Pseudostem Length as an Indicator of the Start of Internode Elongation in Spring and Winter Wheat Cultivars

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To develop an indicator of the start of internode elongation in wheat (*Triticum aestivum* L.) in the warmer regions of Japan, we analyzed the relationships between apical development stage, stem length, and pseudostem length (from the ground to the lamina joint of the uppermost unfolded leaf) in five spring and winter cultivars in the warmer Tokai region of Japan. The time course of apical development differed among cultivars: the winter cultivars reached the double ridges stage (the transition from vegetative to reproductive development) and the following floret differentiation stage later than the spring cultivars in early sowing. Apical development stage was closely related to both stem length and pseudostem length. Internode elongation started at the floret differentiation stage in all cultivars, when the pseudostem length was ca. 5 cm in all cultivars. The present study indicated that pseudostem length is useful as an indicator of the start of internode elongation in wheat cultivation in the warmer regions of Japan.

Key Words: apical development, pseudostem length, spring wheat, start of internode elongation, winter wheat

1. Introduction

The start of internode elongation is a critical event that is associated with the timing of topdressing with nitrogen fertilizer and of frost injury of young spikes in early spring in wheat cultivation in the warmer regions of Japan. Topdressing should be applied after the start of internode elongation, because the application of too much fertilizer before this event promotes abundant tillering and causes lodging through extensive elongation of lower internodes (Eguchi 1983). Frost injury in areas subject to spring frosts is closely related to the earliness of internode elongation, which lifts young spikes above the ground (Inamura et al. 1958).

The calendar date of the start of internode elongation differs among years, sowing times, and cultivars. 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. In the UK, apical development stage is closely related to both the start of internode elongation and pseudostem length, which is measured from the ground to the lamina joint of the uppermost unfolded leaf (Tottman 1977; Baker and Gallagher 1983; Hay 1986). These facts suggest the possibility of judging whether internodes...
have started to elongate from pseudostem length. In the warmer Tokai region of Japan, we showed that internodes of ‘Norin 61’ started to elongate at the floret differentiation stage, and pseudostem length was closely correlated with the apical development stage; as a result, internode elongation begins when pseudostem length is ca. 5 cm, irrespective of year and sowing time (Tanio et al. 2012). These results indicate that pseudostem length could be useful as an indicator of the start of internode elongation. However, whether the same can apply to other cultivars remains to be investigated.

In this study, to develop an indicator of the start of internode elongation in the warmer regions of Japan, we analyzed the relationships between apical development stage, the start of internode elongation, and pseudostem length in five spring and winter wheat cultivars in the warmer Tokai region of Japan.

2. Materials and Methods

1) Plant materials

We grew 5 wheat (Triticum aestivum L.) cultivars which are widely grown in the warmer Tokai region of Japan: ‘Nishinokaori’ (Taya et al. 2003a), ‘Ayahikari’ (Yoshida et al. 2001), ‘Tamaizumi’ (Fujita et al. 2004), ‘Iwainodaichi’ (Taya et al. 2003b), and ‘Satonosora’ (Takahashi et al. 2010), whose planted areas in Tokai region in 2014 (sowing year) were 1623, 3205, 822, 1835, and 982 ha, respectively. ‘Iwainodaichi’ and ‘Satonosora’ are winter wheats and the others are spring wheats. ‘Nishinokaori’ and ‘Tamaizumi’ are red- and white-grained hard wheats, respectively, and the others are red-grained soft wheats.

2) Growth and climate conditions

A total of 20 crops (5 cultivars sown on 2 dates in 2 years) were sown in drained paddy fields (Ultisol, light clay) at Tsu (34° 46' N, 136° 26' E), in the warmer Tokai region of Japan, on November 6 and 22 in 2013 and on November 6 and 21 in 2014 (which we refer to as early and late sowing, respectively, in both years), after rice cultivation. Seeds were sown at 200 seeds 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, P₂O₅, and K₂O were supplied as a basal dressing of a compound fertilizer at 7.0, 7.0, and 7.0 g m⁻², respectively. Topdressings were not applied until heading.

The daily mean temperature during the two cropping seasons was recorded at the National Institute of Vegetable and Tea Science, 500 m from the study fields. The average daily mean temperature for the last 30 years was supplied by the Japan Meteorological Agency (Tsu Local Meteorological Office). The effective day-length was calculated according to the method of Gotoh (1977).

3) Evaluation of plant characteristics

The emergence date of each crop was recorded. During the period from a few weeks before double ridges initiation (a mark of the transition from vegetative to reproductive development) to awn elongation, 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. 4 for...
details; Fig. 2 shows the shoot apex at stage 7). The mean of 10 plants of each sample was calculated, unless otherwise noted. The heading date of each crop was recorded.

![Shoot apex at stage 7 (floret differentiation stage).](image)

**Fig. 2** Shoot apex at stage 7 (floret differentiation stage).

| Sowing year | Sowing date | Cultivar¹ | Emergence date | Date of the following apical development stage² | Heading date |
|-------------|-------------|-----------|----------------|-----------------------------------------------|--------------|
| 2013        | Nov 6       | Nishinokaori | Nov 15         | Jan 9 (15)³ | Feb 16 (13) | Mar 7 (6) | Apr 11 (5) |
|             |             | Ayahikari | Nov 15         | Jan 9 (15) | Feb 18 (15) | Mar 11 (10) | Apr 11 (5) |
|             | Nov 6       | Tamaizumi | Nov 15         | Jan 17 (23) | Feb 24 (21) | Mar 13 (12) | Apr 13 (7) |
|             |             | Iwainodaichi | Nov 15        | Jan 12 (18) | Feb 20 (17) | Mar 11 (10) | Apr 10 (4) |
|             |             | Satonosora | Nov 15         | Jan 21 (27) | Feb 26 (23) | Mar 17 (16) | Apr 14 (8) |
| 2014        | Nov 6       | Nishinokaori | Dec 15         | Feb 18 (55) | Mar 13 (38) | Mar 25 (24) | Apr 21 (15) |
|             |             | Ayahikari | Dec 15         | Feb 6 (43) | Mar 7 (32) | Mar 23 (22) | Apr 17 (11) |
|             | Nov 22      | Tamaizumi | Dec 15         | Feb 17 (54) | Mar 14 (39) | Mar 26 (25) | Apr 21 (15) |
|             |             | Iwainodaichi | Dec 15        | Feb 11 (48) | Mar 8 (33) | Mar 22 (21) | Apr 15 (9) |
|             |             | Satonosora | Dec 15         | Feb 16 (53) | Mar 12 (37) | Mar 24 (23) | Apr 17 (11) |
| 2014        | Nov 6       | Nishinokaori | Nov 15         | Dec 25 (0) | Feb 3 (0) | Mar 1 (0) | Apr 6 (0) |
|             |             | Ayahikari | Nov 15         | Jan 6 (12) | Feb 14 (11) | Mar 7 (6) | Apr 9 (3) |
|             | Nov 6       | Tamaizumi | Nov 15         | Jan 11 (17) | Feb 17 (14) | Mar 8 (7) | Apr 9 (3) |
|             |             | Iwainodaichi | Nov 15        | Jan 17 (23) | Feb 21 (18) | Mar 10 (9) | Apr 7 (1) |
|             |             | Satonosora | Nov 15         | Jan 29 (35) | Feb 25 (22) | Mar 13 (12) | Apr 13 (7) |
| 2014        | Nov 21      | Nishinokaori | Dec 1          | Feb 14 (51) | Mar 8 (33) | Mar 21 (20) | Apr 19 (13) |
|             |             | Ayahikari | Dec 1          | Feb 4 (5) | Mar 5 (30) | Mar 20 (19) | Apr 18 (12) |
|             | Nov 21      | Tamaizumi | Dec 1          | Feb 15 (52) | Mar 7 (32) | Mar 20 (19) | Apr 19 (13) |
|             |             | Iwainodaichi | Dec 1         | Feb 6 (43) | Mar 3 (28) | Mar 18 (17) | Apr 14 (8) |
|             |             | Satonosora | Dec 1          | Feb 12 (49) | Mar 6 (31) | Mar 19 (18) | Apr 18 (12) |

¹ ‘Iwainodaichi’ and ‘Satonosora’ are winter wheats and the others are spring wheats.
² Apical development stages are explained in the footnote to Fig. 4.
³ The difference in calendar date from that of ‘Nishinokaori’ sown on November 6 in 2014 is shown in parentheses.

4) Statistical analyses

Statistical analyses were performed with the analysis tools of Microsoft Excel 2013 (Microsoft Corporation, WA, USA). According to the method of Kawabata (1989), regression analyses were carried out, with cause and effect assigned to explanatory variable (x) and dependent variable (y), respectively, using the mean of 10 plants of each sample. The simple linear regression analysis of the apical development stage against the thermal time (°C•d) that is accumulated daily mean temperature above a base temperature of 0°C was done for each crop. The regression analysis of the pseudostem length that was subjected to logarithmic transformation against the apical development stage was done for each and overall cultivar; then the statistics regarding pseudostem length were converted
to the pseudostem length before logarithmic transformation by exponential transformation. The coefficient of determination ($R^2$) was calculated dividing the regression sum of squares by the total sum of squares.

The analysis of variance (ANOVA) for split-plot design with year, sowing time, and cultivar as block, main-plot, and subplot factors, respectively, was carried out to analyze the effects of year, sowing time, cultivar, and cultivar × sowing time on the calendar date of stage 7 using a set of data on the difference in calendar date from that of ‘Nishinokaori’ sown on November 6 in 2014, and on the pseudostem length at stage 7 using a set of data on the mean of pseudostem length of 11 to 27 plants at stage 7 in each crop; then Tukey’s test was done to determine the significant differences between cultivars.

3. Results

1) Calendar dates of apical development stages

Apical development stage was significantly ($P < 0.001, R^2 > 0.95$) correlated with the thermal time in every crop. By using the regression equation, the dates of stage 3 (double ridges), stage 7 (floret differentiation), and stage 10 (awn elongation) were estimated (Table 1). The time course of apical development differed significantly with year, sowing time (early or late), cultivar, and cultivar × sowing time (e.g., by the ANOVA of the calendar date of stage 7, $P = 0.013, P = 0.004, P = 0.037$, and $P = 0.019$, respectively). Apical development was a little faster in 2014–15 than in 2013–14, probably owing to the generally higher temperatures (Fig. 3). The calendar date of each stage was much earlier in early sowing than in late sowing, mainly because the plants emerged much faster in early sowing. The range among the cultivars in the calendar date of each stage in early sowing was large (e.g., the range in the date of stage 7 among the cultivars sown on November 6 in 2014 was 22 days), whereas that in late sowing was small (e.g., the range in the date of stage 7 among the cultivars sown on November 21 in 2014 was 5 days). In early sowing, the calendar date of each stage of the winter cultivars was later than that of the spring cultivars, except for ‘Iwainodaichi’ sown on November 6 in 2013. In late sowing, on the other hand, there was no difference. The developmental difference between the two winter cultivars in early sowing (Table 1) suggests that the vernalization requirement of ‘Iwainodaichi’ is slightly lower than that of ‘Satonosora’.

These results indicate that the time course of apical development differs among cultivars, and that the calendar dates of the double ridges stage and
plants that had the pseudostem length of 5.0–5.9 cm than those of stages 6 and 8 (stage 6: 18.9%, stage 7: 50.3%, and stage 8: 10.0%). By the ANOVA of the pseudostem length at stage 7, the effects of year, sowing time, and cultivar × sowing time were not significant, but cultivar was significant (P = 0.191, P = 0.188, P = 0.618, and P = 0.015, respectively); ‘Nishinokaori’ was significantly longer than ‘Ayahikari’ and ‘Iwainodaichi’ (Table 3).

On the other hand, pseudostem length increased exponentially with apical development stage (Fig. 4B). The regression was highly significant in every cultivar (P < 0.001, R² ≥ 0.97; Table 3). According to the regression analyses, the mean pseudostem length at stage 7 varied from 5.0 to 5.8 cm among the cultivars and had overlapping 95% prediction interval between 4.9 and 6.3 cm (Table 3). In

2) Relationships between apical development stage, stem length, and pseudostem length

Stem length increased markedly at stage 7 (floret differentiation stage) without differences among cultivars (Fig. 4A), clearly indicating that stems remain as crowns until stage 6, and internodes start to elongate at stage 7, irrespective of cultivar. On the basis of individual plants data (Table 2), the frequency distribution of pseudostem length in the populations of apical development stages 2–10 was all unimodal and differed significantly between populations (e.g., stage 6 vs. stage 7: χ² = 158.9, P < 0.001; stage 7 vs. stage 8: χ² = 185.3, P < 0.001), and the population of stage 7 contained a lot more

floret differentiation stage of winter cultivars are later than those of spring cultivars in early sowing.
addition, the overall regression for the five cultivars was highly significant \((P < 0.001, R^2 = 0.96)\). By this regression, the pseudostem length at stage 7 was 5.3 cm, with 95% prediction interval between 4.2 and 6.6 cm. These results indicate that the difference among cultivars in pseudostem length at stage 7 is reasonably small. Because of the close relationship of apical development stage with both stem length and pseudostem length, stem length increased markedly when pseudostem length was in the vicinity of 5.3 cm in all cultivars (Fig. 4C).

These results indicate that internodes in all cultivars start to elongate at the floret differentiation stage, when pseudostem length is ca. 5 cm in all cultivars.

4. Discussion

Flood and Halloran (1984) showed that the vernalization response gene, which determines...
spring or winter type, plays a critical role in development before the double ridges stage, but has no effect on development after the double ridges stage. Chujo (1966a, b) showed under controlled environment conditions that a mean temperature of 6 to 10°C is effective for vernalization. Our results show that the winter cultivars reached the double ridges and floret differentiation stages later than the spring cultivars in early sowing, but there was no difference in late sowing (Table 1), in agreement with previous results (Araki et al. 1977; Fujita et al. 1995; Fukushima et al. 2005). In early sowing, the mean temperature after emergence in late November was warmer in 2014 than in 2013 (Fig. 3) and the spring cultivars reached the double ridges stage earlier in 2014 than in 2013, but the winter cultivars reached that stage later in 2014 than in 2013 (Table 1). These facts strongly indicate that in early sowing, because the mean temperature after emergence is >10°C, winter cultivars take a longer time to reach the double ridges stage and the following floret differentiation stage (i.e., the start of internode elongation) than spring cultivars, owing to their vernalization requirement. Therefore, to avoid frost injury in early spring, the optimum sowing time for spring cultivars would have a much narrower range than that for winter cultivars, which can be sown earlier than the spring cultivars.

Takegami and Ogo (1956) and Takegami (1956) suggested that the nitrogen topdressing should be applied at the start of internode elongation, the timing of which can be estimated from the appearance of erecting shoots and then verified from the length of the internodes in the base of the longest shoot. The growth habit in winter is classified into three types: erect, with almost vertical shoots; prostrate, with shoots which lie on the surface of the soil; and intermediate, with shoots which grow up at a variable angle (Percival 1921). All three types eventually become erect. Nishio and Nakagawa (1958) and Nishio et al. (1962) revealed that prostrate-type cultivars have sensitivity to vernalization, photoperiod, or both, and that the change of growth habit from prostrate through intermediate to erect is synchronized with apical development. The cultivars that we grew do not have sensitivity to photoperiod (Seki et al. 2011), although the two winter cultivars need vernalization. In the winter after early sowing, the two winter cultivars had a prostrate habit, ‘Nishinokaori’ was erect (as is typical of spring cultivars), and the other cultivars were intermediate. The calendar date of the floret differentiation stage of the prostrate- and intermediate-type cultivars (Table 1) corresponded roughly to the time when the growth habit became erect (data not shown). However, after late sowing, the growth habit was less distinct. Therefore, growth habit could be used as a complementary indicator of the start of internode elongation, depending on cultivar and sowing time.

In the UK, Tottman (1977) revealed that apical development stage is closely correlated with both stem length and pseudostem length regardless of cultivar. In Japan, we showed that apical development stage of ‘Norin 61’ was closely correlated with both stem length and pseudostem length, and that internode elongation began when pseudostem length was ca. 5 cm, irrespective of year and sowing time (Tanio et al. 2012). Our results here show that the same is true of the five other cultivars as well (Fig. 4; Table 2; Table 3). Recently, we reported that vernalization response genes of near-isogenic wheat lines did not influence the pseudostem length at the start of internode elongation (Tanio et al. 2014). These facts strongly indicate that pseudostem length (5 cm) is a useful indicator of the start of internode elongation, irrespective of year, sowing time, or cultivar, in the warmer regions of Japan. This indicator would allow wheat farmers to reduce their efforts to check whether internodes have started to elongate. Additionally, pseudostem length could be useful to evaluate the timing of the start of internode elongation in wheat breeding. Hereafter, it will be essential to confirm these findings in other regions.

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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、東海地域において春播性および秋播性の計5品種の茎頂発育ステージ、茎長および偽茎長（地面から最上位着葉の葉節までの長さ）の関係を解析した。茎頂発育の経時推移は品種によって異なり、早播栽培において秋播性品種は春播性品種に比べて二重隆起形成期（栄養生長から生殖生長への転換期）およびその後の小花分化期が遅かった。茎頂発育ステージは茎長および偽茎長と密接に関係し、すべての品種において、節間伸長開始は小花分化期に起こり、その時の偽茎長は約5 cm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
秋播性小麦、偽茎長、茎頂発育、節間伸長開始期、春播性小麦