The effects of seeding rate on yield, lodging resistance and culm strength in wheat

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ABSTRACT

We compared the effects of four seeding rates, 60, 100, 140, and 180 seeds m⁻², on yield, lodging resistance and culm strength using two Japanese wheat cultivars Ayahikari and Iwainodaichi. With the decreasing seeding rate, maximum tiller number decreased, percentage of productive culms increased and spike number m⁻² decreased, and the spikelet number per spike, percentage of fertile spikelets, grain number per spikelet and grain number per spike increased. Consequently, grain yield was not significantly affected. Lodging was not observed, but the lodging index was significantly affected by the seeding rate and was the highest in the plots sown at 180 seeds m⁻². The bending moment at the breaking point and flexural rigidity of the basal internode with leaf sheaths were highest in the plots sown at 60 seeds m⁻². In conclusion, the culm strength and stem lodging resistance increased with decreasing seeding rate. Section modulus and bending stress, which constitute the bending moment at the breaking point, and the moment of inertia area and Young’s modulus, which represent the flexural rigidity, were highest in plots sown at 60 seeds m⁻². Therefore, the seeding rate was considered to influence the culm morphology and functions of the cell wall components. The effects of the seeding rate on culm characteristics and lodging resistance did not differ between the two cultivars, and ‘Ayahikari’ had consistently stronger culms than ‘Iwainodaichi’. We suggest that low seeding rates method would be suitable for heavily fertilized cultivation for both cultivar with high and low culm strength.

Abbreviations: AMeDAS: the automated meteorological data acquisition system; HSD: honestly significant difference

1. Introduction

The seeding rate for wheat in Japan is decided after considering the germination rate, growing season, soil conditions, etc. The seeding rate of autumn-sown wheat in Japan is generally 100–250 seeds m⁻². It tends to be set high because autumn-sown wheat in Japan is mainly...
grown as an off-season crop on paddy fields, where the germination rate is likely to be low.

The effect of seeding rate on the wheat yield varies, depending on the cultivar and region (Freeze & Bacon, 1990; Ottesen et al., 2007). Conversely, there have been many reports that when the seeding rate increased, the number of grains per spike decreased, but the number of spikes per m² and grain yield increased (Carr, 2003a; 2003b; Faris & De Pauw, 1980; Lafond, 1994; Lafond & Derksen, 1996; Lloveras et al., 2004; Marshal & Ohm, 1987; Ozturk et al., 2006; Roth et al., 1984; Smid & Jenkinson, 1979).

The seeding rate affects lodging resistance as well as the yield (Faris & De Pauw, 1980; Iwabuchi et al., 2000; Stapper & Fischer, 1990; Webster & Jackson, 1993). Because the lodging degree in wheat increased as yield increased, it seems reasonable that lodging occurred frequently in crops with a high seeding rate. In direct-sown rice crops, when the seedling establishment rate was high, the pushing resistance decreased markedly (Yoshinaga et al., 2001), and lodging degree increased (San-oh et al., 2001). Seeding rate affected culm length in wheat (Geleta et al., 2002), with the basal internode being longer in dense planting, resulting in more lodging than in sparse planting (Fukushima et al., 2004). Mizuochi (1988) suggested that the Japanese wheat line ‘Tsukisamu 1’, which exhibited a particularly strong culm, should be grown at a low seeding rate because it could not show the strong culm feature at a high seeding rate. Overall, these studies indicate that the seeding rate affects the length and strength of the wheat culm, affecting resistance to lodging.

To prevent wheat lodging, inhibition of internodal elongation by plant growth regulators such as chloromequat, ethephon, and trinexapac-ethyl is beneficial. However, in Japan, with the exception of Hokkaido, the northern region, few growth regulators are allowed, therefore, high crop yield, with the application of growth regulators and heavy fertilizer, is uncommon. Thus, to prevent lodging under high-yield conditions, methods other than plant growth regulators are necessary.

Of the major cultivars in the warm and temperate wheat-growing regions in Japan, the Japanese noodle wheat cultivar Ayahikari has relatively high culm strength. In contrast, the Japanese noodle wheat cultivar Iwainodaichi has relatively low culm strength (Matsuyama, Okamura & Ookawa, in press). In this study, we investigated the effects of seeding rate on the yield, lodging resistance and culm strength of these two cultivars.

2. Materials and methods

2.1. Plant materials and field management

The Japanese noodle wheat cultivars Ayahikari and Iwainodaichi were used in this study. Field experiments were conducted in the 2013/2014 and 2014/2015 crop seasons on an upland field (light colored Andosol). The site was the National Agriculture and Food Research Organization (NARO) Central Region Agricultural Research Center located in Ibaraki, central Japan (36°0′N latitude, 140°0′E longitude, 24 m above mean sea level). The seeds were sown on 8 November 2013 and 5 November 2014. The seeding rates were 60, 100, 140, and 180 seeds m⁻². A randomised complete block design with three replications was used in all experiments. The plots were approximately 5.4 m², each consisting of eight rows 15 cm inter-row spacing. A chemical fertilizer (N: P₂O₅: K₂O = 0:20:20) was applied at a rate of 4.0 g m⁻² prior to sowing. No chemical nitrogen was added because of the high nitrogen nutrient level of the soil.

Daily precipitation amount (mm day⁻¹) and instantaneous maximum wind speed (m s⁻¹) during grain ripening in the wheat crops were obtained from the automated meteorological data acquisition system of the Japan Meteorological Agency, at the observation point closest to the trial site.

2.2. Measurements of yield characteristics

To determine maximum tiller number m⁻², stem number m⁻² was counted every two or 3 weeks from germination to April. The heading date was determined as the date when 40–50% spikes had emerged. At maturity grain yield m⁻², spike number m⁻², and 1000-grain weight were determined from two randomly selected 1.0 × 0.45 m subsamples from each plot. The percentage of fertile culms was calculated by expressing the spike number m⁻² at maturity as a percentage of the maximum tiller number m⁻². Grain number per spike was calculated from the spike number, 1000-grain weight, and grain yield. Grain yield and 1000-grain weight were corrected to 12.5% moisture content. We also counted spikelet number and fertile spikelet number per spike from a subsample of eight spikes of representative length out of 12 typical spikes sampled from each plot. The percentage of spikelet fertility was calculated by dividing the fertile spikelet number by spikelet number, and the grain number per spikelet was calculated by dividing the grain number per spike by fertile spikelet number per spike.
2.3. Measurements of lodging resistance and culm strength

The physiological parameters of the third internode (the neck internode of the spike was considered to be the first internode) of the main culm, which is closely associated with stem lodging, were investigated. Two weeks after heading, 16 main culms were sampled from each plot to determine the average leaf number and the length of the third internode. The bending load at the breaking of the third internode of 12 representative main culms was measured at a distance of 4 cm between two supporting points, as described by Ookawa and Ishihara (1992), using a TA. XT plus Texture Analyzer (Stable Micro Systems, Godalming, UK). We determined the maximum stress as the bending moment at breaking (gf cm), and the slope of the stress–strain curve as Young’s modulus (kgf mm⁻²). We measured the outer radius (a₁) and inner radius (a₂) of the minor axis in cross-section of the middle part of the internode, as well as the outer radius (b₁) and the inner radius (b₂) of the major axis, to calculate the section modulus (mm³) and the second moment of inertia (mm⁴) as follows:

\[
\text{Section modulus (mm}^3\text{)} = \frac{\pi}{4} \times \frac{a_1^3b_1 - a_2^3b_2}{a_1}
\]

\[
\text{Second moment of inertia (mm}^4\text{)} = \frac{\pi}{4} \times (a_1^4b_1 - a_2^4b_2)
\]

Bending stress (gf mm⁻²) was calculated by dividing the bending moment at breaking by the section modulus, and the flexural rigidity (kgf mm⁻²) was calculated as the product of Young’s modulus and the second moment of inertia.

In 2014/2015, we calculated the percentage degree of reinforcement of the bending moment at breaking and flexural rigidity by the leaf sheath covering by dividing the difference between the measured value of the intact internode and that of the internode, from which leaf sheath had been removed by that of the intact internode.

The lodging index was calculated by dividing the moment of the aerial part (gf cm) by the bending moment at breaking of the intact internode. The moment of the aerial part was obtained as the product of culm length and culm weight at maturity in 2013/2014, or at 2 weeks after heading in 2014/2015.

2.4. Statistical analysis

Software (JMP version 12; SAS Institute Inc., Cary, NC, USA) was used for statistical analyses. Data were analysed using a three-way analysis of variance. The model was defined as a split-plot design, with the two cropping years as the main plot, the two cultivars as the sub-plots, the four seeding rates as sub-sub-plots, and the three replicates as blocks. Tukey’s Honestly Significant Difference test was used for pairwise comparisons of means (P < 0.05).

3. Results

3.1. Overview of the weather and wheat growth during growing season

Seeding establishment was good because of less damages caused by wet soil, pests or disease throughout the two cropping seasons.

The heading dates of ‘Ayahikari’ were 23 April 2014 and 24 April 2015, and those of ‘Iwainodaichi’ were 21 April 2014 and 22 April 2015.

Weather during ripening was calm and dry in both the 2013/2014 and 2014/2015 seasons. There were only 5 days in 2013/2014 and 4 days in 2014/2015 when the maximum instantaneous wind speed exceeded 15 m s⁻¹ (Figure 1). There were only 2 days in 2013/2014 and none in 2014/2015 when the precipitation per day was greater than 50 mm (Figure 1). The grain yield from each plot was greater than the average yield of 327 g m⁻² in 2013/2014 and 329 g m⁻² in 2014/2015 in Ibaraki prefecture (Table 1), and there was no lodging in either cropping season.

3.2. Yield and yield components

Seeding rate significantly affected spike number m⁻² and grain number per spike (Table 1). With decreasing seeding rate, spike number m⁻² decreased and grain number per spike increased, resulting in grain yield not being significantly affected by seeding rate (Table 1). The interaction between cultivars and seeding rate in terms of yield components was significant only with respect to grain number per spike (Table 1). In the case of ‘Ayahikari’, the grain number per spike in plots sown at 60 seeds m⁻² was 14% greater than that in plots sown at 180 seeds m⁻². In the case of ‘Iwainodaichi’, the grain number per spike in plots sown at 60 seeds m⁻² was 33% higher than that in plots sown at 180 seeds m⁻² (Table 1).

The maximum tiller number m⁻² and the percentage of fertile culms were significantly affected by the seeding rate (Table 2). The maximum tiller number m⁻² decreased at the lower seeding rates, whereas the percentage of fertile culms tended to be higher at lower seeding rates (Table 2).

Spikelet number per spike, percentage spikelet fertility and grain number per spikelet were all significantly
affected by seeding rate (Table 3). In response to the reduced seeding rate, the spikelet number per spike, percentage spikelet fertility and grain number per spikelet increased (Table 3). The interaction between cultivars and seeding rate was significant with respect to grain number per spikelet (Table 3). In plots sown at 60 seeds m\(^{-2}\), this
Tables 2. Maximum tiller number per m$^{-2}$ and percentage of productive culms of the four different seeding rates and two cultivars.

| Year          | Cultivar        | Seeding rate (seeds m$^{-2}$) | Maximum tiller number m$^{-2}$ | Percentage of productive culms (%) |
|---------------|-----------------|-------------------------------|-------------------------------|------------------------------------|
| 2013/2014     | Aya hikari      | 60                            | 542                           | 79.4                               |
|               |                 | 100                           | 693                           | 65.5                               |
|               |                 | 140                           | 720                           | 59.4                               |
|               |                 | 180                           | 720                           | 68.5                               |
|               | Iwainodaichi    | 60                            | 531                           | 93.5                               |
|               |                 | 100                           | 649                           | 73.0                               |
|               |                 | 140                           | 733                           | 73.4                               |
|               |                 | 180                           | 858                           | 63.2                               |
| 2014/2015     | Aya hikari      | 60                            | 373                           | 81.7                               |
|               |                 | 100                           | 467                           | 70.0                               |
|               |                 | 140                           | 449                           | 82.8                               |
|               |                 | 180                           | 711                           | 50.8                               |
|               | Iwainodaichi    | 60                            | 476                           | 81.9                               |
|               |                 | 100                           | 724                           | 58.0                               |
|               |                 | 140                           | 627                           | 82.0                               |
|               |                 | 180                           | 653                           | 71.3                               |
| Average       | Iwainodaichi    | 60                            | 503                           | 87.7                               |
|               |                 | 100                           | 687                           | 65.5                               |
|               |                 | 140                           | 680                           | 77.7                               |
|               |                 | 180                           | 756                           | 67.3                               |
| 2013/2014     | Iwainodaichi    | 60                            | 480 a                         | 84.1                               |
|               |                 | 100 a                         | 633 a                         | 66.6                               |
|               |                 | 140 a                         | 632 a                         | 74.4                               |
|               |                 | 180 a                         | 736 a                         | 63.5                               |
| 2014/2015     |                    | 60                            | 503                           | 87.7                               |
|               |                    | 100                            | 687                          | 65.5                               |
|               |                    | 140                            | 680                          | 77.7                               |
|               |                    | 180                            | 756                          | 67.3                               |
| ANOVA         | Cultivar         | 60                            | 542                           | 79.4                               |
|               |                   | 100                            | 693                           | 65.5                               |
|               |                   | 140                            | 720                           | 59.4                               |
|               |                   | 180                            | 720                           | 68.5                               |
|               | Year             | 60                            | 542                           | 79.4                               |
|               |                   | 100                            | 693                           | 65.5                               |
|               |                   | 140                            | 720                           | 59.4                               |
|               |                   | 180                            | 720                           | 68.5                               |
|               | S × C            | 60                            | 542                           | 79.4                               |
|               |                   | 100                            | 693                           | 65.5                               |
|               |                   | 140                            | 720                           | 59.4                               |
|               |                   | 180                            | 720                           | 68.5                               |
|               | C × Y            | 60                            | 542                           | 79.4                               |
|               |                   | 100                            | 693                           | 65.5                               |
|               |                   | 140                            | 720                           | 59.4                               |
|               |                   | 180                            | 720                           | 68.5                               |
|               | S × C × Y        | 60                            | 542                           | 79.4                               |
|               |                   | 100                            | 693                           | 65.5                               |
|               |                   | 140                            | 720                           | 59.4                               |
|               |                   | 180                            | 720                           | 68.5                               |

*** and ** indicate significance at P < 0.001 and P < 0.01, respectively. Any two samples with a common letter are not significantly different (P > 0.05) based on the Tukey honestly significant difference (HSD) test.

Higher seeding rates, implying that the lodging resistance increased as the seeding rate was reduced (Table 4).

The culm lengths of ‘Ayahikari’ and ‘Iwainodaichi’ were not significantly different from one another, whereas the moment of the aerial part of ‘Ayahikari’ was greater than that of ‘Iwainodaichi’ (Table 4). The bending moment at the breaking of the intact internode of ‘Ayahikari’ was also greater than that of ‘Iwainodaichi’ (Table 5). Consequently, the lodging index of ‘Ayahikari’ was smaller than that of ‘Iwainodaichi’, meaning that ‘Ayahikari’ exhibited greater resistance to lodging than did ‘Iwainodaichi’ (Table 4).

3.4. Culm strength

The bending moment at breaking of the internode, without the leaf sheath covering also tended to increase as the seeding rate decreased (Table 5). The degree of reinforcement of the bending moment at the breaking point by the leaf sheath covering was not significantly affected by the seeding rate (Table 5). The section modulus, which represents the thickness of the tissue in cross-section, and the bending stress, which represents the strength derived from the culm cell wall components tended to increase as the seeding rate decreased, when presented as the average of two cultivars and two cropping seasons, but no significant difference was observed because of the high statistical variability (Table 5).

The flexural rigidity of the intact internode was significantly affected by the seeding rate, tending to increase as the seed rate decreased (Table 5). The flexural rigidity of internodes without the leaf sheath covering also tended to increase as the seeding rate decreased, but the differences were not significant (Table 5). The degree of reinforcement of the flexural rigidity by leaf sheath covering was not significantly affected by the seeding rate (Table 5). The second moment of inertia, which is a property of the shape that defined as the capacity of a cross-section to resist bending, was not significantly affected, although it tended to increase as the seeding rate decreased (Table 5). Young’s modulus, representing the elasticity of the internode, was significantly affected by the seed rate (Table 5). The interaction between the two cultivars and the four seeding rates was not significant for any of the parameters described (Table 5). The bending moment at breaking and the flexural rigidity of ‘Ayahikari’ were significantly greater than those of ‘Iwainodaichi’ in both intact internodes and internodes without the leaf sheath covering (Table 5). The section modulus,
the second moment of inertia, and Young’s modulus of ‘Ayahikari’ were also greater than those of ‘Iwainodaichi’ (Table 5). In contrast, ‘Iwainodaichi’ had greater degrees of reinforcement of the bending moment at breaking and of the flexural rigidity of leaf sheath covering (Table 5).

4. Discussion

4.1. The effects of seeding rate on yield and yield components

In this field trial, in response to decreasing seeding rate, spike number per m² decreased, and grain number per spike increased, with the result that the seeding rate did not significantly affect the yield (Table 1). The maximum tiller number m⁻² decreasing as the seeding rate was reduced, while the percentage of fertile culms tended to increase under the same circumstances (Table 2). The interaction between seeding rates and cultivars was significant with respect to grain number per spikelet, where ‘Iwainodaichi’ exhibited a wider range of values than did ‘Ayahikari’ (Table 3). These findings suggest that the variable effect of the seeding rate on grain number per spike between the two cultivars was due to the effect on grain number per spikelet. Accordingly, in the plots sown at the high seeding rate, it seemed that abortion of florets occurred readily, especially in ‘Iwainodaichi’. Some of the florets initiated in each spikelet will abort. If all florets in a spikelet aborted, it was observed as degeneration of the spikelet.

Table 3. Spikelet number per spike, percentage spikelet fertility and grain number per spikelet of the four different seeding rates and the two cultivars.

| Year       | Cultivar  | Seeding rate seeds m⁻² | Spikelet number per spike | Percentage spikelet fertility (%) | Grain number per spikelet |
|------------|-----------|------------------------|---------------------------|----------------------------------|---------------------------|
| 2013/2014  | Ayahikari | 60                     | 17.7                      | 97.9                             | 2.07                       |
|            |           | 100                    | 17.0                      | 95.3                             | 2.01                       |
|            |           | 140                    | 17.0                      | 92.5                             | 2.09                       |
|            |           | 180                    | 16.4                      | 91.4                             | 2.03                       |
|            | Iwainodaichi | 60              | 18.0                      | 98.9                             | 2.27                       |
|            |           | 100                    | 17.2                      | 96.9                             | 2.32                       |
|            |           | 140                    | 17.1                      | 95.9                             | 2.01                       |
|            |           | 180                    | 17.4                      | 95.6                             | 1.87                       |
| 2014/2015  | Ayahikari | 60                     | 19.3                      | 100.0                            | 2.41                       |
|            |           | 100                    | 19.2                      | 99.5                             | 2.21                       |
|            |           | 140                    | 19.3                      | 100.0                            | 2.12                       |
|            |           | 180                    | 18.8                      | 99.8                             | 2.23                       |
|            | Iwainodaichi | 60            | 19.5                      | 99.5                             | 2.36                       |
|            |           | 100                    | 19.0                      | 99.3                             | 2.22                       |
|            |           | 140                    | 18.6                      | 99.1                             | 1.97                       |
|            |           | 180                    | 18.7                      | 98.4                             | 1.85                       |
| Average    |           | 60                     | 18.5                      | 99.0                             | 2.24 a 1.05                |
|            | Ayahikari | 100                    | 18.1                      | 97.4                             | 2.11 a 0.99                |
|            |           | 140                    | 18.1                      | 96.3                             | 2.11 a 0.99                |
|            |           | 180                    | 17.6                      | 95.6                             | 2.13 a 1.00                |
|            | Iwainodaichi | 60          | 18.8                      | 99.2                             | 2.31 a 1.24                |
|            |           | 100                    | 18.1                      | 98.1                             | 2.27 a 1.22                |
|            |           | 140                    | 17.9                      | 97.5                             | 1.99 a 1.07                |
|            |           | 180                    | 18.0                      | 97.0                             | 1.86 a 1.00                |
| 2014/2015  | Ayahikari | 60                     | 18.6                      | a 99.1                            | a 2.28 a                   |
|            |           | 100                    | 18.1                      | ab 97.7                           | ab 2.19 ab                 |
|            |           | 140                    | 18.0                      | b 96.9                            | bc 2.05 bc                 |
|            |           | 180                    | 17.8                      | b 96.3                            | c 2.00 c                  |
|            | Iwainodaichi | 18.1          | 18.2                      | 97.1                             | 2.15                       |
|            |           | 18.2                    | 97.9                      | 2.11                        |
| Average    |           | 60                     | 18.1                      | 97.1                             | 2.15                       |
|            |           | 100                    | 18.2                      | 97.9                             | 2.11                       |
|            |           | 140                    | 17.2                      | 95.6                             | 2.08                       |
|            |           | 180                    | 19.1                      | 99.4                             | 2.17                       |

ANOVA

| Seeding rate | Cultivar | Year | S × C | S × Y | C × Y |
|--------------|----------|------|-------|-------|-------|
|              |          | ns   | **    | ***   | ns    |

The number in italics is the ratio when the value of the seeding rate 180 m⁻² is considered as 1. ***, **, and * indicate significance at P < 0.001, P < 0.01, and P < 0.05, respectively. Any two samples with a common letter are not significantly different (P > 0.05), based on the Tukey honestly significant difference (HSD) test.
Table 4. Lodging index, culm length and moment of aerial part of the four different seeding rates and two cultivars.

| Year     | Cultivar         | Seeding rate seeds m⁻² | Lodging index | Culm length (cm) | Moment of aerial part (gf cm) |
|----------|------------------|------------------------|---------------|-----------------|-------------------------------|
| 2013/2014| Aya hikari       | 60                     | 0.59          | 79.3            | 736                           |
|          |                  | 100                    | 0.74          | 80.4            | 685                           |
|          |                  | 140                    | 0.72          | 82.1            | 653                           |
|          |                  | 180                    | 0.76          | 84.1            | 622                           |
|          | Iwainodaichi     | 60                     | 0.65          | 74.8            | 529                           |
|          |                  | 100                    | 0.69          | 80.7            | 540                           |
|          |                  | 140                    | 0.79          | 80.5            | 529                           |
|          |                  | 180                    | 0.91          | 83.1            | 557                           |
| 2014/2015| Aya hikari       | 60                     | 0.69          | 71.2            | 762                           |
|          |                  | 100                    | 0.79          | 75.3            | 806                           |
|          |                  | 140                    | 0.72          | 74.3            | 814                           |
|          |                  | 180                    | 0.82          | 75.0            | 781                           |
|          | Iwainodaichi     | 60                     | 0.72          | 69.6            | 576                           |
|          |                  | 100                    | 0.85          | 72.1            | 588                           |
|          |                  | 140                    | 0.92          | 73.5            | 584                           |
|          |                  | 180                    | 0.86          | 74.3            | 558                           |
|          | Average          |                        | 0.64          | 75.2            | 749                           |
|          | Ayahikari        | 100                    | 0.77          | 77.8            | 746                           |
|          |                  | 140                    | 0.72          | 78.2            | 734                           |
|          |                  | 180                    | 0.79          | 79.5            | 702                           |
|          | Iwainodaichi     | 60                     | 0.68          | 72.2            | 552                           |
|          |                  | 100                    | 0.77          | 76.4            | 564                           |
|          |                  | 140                    | 0.85          | 77.0            | 557                           |
|          |                  | 180                    | 0.88          | 78.7            | 557                           |
| 60       |                  |                        | 0.66          | 73.7            | b 651                          |
| 100      |                  |                        | 0.77          | 77.1            | a 655                          |
| 140      |                  |                        | 0.79          | 77.6            | a 645                          |
| 180      |                  |                        | 0.84          | 79.1            | a 630                          |
| Ayahikari|                | 0.73                    | 77.7          | 733                           |
| Iwainodaichi|           | 0.80                    | 76.1          | 558                           |
| 2013/2014|                | 0.73                    | 80.6          | 606                           |
| 2014/2015|                | 0.80                    | 73.2          | 684                           |

ANOVA

| Seeding rate | Cultivar | Year | S × C | S × Y | C × Y | S × C × Y |
|--------------|----------|------|-------|-------|-------|-----------|
| **           | *        | ***  | -     | -     | -     | ns        |

***, ** and * indicate significance at P < 0.001, P < 0.01, and P < 0.05, respectively.

The moment of the aerial part was obtained as the product of culm length and culm weight at maturity in 2013/2014, or at 2 weeks after heading in 2014/2015. Any two samples with a common letter are not significantly different (P > 0.05) based on the Tukey honestly significant difference (HSD) test.

Stockman, 1980; Thorne & Wood, 1987). The findings from this study suggested that competition for assimilation products during this period in the plots at the high seeding rate seemed to be more intense than that in the plots at the low seeding rate, especially in ‘Iwainodaichi’.

With respect to the development of tillering, non-productive tillers caused loss of dry matter due to competition for assimilation products and decreased yield potential (Berry et al., 2003; Foulkes et al., 2011; Sharma, 1995). Because the canopy structure is affected by the tiller number, seeding rate is presumed to have influenced respiration and photosynthesis of the canopy. In this study, the plots with the lowest seeding rate, where the percentage abortion of tillers and florets was relatively low, exhibited grain yields which were higher than those in the high-seeding-rate plots (Table 1). It was inferred from these findings that the lower seeding rate minimises abortion of florets and tillers and thus is relatively efficient in terms of resource use and in terms of grain yield.

4.2. The effects of seeding rate on lodging resistance

In this study, lodging index was calculated by dividing the moment of the aerial part by the bending moment at breaking of the intact internode. The moment of the aerial part was not significantly affected by seeding rate because culm weight increased and culm length decreased, with decreasing seeding rate (Table 4). Regarding the effect of seeding rate on culm length, it was inferred that the low transmission of solar radiation into the canopy of high-seeding-rate crops further promoted stem elongation in crops sown at high seeding rates. Meanwhile, the bending moment at breaking in the plots sown at a low seeding rate was significantly lower than that in the plots sown at a high seeding rate (Table 5), so that lodging index in the low seeding rate crop was lower (Table 4). This was consistent with previous reports, which had suggested that high seeding rate tended to promote lodging (Faris & De Pauw, 1980; Iwabuchi et al., 2000; Stapper & Fischer, 1990; Webster & Jackson, 1993). The lodging index, calculated with the moment of the aerial part and the bending moment at breaking of the basal internode of wheat and barley cultivars, was previously reported to be correlated with lodging resistance observed in fields (Oda et al., 1966), and have been used to determine the difference of lodging resistance among cultivars and breeding lines (Ma, 2009). The weather during ripening in this study was calm and dry in both trial years (Figure 1), so that there was no lodging despite the high yield (Table 1). However, the findings suggested that lodging resistance increased with decreasing seeding rate.

4.3. The effects of seeding rate on culm strength

The bending moment at breaking of the intact internode, related to resistance to stem breaking-type lodging, and the flexural rigidity of the intact internode, related to resistance to stem bending-type lodging both increased significantly in response to reduced seeding rate (Table 5). Therefore, the wheat culms in the plots with a low seeding rate were stronger than those in the plots with a high seeding rate. Regarding
Table 5. Physiological parameters, representing culm strength, of the four different seeding rates and two cultivars.

| Year       | Cultivar      | Seeding rate seeds m⁻² | Intact internode | Intermode without leaf sheath covering | Degree of reinforcement by leaf sheath covering (%) | Section modulus (mm⁴) | Bending stress (gf mm⁻²) | Intact internode | Intermode without leaf sheath covering | Degree of reinforcement by leaf sheath covering (%) | Second moment of inertia (mm⁻⁶) | Young's modulus (kgf mm⁻²) |
|------------|---------------|------------------------|-----------------|----------------------------------------|-----------------------------------------------|-----------------------|--------------------------|-----------------|----------------------------------------|-----------------------------------------------|---------------------------------|--------------------------|
|            | Aya hikari    | 60                     | 1243            | -                                      | -                                             | 10.7                  | 1169                     | 822             | -                                      | -                                             | -                               | 27.0                     |
| 2013/2014  |               | 100                    | 922             | -                                      | -                                             | 8.34                  | 1118                     | 479             | -                                      | -                                             | -                               | 19.5                     |
|            |               | 140                    | 917             | -                                      | -                                             | 8.88                  | 1032                     | 471             | -                                      | -                                             | -                               | 21.0                     |
|            |               | 180                    | 821             | -                                      | -                                             | 8.23                  | 999                      | 421             | -                                      | -                                             | -                               | 19.1                     |
|            |               | 2013/2014              |                |                                        |                                                |                      |                          |                 |                                        |                                                |                                 |                          |
| 2014/2015  |               | 60                     | 824             | -                                      | -                                             | 6.90                  | 1195                     | 370             | -                                      | -                                             | -                               | 15.1                     |
|            |               | 100                    | 799             | -                                      | -                                             | 6.94                  | 1148                     | 362             | -                                      | -                                             | -                               | 15.4                     |
|            |               | 140                    | 684             | -                                      | -                                             | 6.31                  | 1107                     | 277             | -                                      | -                                             | -                               | 13.8                     |
|            |               | 180                    | 615             | -                                      | -                                             | 5.18                  | 1198                     | 212             | -                                      | -                                             | -                               | 10.5                     |
|            | Iwaino daichi | 60                     | 824             | -                                      | -                                             | 6.90                  | 1195                     | 370             | -                                      | -                                             | -                               | 15.1                     |
| 2014/2015  |               | 100                    | 824             | -                                      | -                                             | 6.94                  | 1148                     | 362             | -                                      | -                                             | -                               | 15.4                     |
|            |               | 140                    | 684             | -                                      | -                                             | 6.31                  | 1107                     | 277             | -                                      | -                                             | -                               | 13.8                     |
|            |               | 180                    | 615             | -                                      | -                                             | 5.18                  | 1198                     | 212             | -                                      | -                                             | -                               | 10.5                     |
|            | Ayahikari     | 60                     | 1175            | -                                      | -                                             | 10.53                 | 1118                     | 704             | -                                      | -                                             | -                               | 27.0                     |
| Average    | 60                     | 1175                 | -              | -                                      | -                                             | 10.53                 | 1118                     | 704             | -                                      | -                                             | -                               | 27.0                     |
|            | Ayahikari     | 100                    | 971             | -                                      | -                                             | 9.63                  | 1030                     | 528             | -                                      | -                                             | -                               | 24.1                     |
|            |               | 140                    | 1026            | -                                      | -                                             | 10.31                 | 1005                     | 567             | -                                      | -                                             | -                               | 25.2                     |
|            |               | 180                    | 890             | -                                      | -                                             | 9.37                  | 957                      | 472             | -                                      | -                                             | -                               | 23.0                     |
|            | Iwainodaichi  | 60                     | 817             | -                                      | -                                             | 7.34                  | 1150                     | 364             | -                                      | -                                             | -                               | 16.4                     |
|            |               | 100                    | 750             | -                                      | -                                             | 7.33                  | 1033                     | 336             | -                                      | -                                             | -                               | 16.3                     |
|            |               | 140                    | 660             | -                                      | -                                             | 6.64                  | 1013                     | 275             | -                                      | -                                             | -                               | 14.6                     |
|            |               | 180                    | 632             | -                                      | -                                             | 6.02                  | 1075                     | 225             | -                                      | -                                             | -                               | 12.7                     |
|            | Ayahikari     | 100                    | 861             | b                                      | 803 a                                     | 6.8                   | 8.48                     | 1031            | 432 b                                     | 361                             | 18.7                            | 20.2                     |
|            |               | 140                    | 843             | b                                      | 769 ab                                    | 12.8                  | 8.47                     | 1009            | 421 b                                     | 345                             | 30.0                            | 19.9                     |
|            |               | 180                    | 761             | c                                      | 715 b                                     | 12.7                  | 7.70                     | 1016            | 349 c                                     | 297                             | 25.1                            | 17.8                     |
|            | Iwainodaichi  | 1015                   | 961             | 8.5                                     | 9.96                                     | 1027                  | 568                      | 483             | 16.7                                     | 24.8                            | 22.9                            |                          |
| 2014/2015  | Ayahikari     | 715                     | 605             | 13.4                                    | 6.83                                     | 1068                  | 300                      | 197             | 33.1                                     | 15.0                            | 20.0                            |                          |
|            |               | 853                     | -              | 7.68                                    | 1121                                     | 427                   | -                        | -               | -                                       | 17.7                            | 23.3                            |                          |
|            |                | 877                     | 783             | 10.9                                    | 9.11                                     | 975                   | 441                      | 340             | 24.9                                     | 22.1                            | 19.6                            |                          |

ANOVA

| Seeding rate | Cultivar | Year | S × C | S × Y | C × Y | S × C × Y |
|--------------|----------|------|------|-------|-------|-----------|
| ***          | ***      | ns   | ns   | ns    | ns    | ns        |
| ***          | ***      | ns   | ns   | ns    | ns    | ns        |
| ns           | ***      | ns   | ns   | ns    | ns    | ns        |
| ***          | ***      | ns   | ns   | ns    | ns    | ns        |

***, ** and * indicate significance at P < 0.001, P < 0.01, and P < 0.05, respectively. Any two samples with a common letter are not significantly different (P > 0.05) based on the Tukey honestly significant difference (HSD) test.
the bending moment at breaking and flexural rigidity, the degree of reinforcement by leaf sheath covering were not affected by the seeding rate (Table 5). The high seeding rate reduced the strength of the internode without leaf sheath covering (Table 5), suggesting that the seeding rate affected the structure of the culm or cell wall components, rather than the leaf sheath.

Both of section modulus and bending stress tended to increase as the seeding rate decreased (Table 5). The second moment of inertia and Young’s modulus also tended to increase as the seeding rate decreased (Table 5). Hence, these data suggest that the seeding rate affected both culm morphology and a function of culm cell wall components.

The thickness of cortical fibre tissue is regarded as being important for strong culm properties in rice (Matsuda et al., 1983). The rice cultivar ‘Leaf Star’, for example, with excellent resistance to lodging has thick cortical fibre tissue (Ookawa et al., 2014). The concentrations and densities of lignin, celluloses and hemicellulose constituting the cell wall also influence culm strength (Kokubo et al., 1989; Li et al., 2003; Matsuyama et al., 2014; Ookawa & Ishihara, 1993). It can be inferred that the seeding rate changed the canopy structure and affected not only internodal elongation but also thickening and accumulation of cell wall components.

4.4. The difference in lodging index and culm strength between two cultivars

The effects of seeding rate on culm strength and lodging resistance did not differ between ‘Ayahikari’ and ‘Iwainodaichi’, because the [cultivar × seeding rate] interaction for neither parameter was significant about both lodging index and culm strength (Table 2). Meanwhile, it was confirmed that ‘Ayahikari’ had greater resistance to lodging because of a high bending moment at breaking of the intact basal internode and a low lodging index (Table 4), as previously reported (Matsuyama et al., in press). Therefore, a cultivar such as Ayahikari, with high lodging resistance, should demonstrate marked lodging resistance when it is sown at a lower seeding rate. That would encourage application heavy fertiliser treatment necessary to achieve high yields.

Regarding the reinforcement of the bending moment at breaking and flexural rigidity by leaf sheath covering, ‘Iwainodaichi’ outperformed ‘Ayahikari’ (Table 5). The decline of reinforcement of culm strength by leaf sheath covering has been suggested to be caused by the senescence of the leaf sheath (Ookawa & Ishihara, 1992). Although ‘Iwainodaichi’ had a relatively weak culm, the greater reinforcement of culm strength by leaf sheath covering seemed to be beneficial to maintaining lodging resistance.

5. Conclusion

Culm strength and lodging resistance changed depending on the seeding rate regardless of cultivar characteristics associated with culm strength. Coincidently, wheat cultivars demonstrated greater culm strength and lodging resistance, when cultivated at a low seeding rate. It was suggested that the low seeding rates method would be suitable for heavily fertilized cultivation in both cases of cultivar with high culm strength and low culm strength. Spike number per m² decreased, and grain number per spike increased, as a result of decreased seeding rate, so the grain yield in plots sown at low seeding rate were almost the same or slightly higher than that in plots sown at high seeding rate. The optimal seeding rate to obtain high yields differs depending on the environment and cultivars. Both ‘Ayahikari’ and ‘Iwainodaichi’ have a relatively long spike (Taya et al., 2002; Yoshida et al., 2001), and tend to gain high grain number per spike. It is assumed that these cultivars with the high number of grains per spike are suitable for the practice of low seeding rate that keeps high yield and improves lodging resistance.

Except for the situation in Hokkaido, wheat in Japan is grown as an off-season crop in paddy fields. Because of concerns regarding poor seedling establishment caused by wet soil, farmers have tended to set seeding rates high. But recently, long-term upland crop rotation and improvement of drainage such as the introduction of underground drains or sloping fields using a laser leveller, which contribute to the improvement of seedling establishment, are becoming popular. Under these conditions of good seedling establishment, lowering the seeding rate that improve lodging resistance could be a cultivation technique that would be widely adopted by farmers.

Disclosure statement

No potential conflict of interest was reported by the authors.

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