated internode \( (\geq 0.30 \text{ cm}) \), in the wheat crop (cv. Norin 61) sown on November 16 in 2010.

| Date   | No. of plants | No. of total leaves | No. of unfolded leaves | Internode length (cm) | Stem length (cm) | Pseudostem length (cm) | Apical stage |
|--------|---------------|---------------------|------------------------|-----------------------|------------------|------------------------|-------------|
|        | N5 | N6 | N7 | N8 | N9 | N10 | N11 |               |                   |               |               |             |
| Mar 9  | 27 | 9  | 6  | —  | —  | —  | —  | 1.83a | 0.29d | —  | —  | —  | 2.45a | 6.8a | 8.0a |
|        | 41 | 10 | 6  | —  | —  | —  | —  | 1.27b | 0.50c | —  | —  | —  | 2.15b | 6.0b | 7.6bc |
|        | 3  | 10 | 7  | —  | —  | —  | —  | 0.67b | 0.76b | —  | —  | —  | 1.95abc | 6.2b | 8.7ab |
|        | 3  | 10 | 6  | —  | —  | —  | —  | 0.69b | 0.69b | —  | —  | —  | 1.24d | 4.9c | 7.5c |
|        | 14 | 10 | 7  | —  | —  | —  | —  | 1.16a | —  | —  | —  | —  | —  | 1.74c | 6.9a | 7.9a |
| All    | 9.7| 6.2| —  | —  | —  | —  | —  | 1.15 | 0.56 | —  | —  | —  | 2.10 | 6.3 | 7.7 |
| Mar 22 | 20 | 9  | 7  | —  | —  | —  | —  | 1.97a | 2.11c | 0.34 | —  | —  | 4.73b | 11.5a | 10.0a |
|        | 33 | 10 | 7  | —  | —  | —  | —  | 1.34b | 3.32b | 0.57b | —  | —  | 5.64a | 11.0a | 9.9a |
|        | 9  | 10 | 7  | —  | —  | —  | —  | 3.02 | 0.67a | —  | —  | —  | 5.05ab | 10.9a | 9.9a |
| All    | 9.7| 7.9| —  | —  | —  | —  | —  | 1.36 | 3.02 | 0.51 | —  | —  | 5.26 | 11.1 | 9.9 |

N6, N7, and N8 indicate the internode subtending the 6th, 7th, and 8th leaf, respectively, and N10 or N11 is the peduncle. Underline indicates the internode subtending the uppermost unfolded leaf. Means followed by the same letter within a column are not significantly different at \( P<0.05 \) according to the Aspin-Welch \( t \)-test.

\(^{1}\) Including internodes \(< 0.30 \text{ cm}\).
gate first, followed by the leaf sheath, then the subtending internode; and the elongation of each organ is followed by that of the corresponding organ of the phytomer above; this is true in maize (Sharman 1942), rice (Sato 1952; Seko et al. 1956), and wheat (Ichii 1978; Gallagher 1979; Kirby 1988). When a lamina has just unfolded (i.e., the lamina joint is just visible), the leaf sheath ends its main elongation and the subtending internode begins its main elongation (Ichii 1978). Matsuba (1997) showed that the position of the GA$_3$-sensitive internode of rice was closely related to the plant age (expressed in leaf number), and that a signal to induce internode elongation was generated at the stage from flag leaf initiation to first bract initiation, when the internode sensitive to the signal at this time started to elongate. Our results indicate that internodes started to elongate at the floret differentiation stage in wheat, in agreement with those of Baker and Gallagher (1983), Kirby et al. (1985), and Craufurd and Cartwright (1989). In the crop sown on November 16 in 2010 and examined on March 9 in 2011 (Table 2), the position (N6 or N7) of the lowermost elongated internode was significantly related to the number (6 or 7) of unfolded leaves (contingency test: $\chi^2 = 41.9, P < 0.001$). These facts strongly indicate that a signal to induce wheat internode elongation is generated at the floret differentiation stage, prompting the internode that is sensitive to the signal at this time to start elongation.

Apical development is related not only to the start of internode elongation, but also directly to yield components. Therefore, it is important to determine the apical development stage in wheat production. Halse and Weir (1970) studied wheat phenological development under controlled environmental conditions and showed that genetic factors, vernalization, photoperiod, and temperature had significant effects on apical development. Our results indicate that the time course of apical development differed with year and (greatly) with sowing time (Fig. 2, Table 1). Therefore, a useful indicator of the apical development stage is needed. The apical development stage of transplanted rice can be estimated from the plant age (expressed in leaf number), because apical development is closely correlated with the development of the subtending leaves (Nemoto et al. 1995). On the other hand, the peak of the wheat sowing time varies with year and its period is also apt to be long, because rain can interfere with sowing. In addition, the total number of leaves differs with sowing time and cultivar (Fukushima et al. 2001; Fukushima et al. 2003). Therefore, for estimating the apical development stage from the plant age (expressed in leaf number), it would be necessary to take account of the sowing time and cultivar.

Our results indicate that pseudostem length was closely correlated with apical development stage in the warmer Tokai region of Japan ($r^2 = 0.95$, which means $r = 0.97$). This result agrees with that of Tottman (1977) in the UK ($r = 0.96$). However, the studies differed in the type of regression (curvilinear versus linear) and pseudostem length at the floret differentiation stage (5.6 and 9.8 cm, respectively). These discrepancies might be due to differences in the standards for the apical development stage and growing period. Our results also indicate that the apical development stage could be estimated from the pseudostem length within a 95% confidence limit of $\pm 1.2$ stages (Fig. 3B). However, the pseudostem length did not differ widely as a function of stage from stages 2 to 6, whereas that from stages 8 to 10 varied considerably, probably because of differences in the lengths of the elongated internodes. Therefore, it seems likely that it would be difficult to estimate these stages from the pseudostem length, whereas it could be possible to estimate stage 7 (floret differentiation stage) with reasonable accuracy.

We found that the apical development stage was closely related to both the start of internode elongation and pseudostem length, with the result that internode elongation began when the pseudostem length was ca. 5 cm. As these facts were based on main stems, it seems reasonable to
assume that internode elongation begins when the longest pseudostem is ca. 5 cm long. Therefore, pseudostem length could be useful as an indicator of the start of internode elongation, and could be used as a tool for wheat cultivation in the warmer regions of Japan. It will be necessary to confirm this relationship for other cultivars, growing regions, and cultivation methods.

**Acknowledgements**

We thank T. Uemura, T. Izumi, and M. Arakaki (National Institute of Vegetable and Tea Science) and O. Sakaue (National Agricultural Research Center) for their technical assistance. Thanks are due to the Iwaki Farmer Group for allowing us to use their fields. We are grateful to the National Institute of Vegetable and Tea Science for the meteorological data. We thank Y. Watanabe (National Agricultural Research Center) for his reading of this manuscript. This study was supported by a Grant-in-Aid for research programs in crop production in paddy fields from the Ministry of Agriculture, Forestry and Fisheries of Japan.

**Summary**

To develop a useful indicator of the start of internode elongation in wheat in the warmer regions of Japan, we analyzed the relationships between the apical development stage, stem length, and pseudostem length (from the ground to the lamina joint of the uppermost unfolded leaf) of the main shoot in wheat cultivar ‘Norin 61’. The time course of apical development differed with year and (greatly) with sowing time. Nevertheless, stem elongation was synchronized with apical development, and the internodes probably started to elongate at the floret differentiation stage. In addition, pseudostem length was highly correlated with the apical development stage (5.6 cm at the floret differentiation stage). These close relationships show that internode elongation began when the pseudostem length was ca. 5 cm. Therefore, pseudostem length could be useful as an indicator of the start of internode elongation for wheat cultivation in the warmer regions of Japan.

**Key Words**

apical development stage, floret differentiation stage, pseudostem length, start of internode elongation, stem length, wheat

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要旨
日本温暖地における小麦の節間伸長開始期の指標を開発するため、小麦品種「農林61号」を用いて、主茎について頂端発育ステージ、茎長および偽茎長（地面から最上位展開葉の葉節までの長さ）の関係を解析した。頂端の発育の経時推移は年次と播種日によって異なり、特に播種日による変動が大きかった。しかし、茎の伸長と頂端の伸育との間には同調的関係が認められ、節間伸長開始は小花分化期に起こった。また、偽茎長と頂端発育ステージとの間には高い相関が認められ、小花分化期の偽茎長は5.6cmであった。これらの密接な関係の結果、節間伸長開始期は偽茎長が約5cmのときであった。したがって、日本温暖地の小麦栽培において、偽茎長は節間伸長開始期の指標として有用であると考えられた。

キーワード
偽茎長、茎長、小麦、小花分化期、節間伸長開始期、頂端発育ステージ