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REVIEW

Breeding and Agronomic Research on Lodging Resistance and Culm Strength of Japanese Wheat Cultivars

Hiromi MATSUYAMA*

Central Region Agricultural Research Center, National Agriculture and Food Research Organization, Tsukuba, Japan

Abstract

Here, Japanese wheat breeding and agronomic studies on lodging resistance, focusing on culm strength are discussed. In Japan, the selection of short-culm wheat varieties is preferred for breeding purposes to date due to their lodging resistance, whereas culm strength has only marginally improved. However, improving culm strength was suggested to help improve lodging resistance in short-culm varieties. Thus, among the 18 typical and predominant wheat varieties, "Yumechikara" showed maximum bending moment at the breaking of the basal internode and produced the strongest culm. Meanwhile, among other varieties that produced strong culms, some demonstrated considerable bending stress and medium section modulus, whereas some showed medium bending stress and large section modulus. Improved varieties with higher lodging resistance may be produced by crossbreeding of varieties with different levels of culm strength. Regarding the effects of crop management, decreased seeding rates resulted in shorter culm length and increased bending moment at the breaking point of the basal internode, which indicated higher lodging resistance. Therefore, low seeding rates may be suitable for heavily fertilized wheat crops, requiring high lodging resistance.

Discipline: Crop Science
Additional key words: bending moment at breaking, seeding rate

Introduction

Improving wheat lodging resistance is indispensable for achieving consistently high yields; further, wheat lodging may be prevented through inhibition of internodal elongation by applying plant growth regulators such as chlormequat, ethephon, or trinexapac-ethyl. However, in Japan, except in the northern region, Hokkaido, few growth regulators are permitted for agricultural use; therefore, high crop yields based on the application of growth regulators and heavy fertilization are rather uncommon. Thus, alternatives to growth regulator treatments are necessary to prevent lodging while aiming for high yields.

In Europe, wheat lodging is categorized into two types: stem lodging, in which case the culm bends and breaks, and root lodging, in which case straight culm tilts and lodging occurs from the root (Pinthus 1973). Culm length and strength, panicle weight, and root development are important factors for preventing the lodging of grain crops, including wheat (Pinthus 1973). In contrast to Pinthus (1973), who assumed root lodging was more critical, whereby he focused on the root system, Berry et al. (2004) examined culm strength in detail, and developed a wheat lodging model by clarifying the physical mechanism of lodging, including external factors such as wind speed and rainfall. Subsequently, they identified the ideal shape of the wheat plant for the highest resistance to lodging (Berry et al. 2007).

In Japan, wheat lodging is categorized into three types: stem-breaking lodging, stem-bending lodging, and root lodging. Among these, stem-bending lodging is particularly common in wheat crops in Japan. Thus, to date, the Japanese breeding of wheat varieties has focused on the production of short-culm varieties for improving lodging resistance; however, presumably, not only culm length but also culm strength, affected lodging resistance in Japanese wheat. Oda et al. (1966) investigated

*Corresponding author: matsuyama.hiromi@affrc.go.jp
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differences in lodging resistance and culm strength in a wide range of barley and wheat varieties used in the United States, Europe, and Japan, and they found that wheat lodging resistance is lower in Japanese than in overseas varieties, whereas that of Japanese barley was higher than that of overseas varieties. Regarding lodging resistance of Japanese barley, physical traits and cell wall components related to culm strength (Hozyo & Oda 1965a, b; Kokubo et al. 1989) and effects of shading and inter-row space on culm strength (Hozyo & Oda 1965c, 1967) have been examined. However, few studies on lodging in wheat, compared to barley, have been conducted in Japan. Indeed, lodging resistance and culm strength of Japanese wheat, including recently produced varieties have never been examined. Additionally, potential effects of cultivation methods on lodging resistance of Japanese wheat remained unclear.

This paper discusses recent breeding efforts and agronomic studies regarding lodging resistance, focusing on culm strength of Japanese wheat. A "core collection of Japanese wheat varieties" (Kojima et al. 2017) and 18 typical wheat varieties currently predominant in areas from Hokkaido to Kyushu were examined to elucidate changes in lodging resistance in novel wheat varieties, and to identify the characteristics of major varieties. Moreover, the effects of nitrogen topdressing and seeding rates on lodging resistance and culm strength of Japanese high-yielding varieties are discussed.

Measuring lodging resistance and culm strength

The physiological parameters of the third internode (the neck internode of the spike was deemed the first internode) of the main culm, which is closely associated with stem lodging, were investigated 2 weeks after heading. The bending load at the breaking of the basal internode was measured at a distance of 4 cm between two supporting points (Ookawa & Ishihara 1992) using a TA. XT plus Texture Analyzer (Stable Micro Systems, Godalming, UK). The bending moment at breaking (gf cm) was considered the maximum stress. The outer and inner radii (a_1 and a_2, respectively) of the minor axis in the cross-section of the middle part of the internode were measured, and the outer and inner radii of the major axis (b_1 and b_2, respectively), to calculate the section modulus (mm^3) as follows:

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

The bending stress (gf mm^{-2}) was calculated by dividing the bending moment at breaking by the section modulus.

Lodging resistance and culm strength of native and breeding Japanese wheat varieties

1. Changes in lodging resistance and culm strength in Japanese wheat breeding

A core collection is a set of representative varieties and lines selected to reflect the genetic variation within numerous conserved genetic resources. A "Core collection of Japanese wheat varieties" was created in the gene bank project "Creation of the Japanese wheat core collection" (2009-2011) and preserved at the Research Center for Genetic Resources, National Agriculture and Food Research Organization (NARO). This collection comprised 44 native varieties and varieties produced through pure line selection, 51 varieties produced through modern hybrid breeding, and the genetic standard line "Chinese Spring." Of these 96 varieties, 94 (excluding "Saitama No. 27" [ID: JWC50] and "Chinese Spring" [ID: JWC96], which showed problems at the time of sowing; Table 1) were tested in the field. The test site was the NARO Central Region Agricultural Research Center located in Ibaraki, central Japan (36°0′ N, 140°0′ E, at an elevation of 24 m above mean sea level). A total of 34 seeds of each variety were sown on November 6, 2009 and November 5, 2010, at 80 and 5 cm inter-row and inter-hill spacing, respectively.

Prior to the establishment of "HACHIMAN KOMUGI" in 1973, culm lengths varied substantially, whereas after this, culm length typically did not exceed 100 cm (Fig. 1), indicating selection of short-culm varieties that are more lodging resistant. However, regarding the bending moment at breaking of the basal internode, few varieties were lower than the average of the 94 varieties tested, even among the wheat varieties produced after the 1970s. Thus, in reality, culm strength was hardly increased through breeding selection in Japan.

Culm length is a trait typically investigated during the breeding process; furthermore, it can be assessed visually, whereas characteristics related to culm strength are more difficult to judge in this manner. In addition, culm length is a relatively simple trait determined by a single gene, whereas culm strength is a complex characteristic depending on multiple traits. Therefore, selection of varieties with high culm strength likely difficult to implement in the wheat breeding process.

Additionally, genes affecting culm length may negatively affect yield (Kashiwagi et al. 2007). Varieties with short-culm length reportedly showed increased leaf area density, decreased CO_2 and water vapor diffusion, and decreased photosynthesis (Kuroda et al. 1989). Wheat varieties used in Japan over the past 40 years typically show a comparably short culm length (80 cm-85 cm);

thus, further reduction of the culm length may not be desirable concerning grain yield.

2. The correlation between lodging resistance and culm strength

Among the 94 varieties of the "Core collection of Japanese wheat varieties" used in the field test, 57 varieties showing lodging in both years were categorized according to culm length. The classification was made using three categories of equal range between minimum culm length (65.4 cm, for "KOMUGI NOURIN 10") and maximum culm length (149.5 cm, for "SAPPORO HARU KOMUGI"). Varieties with culms shorter than 93.4 cm were categorized in the short-culm group, varieties with culm lengths between 93.4 cm- 121.5 cm were classified as the intermediate-culm group, and varieties with culm lengths of 121.5 cm or more were classified as the long-culm group. Then, the relationship between each trait and the number of days from heading to lodging was analyzed.

In the intermediate- and long-culm groups, a significant negative correlation between culm length and the number of days from heading to lodging was observed (Fig. 2). In turn, in the short-culm group (< 93.4 cm), there was no significant correlation between culm length and the number of days from heading to lodging; however, a significant positive correlation was detected between the section modulus of the basal internode (the value of strength determined by the shape of the cross section) and the number of days (Fig. 2). Therefore, increasing culm strength may help improve lodging resistance in short-culm wheat varieties (Matsuyama et al. 2014).

Culm strength of typical wheat varieties used in Japan in recent years

1. Culm characteristics of varieties with strong culms

We compared culm characteristics of 18 typical wheat varieties grown in each region of Japan recently (Table 2). The test site was the NARO Central Region Agricultural Research Center. Fifty seeds of each variety were sown on November 14, 2013, and on November 13, 2014, at 70 and 5 cm inter-row and inter-hill spacing, respectively.

Among the 18 varieties under study, "Yumechikara" grown in the Hokkaido region in 2010 showed the largest bending moment at breaking of the basal internode (Fig. 3). In turn, "Yukichikara," "Kinunonami," "Ayahikari," and "Chikugoizumi" showed large bending moments at breaking. Among these, "Yukichikara" and

Table 1. The 94 varieties of a "Core collection of Japanese wheat varieties" tested in this study

ID	Varieties	ID	Varieties	ID	Varieties	ID	Varieties
JWC 01	AKAGAWA AKA	JWC 25	SAKOBORE	JWC 49	KOUNOSU 25	JWC 74	AOBA KOMUGI
JWC 02	SHIRO HADA	JWC 26	SHIN CHUNAGA	JWC 51	KANTOU 107	JWC 75	HITSUMI KOMUGI
JWC 03	DOUSON 1	JWC 27	HATAKEDA KOMUGI	JWC 52	IGA CHIKUGO OREGON	JWC 76	FURUTSU MASARI
JWC 04	SAPPORO HARU KOMUGI	JWC 28	YUUSHOUKI 347	JWC 53	GOKUWASE 4-15	JWC 77	YUKICHABO
JWC 05	SOUSHUU 2	JWC 29	HIROSHIMA SHIPUREE	JWC 54	KOMUGI NOURIN 1	JWC 78	HIKARI KOMUGI
JWC 06	SHISEN 1	JWC 30	MUBOU CHINKO	JWC 55	HARUMAKI KOMUGI NOURIN 3	JWC 79	FUKUHO KOMUGI
JWC 07	ZAIRAI FURUTZ	JWC 31	HIRAKI KOMUGI	JWC 56	KOMUGI NOURIN 9	JWC 80	FUKUWASE KOMUGI
JWC 08	NISHIMURA	JWC 32	NAKA SOUSHUU	JWC 57	KOMUGI NOURIN 10	JWC 81	ABUKUMA WASE
JWC 09	SHIRASAYA	JWC 33	HOUMAN	JWC 58	KOMUGI NOURIN 16	JWC 82	HOKUSHIN
JWC 10	FUKOKU	JWC 34	SEKICHIKU 1	JWC 59	KOMUGI NOURIN 26	JWC 83	CHIHOKU KOMUGI
JWC 11	AKAGARA IBARAKI 1	JWC 35	ESHIMA SHINRIKI	JWC 60	KOMUGI NOURIN 27	JWC 84	HARUYUTAKA
JWC 12	SHIRO SANJAKU	JWC 36	IGA CHIKUGO	JWC 61	KOMUGI NOURIN 39	JWC 85	NANBU KOMUGI
JWC 13	AKA BORO 1	JWC 37	SHIRO KOMUGI	JWC 62	KOUSHITSU KOMUGI NOURIN 42	JWC 86	KITAKAMI KOMUGI
JWC 14	NITTA WASW	JWC 38	CHIKUZEN	JWC 63	KOMUGI NOURIN 50	JWC 87	SHIRANE KOMUGI
JWC 15	SUNEKIRI 15	JWC 39	ICHIGOU HAYA KOMUGI	JWC 64	KOMUGI NOURIN 53	JWC 88	BANDOU WASE
JWC 16	AKA BOUZU	JWC 40	SHIRO BUNBU	JWC 65	KOMUGI NOURIN 55	JWC 89	SHIROGANE KOMUGI
JWC 17	HOSOGARA	JWC 41	ASO ZAIRAI (YUUBOU KAPPU)	JWC 66	KOMUGI NOURIN 61	JWC 90	CHIKUGOIZUMI
JWC 18	SHIRO DARUMA	JWC 42	SOTOME	JWC 67	KOMUGI NOURIN 67	JWC 91	KOMUGI NOURIN 20
JWC 19	AKA DARUMA	JWC 43	SADA BOUZU	JWC 68	HARUMAKI KOMUGI NOURIN 75	JWC 92	FUJIMI KOMUGI
JWC 20	WASE KOMUGI	JWC 44	NOBEOKABOUZU KOMUGI	JWC 69	HOKUEI	JWC 93	SHIRASAGI KOMUGI
JWC 21	AKA KOMUGI	JWC 45	SAKIGAKE 1	JWC 70	MUKA KOMUGI	JWC 94	JUNREI KOMUGI
JWC 22	SHIBU SHIRAZU	JWC 46	AKASABI SHIRAZU 1	JWC 71	HOROSHIRI KOMUGI	JWC 95	HACHIMAN KOMUGI
JWC 23	KOSHIGUN ZAIRAISHU	JWC 47	HONKEI 275	JWC 72	TAKUNE KOMUGI		
JWC 24	SHIRO CHABO	JWC 48	HOKKAI 240	JWC 73	HARUHIKARI		

"ID" is the gene bank ID at Research Center for Genetic Resources, National Agriculture and Food Research Organization (NARO).
"Saitama No. 27" [ID: JWC50] and "Chinese Spring" [ID: JWC96] showed problems at the time of sowing and could not be used in the analysis.

"Chikugoizumi" showed large bending stress and medium section modulus, whereas "Kinunonami" and "Ayahikari" showed medium bending stress and large section modulus.

The high-yielding rice variety "Leaf star," which produces extremely strong culms (Kato et al. 2010), likely inherited the large section modulus from "Chugoku 117," and the high maximum bending stress from "Koshihikari" (Ookawa & Ishihara 1997). However, in wheat, improved varieties with higher lodging resistance may be produced through crossbreeding of varieties with different levels of culm strength (Matsuyama et al. 2020). Measuring physical properties associated with culm strength is expected to accelerate wheat breeding aimed at improving lodging resistance.

2. Correlation between culm strength and yield

The cross-sectional area of the basal internode was significantly and positively correlated with spikelet number per spikelet in the 18 wheat varieties tested (Fig. 4). Ookawa et al. (2010) identified an effective quantitative trait locus (QTL) associated with culm strength, which was designated STRONG CULM2 (*SCM2*). Moreover, they found that *SCM2* was identical to ABERRANT PANICLE ORGANIZATION1 (*APO1*), which was previously reported to affect panicle structure (Terao et al. 2010). Additionally, a near-isogenic line carrying *SCM2* showed enhanced culm strength and higher spikelet numbers because of the pleiotropic effects of this gene. Similar factors affecting culm strength and

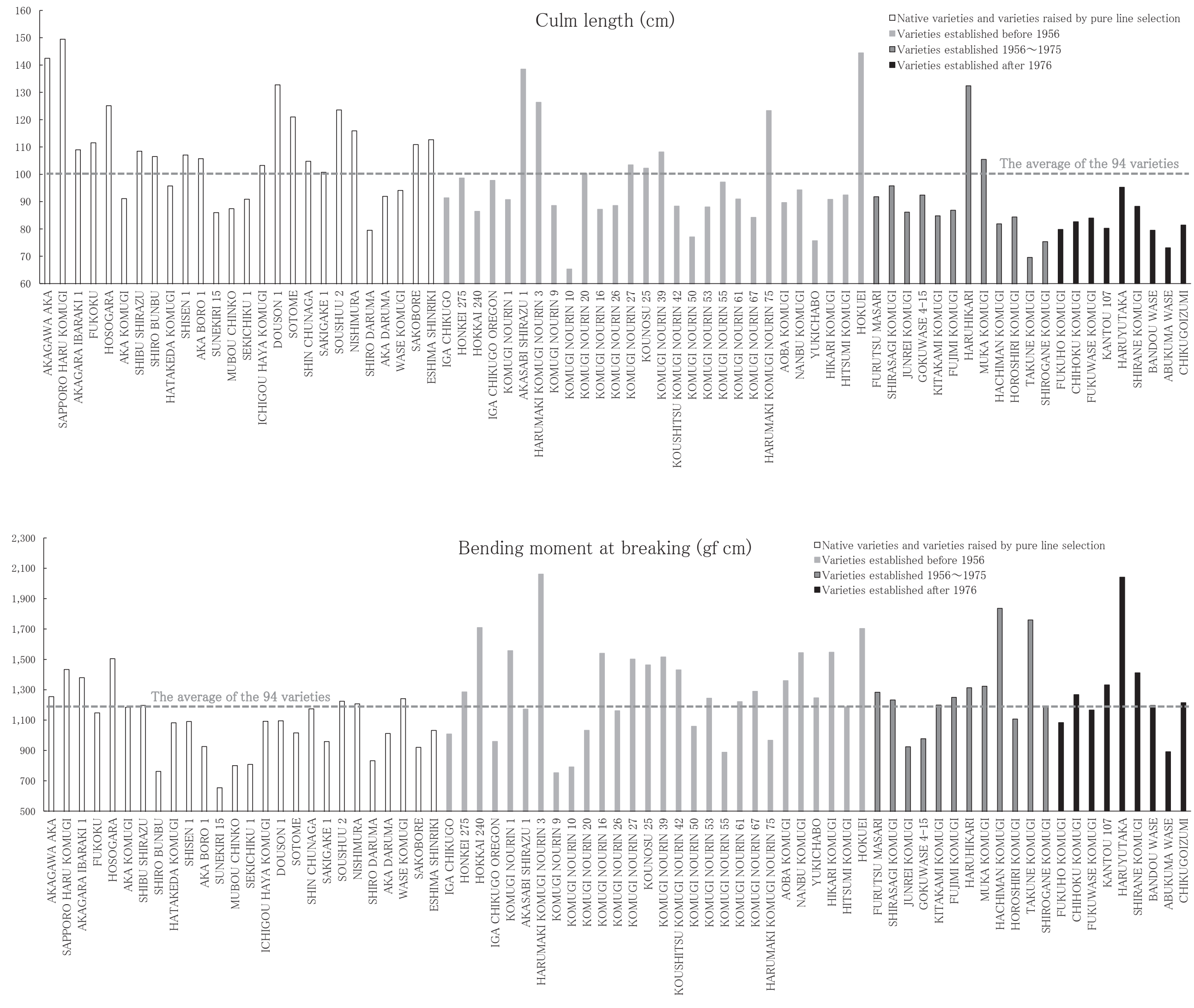

Fig. 1. Culm length and the bending moment at breaking of the basal internode of the 94 varieties arranged in order of establishment year

spikelet numbers are expected to occur also in wheat; thus, increasing culm strength and improving sink capacity in wheat variety breeding may not necessarily constitute a conflict.

Cultivars bred in the Hokkaido region showed larger cross-sectional areas and more spikelets number per spike than cultivars bred in the Kyushu region. Meanwhile, cultivars bred in the Kanto region showed intermediate values for the same parameters (Fig. 4). Different varieties produced in the same region are typically selected under similar conditions and frequently originate from a common parent, whereas they are likely to share some characteristics. For example, varieties bred in Hokkaido show vertical and closed tiller posture, whereas those bred in Kyushu produced tilted spread tillers. In paddy rice, the strength of the basal part is superior when the proportion of productive tillers is high (Yoshinaga et al. 2001); moreover, culm-related traits may differ between regions due to tillering characteristics associated with the respective plant types.

Effects of crop management on wheat lodging resistance and culm strength

1. Nitrogen topdressing

Supplemental nitrogen is indispensable for increasing wheat yield, but with increasing amounts of topdressing nitrogen, culm length increases, culm strength decreases, and the risk of lodging increases (Crook & Ennos 1995, Kurai et al. 1998, Berry et al. 2000). The effects of the

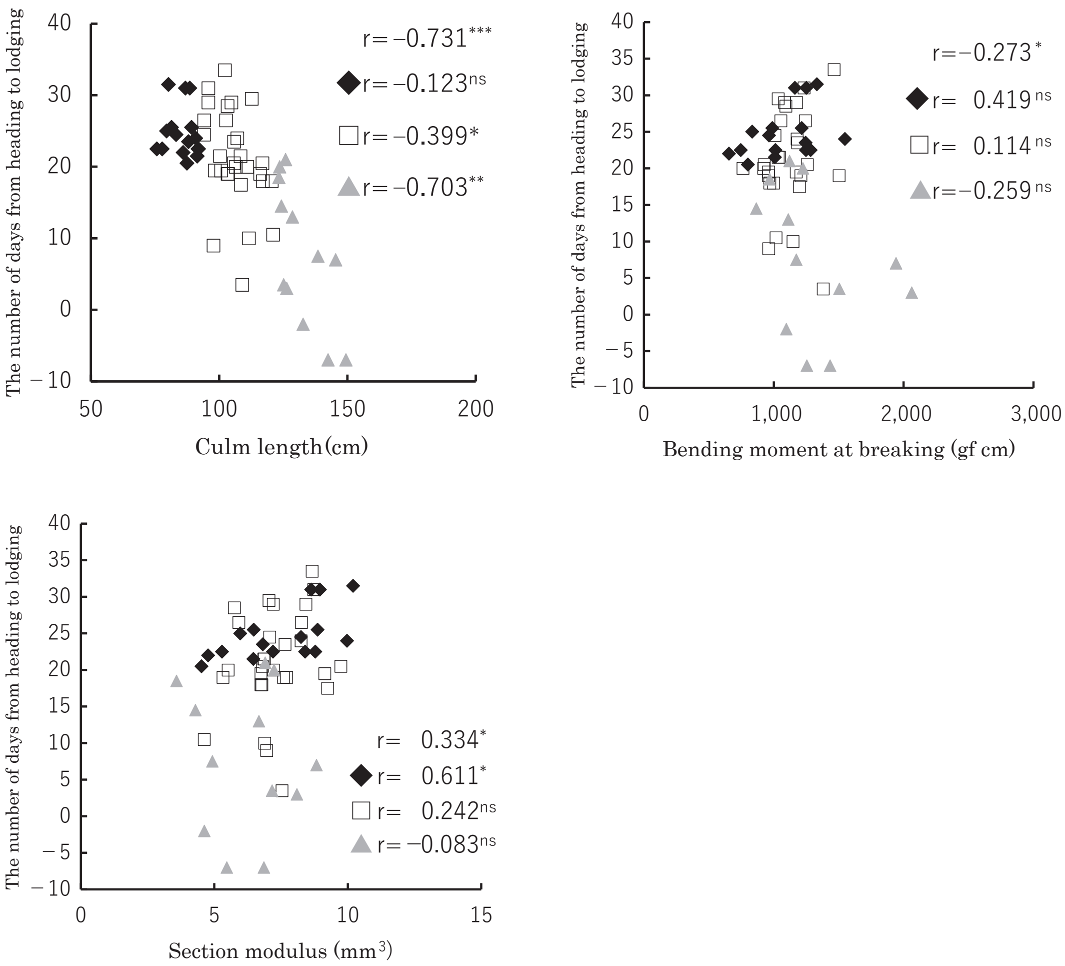

Fig. 2. Correlation between the number of days from heading to lodging and culm length, bending moment at breaking, and section modulus of the basal internode of the 57 varieties

◆: short-culm group (< 93.4 cm)

□: intermediate-culm group (93.4 cm-121.5 cm)

▲: long-culm group (> 121.5 cm)

“r” is the correlation coefficient value

*, **, and ***: significant at the 0.05, 0.01 and 0.001 levels; ns: not significant

timing of supplemental nitrogen on lodging resistance and culm strength were examined by field tests using Japanese noodle wheat cultivars “Ayahikari” and “Iwainodaichi.” The test site was at the NARO Institute of Crop Science in Ibaraki, central Japan (36°0′ N, 140°0′ E, at an elevation of 24 m above mean sea level). Seeds were sown at 140 seeds m^{-2} on November 5, 2013 and on October 28, 2014, with 15 cm inter-row spacing. Supplemental nitrogen (ammonium sulfate; 80 kg/ha) was applied at three different growth stages, representing three treatments. The three stages were GS30 (ear at 1 cm), GS32 (second node detectable), and GS39 (flag-leaf ligule just visible), according to Zadoks growth stages (Tottman 1987). A fourth treatment without supplemental nitrogen was used as control.

The supplemental nitrogen application decreased the bending moment at breaking of the basal internode at GS30 and GS32 (Fig. 5). The supplemental nitrogen administration at GS30 increased culm length, and accordingly, application at GS32 (after the jointing stage) appeared comparably more beneficial than that before the jointing stage. However, under high-yield cultivation conditions, nitrogen administration near the jointing stage appears to be indispensable. The side effect of a greater risk of lodging may be ameliorated by strong-culm cultivars or methods other than nitrogen fertilization (Matsuyama & Ookawa 2021).

2. Seeding rate

The seeding rate is an important crop management factor, along with nitrogen fertilization. We compared the effects of four seeding rates (60, 100, 140, and 180 seeds m^{-2}) on lodging resistance and culm strength using the cultivars “Ayahikari” and “Iwainodaichi.” The study site was the NARO Central Region Agricultural Research Center. Seeds were sown on November 8, 2013, and on November 5, 2014, at 15 cm inter-row spacing.

Table 2. The 18 typical wheat varieties grown in each region of Japan

Region	Varieties
Hokkaido	HARUYUTAKA HOKUSHIN KITAHONAMI YUMACHIKARA
Tohoku	NANBU KOMUGI YUKICHIKARA SHIRANEKOMUGI YUMEKAORI
Kanto	AYAHIKARI KINUNONAMI YUMESHIHOU SATONOSORA
Tokai	KINUAKARI
Kyushu	KOMUGI NOURIN 61 SHIROGANE KOMUGI CHIKUGOIZUMI IWAINODAICHI NISHINOKAORI

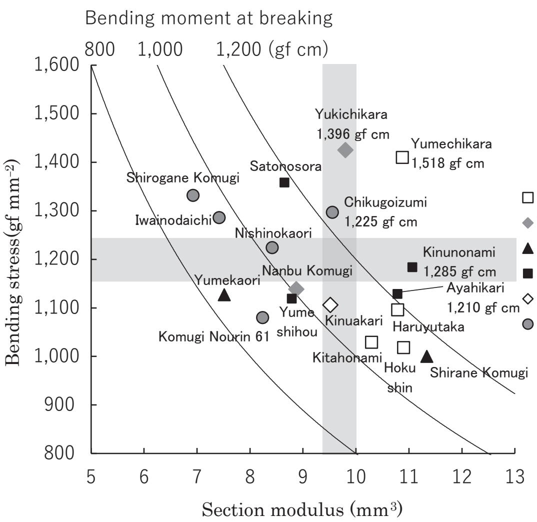

Fig. 3. Bending stress and section modulus among the 18 typical wheat varieties grown in each region of Japan

The gray range is the range of mean ± standard error of the 18 varieties.

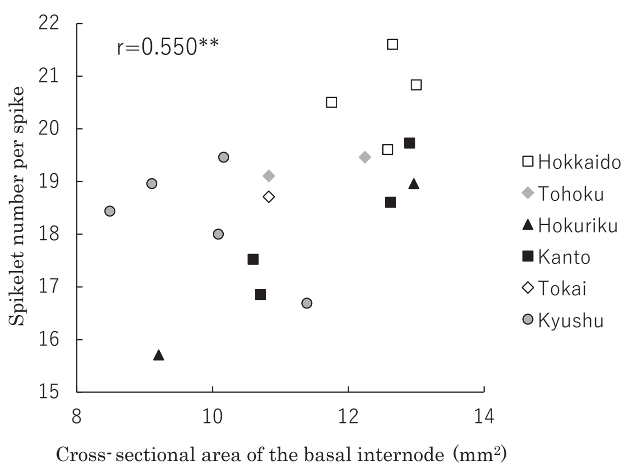

Fig. 4. Correlation between spikelet number per spike and cross-sectional area of the basal internode among the 18 typical wheat varieties grown in each region of Japan

Culm length decreased, and the bending moment at the breaking of the basal internode increased with a decrease in seeding rate, indicating improved lodging resistance (Fig. 6). Additionally, grain yield was not significantly affected in this case. Therefore, low seeding rates may be better suited for heavily fertilized wheat crops that require high lodging resistance (Matsuyama & Ookawa 2019).

Except for the condition of Hokkaido, wheat in Japan is grown in paddy fields as an off-season crop. Owing to concerns regarding poor seedling establishment in wet soils, farmers tend to use a high seeding rate; however, recently, long-term upland crop rotation and improvement of drainage, such as through the introduction of underground drains or sloping fields established using a laser leveler, which contributes to improving seedling establishment, have become popular. Under such conditions of highly successful seedling establishment, lower seeding rates may be better management practice to improve lodging resistance in wheat.

Conclusion and perspectives

During the “Green Revolution,” short-culm varieties for cultivation under heavy fertilization were developed through crossings with “KOMUGI NOURIN 10” that carries semi-dwarf genes *Rht1* and *Rht2*, thereby facilitating mass production of wheat. Even in

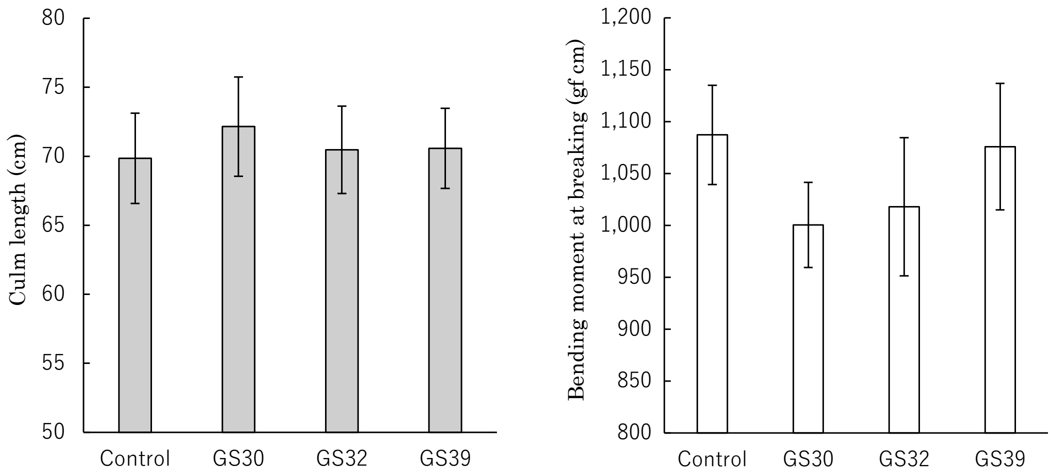

Fig. 5. Effects of timing of supplemental nitrogen on culm length and bending moment at breaking of the basal internode
Bars indicate standard deviation.

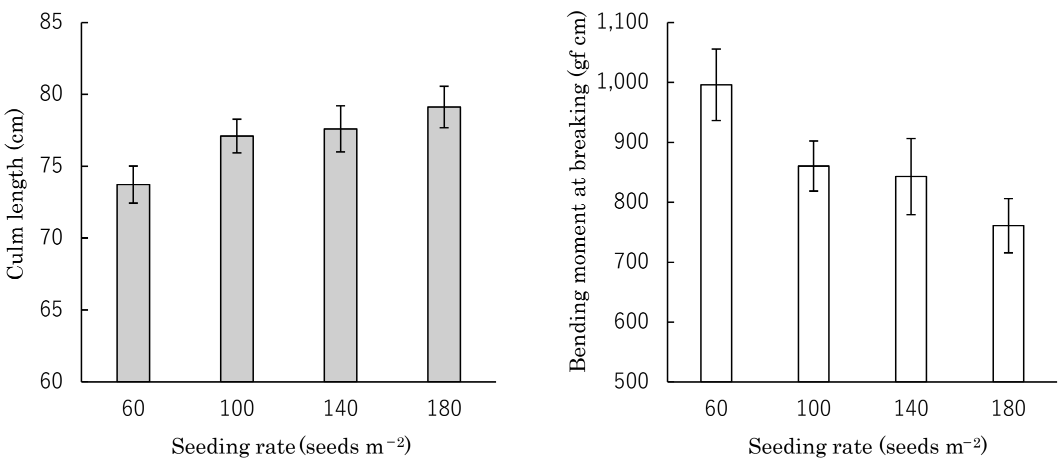

Fig. 6. Effects of seeding rates on culm length and bending moment at breaking of the basal internode
Bars indicate standard deviation.

the present-day breeding of Japanese wheat varieties, lodging resistance has been improved mainly through developing short-culm varieties, and most of the varieties produced in recent years are short-culm varieties carrying either *Rht1* or *Rht2* (Kojima et al. 2017). However, even short-culm varieties may exhibit lodging at yields exceeding approximately 600 g m^{-2}. Therefore, significant improvement of lodging resistance is necessary to achieve higher wheat yields.

High-yielding wheat varieties cultivated in the United Kingdom, Germany, and New Zealand, representing the world's high-yield regions, have been improved to a panicle weight type with numerous grains per spike and a large 1,000-grain weight (Reynolds et al. 2012). Most of the high-yielding paddy rice varieties produced recently in Japan are also panicle weight types (Fukushima 2020) that are prone to lodging due to the large above-ground moment; thus, they depend on higher lodging resistance.

These studies indicate markedly inter-variety differences in wheat culm strength, in addition to variations in culm strength characteristics. Therefore, it is possible to develop high-yielding wheat varieties with strong culms and extremely high resistance to lodging by crossing varieties with different culm strength characteristics. Nonetheless, to characterize culm strength, first, it is necessary to measure the physical properties of culms in varieties and lines that can be used as breeding materials.

QTL analyses of rice showed that *APO1/SCM2* and *FC1/SCM3* originated from different ecotypes and they were identified as genes associated with culm strength; thus, culm strength can be increased through an accumulation of these genes, as in "Koshihikari" (Ookawa et al. 2010, Yano et al. 2015). QTL analyses and genome-wide association studies are expected to promote the identification of genes and QTLs associated with culm strength; furthermore, the discovery of orthologs of culm and ear morphogenesis genes identified in rice may help improve lodging resistance and yield in Japanese wheat varieties.

Finally, the results of our crop management tests showed that culm strength and lodging resistance of wheat were improved by a reduction in seeding rate. Some wheat farmers in Hokkaido, who pursue advanced high-yielding cropping in upland fields using plant growth regulators to reduce culm growth, also manage the number of stems by optimizing seeding rates and fertilization to prevent lodging. Thus, even in wheat that is grown in paddy fields as an off-season crop, high-yielding crop management to achieve both lodging resistance and yields by reducing the seeding rates will be developed and disseminated in the future.

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References

Berry, P. M. et al. (2000) Controlling plant form through husbandry to minimise lodging in wheat. *Field Crops* Res., **67**, 59-81.

Berry, P. M. et al. (2004) Understanding and reducing lodging in cereals. *Adv. Agron*., **84**, 217-271.

Berry, P. M. et al. (2007) Ideotype design for lodging-resistant wheat. *Euphytica*, **154**, 165-179.

Crook, M. J. & Ennos, A. R. (1995) The effect of nitrogen and growth regulators on stem and root characteristics associated with lodging in two cultivars of winter wheat. *J. Exp. Bot*., **46**, 931-938.

Fukushima, A. (2020) Varietal characteristics and cultivation techniques of rice for business use and feed in the Tohoku region of Japan. *Jpn. J. Crop Sci*., **89**, 1-7 [In Japanese with English summary].

Hozyo, Y. & Oda, K. (1965a) Studies on the stiffness of culms in barley plants (*Hordeum sativum*, JESSEN): 2. The development of physical properties in culms. *Jpn. J. Crop Sci*., **33**, 259-262 [In Japanese with English summary].

Hozyo, Y. & Oda, K. (1965b) Studies on the stiffness of culms in barley plants (*Hordeum sativum*, JESSEN): 4. The chemical constitution of culms. *Jpn. J. Crop Sci*., **33**, 268-271 [In Japanese with English summary].

Hozyo, Y. & Oda, K. (1965c) Studies on the stiffness of culms in barley plants (*Hordeum sativum*, JESSEN): 5. Effects of shading on development in culms. *Jpn. J. Crop Sci*., **33**, 272-276 [In Japanese with English summary].

Hozyo, Y. & Oda, K. (1967) Studies on the stiffness of culms in barley plants (*Hordeum sativum*, JESSEN): 14. The interrelationship of planting density and culm strength. *Jpn. J. Crop Sci*., **36**, 85-93 [In Japanese with English summary].

Kashiwagi, T. et al. (2007) Improvement of resistance to bending-type lodging in rice. *Jpn. J. Crop Sci*., **76**, 1-9 [In Japanese with English summary].

Kato, H. et al. (2010) Breeding of the rice cultivar "Leaf Star" with high stem and leaf yield for whole crop silage. *Bull. Nat. Inst. Crop Sci*., **11**, 1-15 [In Japanese with English summary].

Kojima, H. et al. (2017) Development and evaluation of the core collection of Japanese wheat varieties. *Bull. NARO Inst. Crop Sci*., **1**, 1-13 [In Japanese with English summary].

Kokubo, A. et al. (1989) Culm strength of barley: Correlation among maximum bending stress, cell wall dimensions, and cellulose content. *Plant Physiol*., **91**, 876-882.

Kurai, K. et al. (1998) Change of growth by the phase of top dressing and the improved method of fertilizer application in wheat. *Bull. Tochigi Agric. Exp. St*., **4**, 1-12 [In Japanese with English summary].

Kuroda, E. et al. (1989) Analysis on difference of dry matter production between rice cultivars with different plant height in relation to gas diffusion inside stands. *Jpn. J. Crop Sci.*, **58**, 374-382 [In Japanese with English summary].

Matsuyama, H. et al. (2014) Varietal difference in lodging resistance and culm characteristics of wheat. *Jpn. J. Crop Sci.*, **83**, 136-142 [In Japanese with English summary].

Matsuyama, H. & Ookawa, T. (2019) The effects of seeding rate on yield, lodging resistance and culm strength in wheat. *Plant Prod. Sci.*, **23**, 322-332.

Matsuyama, H. et al. (2020) The characteristics influencing strong culm associated with lodging resistance of main wheat cultivars in Japan. *Jpn. J. Crop Sci.*, **89**, 119-125 [In Japanese with English summary].

Matsuyama, H. & Ookawa, T. (2021) Effects of timing of supplemental nitrogen application on lodging resistance and yield of wheat (*Triticum aestivum* L.). *Jpn. J. Farm Work Res.*, **56**, 17-27.

Oda, K. et al. (1966) Varietal analysis of physical characters in wheat and barley plants relating to lodging and lodging index. *Bull. Nat. Inst. Agric. Sci.*, **D15**, 55-85 [In Japanese with English summary].

Ookawa, T. & Ishihara, K. (1992) Varietal difference of physical characteristics of the culm related to lodging resistance in paddy rice. *Jpn. J. Crop Sci.*, **61**, 419-425 [In Japanese with English summary].

Ookawa, T. & Ishihara, K. (1997) Genetic characteristics of breaking strength of basal culm related to lodging resistance in a cross between Koshihikari and Chugoku 117. *Jpn. J. Crop Sci.*, **66**, 603-609 [In Japanese with English summary].

Ookawa, T. et al. (2010) New approach for rice improvement using a pleiotropic QTL gene for lodging resistance and yield. *Nat. Comm.*, **1**, 132.

Pinthus, M. J. (1973) Lodging in wheat, barley, and oats: The phenomenon, its causes, and preventive measures. *Adv. Agron.*, **25**, 209-263.

Reynolds, M. et al. (2012) Achieving yield gains in wheat. *Plant Cell Environ.*, **35**, 1799-1823.

Terao, T. et al. (2010) A gene controlling the number of primary rachis branches also controls the vascular bundle formation and hence is responsible to increase the harvest index and grain yield in rice. *Theor. Appl. Genet.*, **120**, 875-893.

Tottman, D. R. (1987) The decimal code for the growth stages of cereals, with illustrations. *Ann. Appl. Biol.*, **110**, 441-454.

Yano, K. et al. (2015) Isolation of a novel lodging resistance QTL gene involved in strigolactone signaling and its pyramiding with a QTL gene involved in another mechanism. *Mol. Plant*, **8**, 303-314.

Yoshinaga, S. et al. (2001) Improvement of lodging resistance in submerged direct seeding rice (*Oryza sativa* L.) cultivation using a newly developed ‘Shooting hill-seeder’. Effects of seedling density on the lodging resistance of hill-seeded rice as compared with that of broadcast-seeded rice. *Jpn. J. Crop Sci.*, **70**, 186-193 [In Japanese with English summary].