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NOTES AND INSIGHTS

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A comparison of mechanical characteristics among *Setaria viridis* var. *minor*, *Setaria italica*, and *Setaria* × *pycnocoma* species of the family Poaceae

Masayuki Shiba | **Ryosuke Sato** | **Tatsuya Fukuda**

Graduate School of Integrative Science and Engineering, Tokyo City University, Setagaya, Japan

Correspondence
Masayuki Shiba and Tatsuya Fukuda, Graduate School of Integrative Science and Engineering, Tokyo City University, 1-28-1 Tamazutsumi, Setagaya, Tokyo 158-8557, Japan.
Email: msykshiba48@gmail.com; tfukuda@tcu.ac.jp

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Abstract

Setaria viridis var. *minor* and *Setaria* × *pycnocoma* occur sympatrically in various places in Japan, despite their different morphological and mechanical traits. Morphological and mechanical analyses were performed to determine whether the putative hybrid *S.* × *pycnocoma* possessed the morphological and mechanical characteristics of its ancestral species, *S. viridis* var. *minor* and *Setaria italica*. Our results indicated that *S. italica* had the highest panicle weight and longest culm with the lowest culm mechanical strength and *S. viridis* var. *minor* had the lightest panicle weight and shortest culm with the highest culm mechanical strength. *S.* × *pycnocoma* had a wide range of culm strengths, including mechanical properties of both ancestral species, which suggested that the intermediate mechanical characteristics of this species had been gained by repeated introgression within themselves.

KEYWORDS

culm, hybrid, mechanical characteristics, *Setaria*, three-point bending test

1 | INTRODUCTION

Natural hybridization has often been viewed as an unimportant phenomenon in evolution because crosses between genetically divergent lineages often result in offspring with reduced fertility or viability (Mayr, 1963). In cases where natural hybridization has been implicated directly in evolutionary processes, it has often played a role in finalizing speciation (Howard, 1993). Alternatively, in cases where natural hybrids are stable over time, they have often been considered impediments to continuing evolutionary divergence rather than evolutionarily necessary in their own right (Arnold, 1992; Rieseberg et al., 2000). Interspecific hybrids are particularly favorable materials for introducing novel genetic traits from wild species into crops to generate genetic divergence (Allard, 1960), and the grass family has hybrids between crop and wild species (Arriola & Ellstrand, 1996; Urfusová et al., 2021).

The genus *Setaria* belongs to the Poaceae and is widespread worldwide (Wang et al., 1995). *Setaria viridis* (L.) P. Beauv. var. *minor* (Thunb.) Ohwi is an annual grass growing on fields and roadsides (Dekker, 2003), and the height of the culm varies from 20 to 70 cm (Ohwi, 1982) (Figure. 1a). This species is of interest as a potentially powerful model system for analyzing C_4 photosynthesis as it uses the NADP-malic enzymatic subtype C_4 photosynthetic system to fix C (Brutnell et al., 2010; Li & Brutnell, 2011). In addition, *S. viridis* var. *minor* has features including a small body, diploidy, a short life cycle, a

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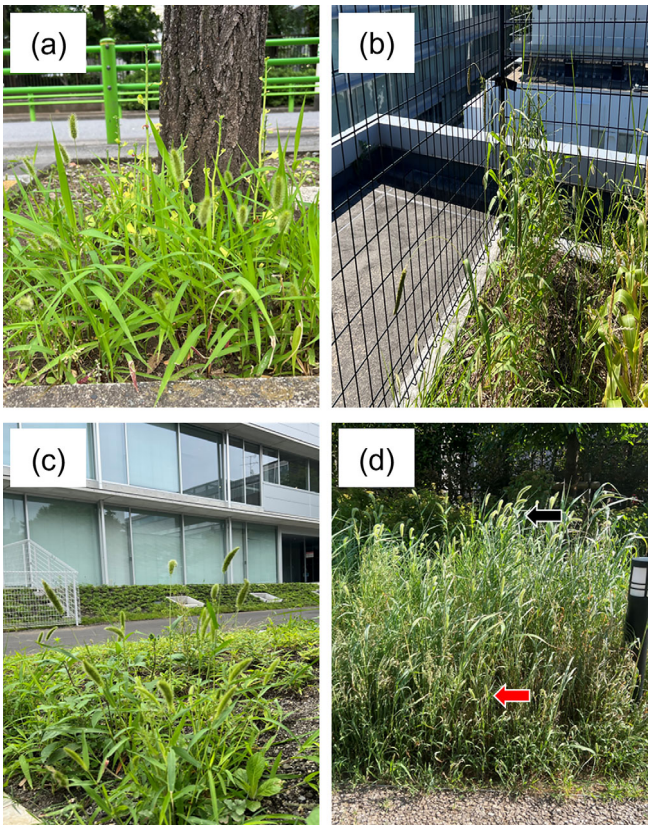


FIGURE 1 (a) *Setaria viridis* var. *minor*. (b) *Setaria italica*. (c) *Setaria* × *pycnocoma*. (d) Mixed population of *S. viridis* var. *minor* and *S.* × *pycnocoma*. Red arrows indicate *S. viridis* var. *minor*, black arrows indicate *S.* × *pycnocoma*.

small genome, and a single inflorescence that produces hundreds of seeds. Therefore, this plant has been transformed efficiently via CRISPR–Cas9 and the resulting transformants have been used in various studies other than C_4 photosynthesis research in recent years (Ferreira et al., 2019; Hunter et al., 2020; Junqueira et al., 2018; Ribeiro et al., 2017; Rodríguez et al., 2020; Saha et al., 2016; Yang et al., 2018). Also, *S. viridis* var. *minor* has a close phylogenetic relation with *Setaria italica* (L.) Beauv. (Christin et al., 2009; Kim et al., 2015; Vicentini et al., 2008). Both species are predominantly self-pollinating (Li & Brutnell, 2011) and possess the same number of chromosomes (Nani et al., 2015). *S. italica*, one of the oldest cereals in the Old World, is thought to have played a crucial role in ancient civilization as a staple crop and, in modern times, has been broadly cultivated in East Asian countries, including Japan, Korea, and China, as well as Western Europe and parts of Africa (Purugganan & Fuller, 2009) (Figure 1b). Like *S. viridis* var. *minor*, this species is also a model plant used in studies of C_4 grass biology and other agronomic traits (Brutnell, 2015; Doust et al., 2009; Lata et al., 2013; Li & Brutnell, 2011; Xianmin et al., 2014). In addition to *S. viridis* var. *minor* and *S. italica*, we also considered a putative hybrid, *Setaria* × *pycnocoma* (Steud.) Henrard (Darmency et al., 1987; Darmency & Pernès, 1985; Li et al., 1945) (Figure 1c), which grows in the fields and by the roadside along with *S. viridis* var. *minor*. In general, hybrids typically display a mosaic of parental and intermediate morphological characters. Therefore, although hybrids were previously considered to have morphological characteristics intermediate between two recognized species, extreme and novel characteristics appear rather often in hybrids (Grant, 1981).

The longer the culm height and the heavier the panicle, the higher the risk of lodging in Poaceae. Culm lodging refers to a permanent displacement of a culm from its vertical orientation caused by breakage or bending of the stem, thereby causing the shoots to lean towards the ground under unfavorable conditions (Dahiya et al., 2018; Hu et al., 2013; Sterling et al., 2003). It is one of the most prominent obstacles in plant growth that reduces seed number and quality (Liu et al., 2018). For example, lodging can cause yield losses by more than 50% (Fischer & Stapper, 1987; Tripathi et al., 2005; Weibel & Pendleton, 1964), and Pinthus (1974) suggested that the losses could be as prominent as those caused by plant diseases and insect pests in high-yielding environments. Stem lodging affects various plant species worldwide, and the height and strength of the stem are critical factors determining stem lodging resistance (Kashiwagi et al., 2005; Verma et al., 2005; Yao et al., 2011).

Hybrids have been involved in not only evolutionary radiation (Anderson & Stebbins, 1954; Grant & Grant, 2019; Meier et al., 2019) and diversification (Mitchell & Whitney, 2021), but also adaptation (Campbell & Snow, 2007; Hovick et al., 2012; Mitchell et al., 2019) and speciation (Rieseberg et al., 2003; Soltis & Soltis, 2009), suggesting that *S.* × *pycnocoma* could have some characteristic traits that are different from those of *S. viridis* var. *minor* and *S. italica*. Interestingly, *S. viridis* var. *minor* and *S.* × *pycnocoma* with different culm lengths and panicle weights grow sympatrically. It is questionable whether the culm strength of *S.* × *pycnocoma*, which is longer than that of *S. viridis* var. *minor*, shows different values between them. For example, the large panicle of *S. italica* is expected to have stronger culms to support the large panicle than those of *S. viridis* var. *minor*. Therefore, the differentiation of mechanical traits can be revealed by comparing the culm strength of the two original hybrids (*S. viridis* var. *minor*, *S. italica*) and the hybrid *S.* × *pycnocoma*. Lodging resistance in Poaceae is related to breaking strength, which determines the mechanical strength of culms (Ookawa & Ishihara, 1992). The aim of this study was to compare Young's modulus, bending strength, and breaking strain of culms of *S. viridis* var. *minor*, *S.* ×

pycnocoma, and *S. italica* and to evaluate their mechanical properties to determine the differentiation of mechanical traits in the hybrid *S.* × *pycnocoma*.

2 | MATERIALS AND METHODS

The *S. viridis* var. *minor* and *S.* × *pycnocoma* examined in this study were collected from soil along the road within the Tokyo City University Setagaya campus and determined as wild specimens (Figure 1d). The former was collected on July 11–12, and the latter was collected during the period of July 1–4. We used seeds of *S. italica* (Kajiwara rice store Co., Kyoto, Japan). *S. italica* was cultivated in the outdoor experimental garden of the university (Tamazutsumi, Setagaya-ku, Tokyo, Japan; 35°35′56″N, 139°39′11″E) and individuals grown from seed were used for the experiments. The cultivation period was between May 10 and September 6. The same soil as that of *S. viridis* var. *minor* and *S.* × *pycnocoma* was used for cultivating *S. italica*. *S. italica* was harvested on September 6. All species were collected at the beginning of ear emergence.

For morphological analysis, we measured the length of culms for each sample. Measurements were taken for 30 individuals each of *S. viridis* var. *minor* and *S.* × *pycnocoma* and 10 individuals of *S. italica*. These measurements were performed using a digimatic caliper (CD-15CXR; Mitutoyo, Japan).

For mechanical analysis, Young's modulus, bending strength, and breaking strain at the culm of the top were measured and calculated using a three-point bending test (Figure 2). Measurements were taken for 12 individuals each of *S. viridis* var. *minor* and *S.* × *pycnocoma* and 10 individuals of *S. italica*. In the three-point bending test, the specimen is placed on two supports, a point load is applied to the sample while the upper support descends at a constant rate, and the load and deflection during bending are measured. A force tester (MCT-1150, A&D, Japan) equipped with a load cell (USM-500 N, A&D, Japan) with a resolution of 0.1 N was used in this study. An optional fixture (JM-B1-500N, A&D, Japan) was also attached to run the three-point bending test. The test conditions were as follows: the distance between the two lower supports was 30 mm, and the lower support was placed so that the upper support was positioned in the center between the lower supports. The upper support was moved downward at a constant speed (10 mm/min). Before testing, the culms were cut apart between 30 mm and 35 mm using a razor. The length and average diameter of the detached culms were measured using a digimatic caliper (CD-15CXR; Mitutoyo, Japan), and volume was calculated and tested. Loads and deflections

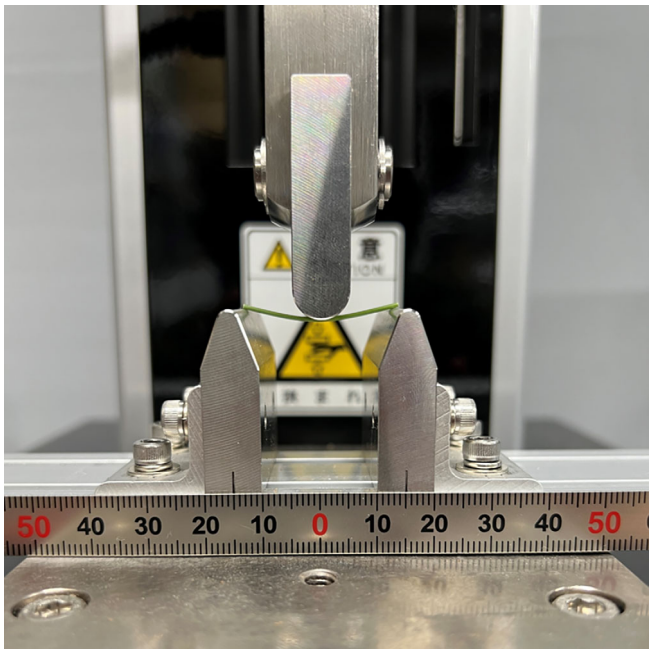


FIGURE 2 The three-point bending test used in this study.

were recorded during the three-point bending test using MCT-Logger software (A&D, Tokyo, Japan). The three-point bending tests were conducted until the samples broke. The data sampling frequency was set to 60 Hz. From the test results, the bending stress σ was calculated using Equation (1):

$$\sigma = \frac{8PL}{\pi D^3}, \tag{1}$$

where P is the measured load, L is the distance between supports, and D is the average diameter of the sample. The bending strength σ_{max} was calculated using the load at break P_{max} in Equation (1). Strain ε was calculated using Equation (2):

$$\varepsilon = \frac{6D\rho}{L^2} \times 100\%, \tag{2}$$

where ρ represents the measured deflection. The deflection at breaking (ρ_{max}) was used to calculate the strain at breaking (ε_{max}). After testing, the material was dried at 100°C for 72 h using an incubator (FS-405, Advantec, Japan), and the dry weight was measured using an electronic balance (ATX224R, Shimadzu, Japan) to calculate the dry weight per unit volume. Young's modulus E, which represents resistance to deformation, was calculated for values in the 0.05–0.25% strain range of the deformed bending stress–strain curve.

We used Koneko software for statistical analysis (Ogura, 2012). Each measured variable was compared using the Tukey–Kramer test of multiple comparisons.

3 | RESULTS

We measured the culm length as well as the panicle length and weight of *S. viridis* var. *minor*, *S. italica*, and *S.* × *pycnocoma*. The culm of *S. viridis* var. *minor* (mean ± SE: 36.65 ± 1.55 cm) was significantly shorter than those of *S.* × *pycnocoma* (mean ± SE: 69.82 ± 2.73 cm) and *S. italica* (mean ± SE: 76.23 ± 4.45 cm).

A comparison of the panicle length of these species revealed that the panicle of *S.* × *pycnocoma* was significantly longer than those of *S. italica* and *S. viridis* var. *minor* (Figure 3a). However, a comparison of the panicle weight of these species revealed that the panicle weight of *S. italica* was significantly higher than those of *S.* × *pycnocoma* and *S. viridis* var. *minor* (Figure 3b).

Dry weight per unit culm volume was significantly lower in *S.* × *pycnocoma* than in *S. italica* and *S. viridis* var. *minor* (Figure 4).

The selected mechanical properties, including bending strength, strain, and apparent Young's modulus, were determined using the three-point bending test. Generally, the relation between stress and strain of a particular material is displayed as its stress–strain curve, which is unique for each material and estimated by recording the amount of bending stress at distinct tensile or compressive strain intervals. These curves reveal many of the properties of a material. The bending strength of *S. viridis* var. *minor* was greater than that of *S. italica* and *S.* × *pycnocoma* (Figure 5a), whereas its breaking strain was lower than those of *S. italica* and *S.* × *pycnocoma* (Figure 5b). Young's modulus was highest for *S. viridis* var. *minor* and smallest for *S. italica*, and Young's modulus of *S.* × *pycnocoma* was not significantly different from those of the other two species (Figure 5c).

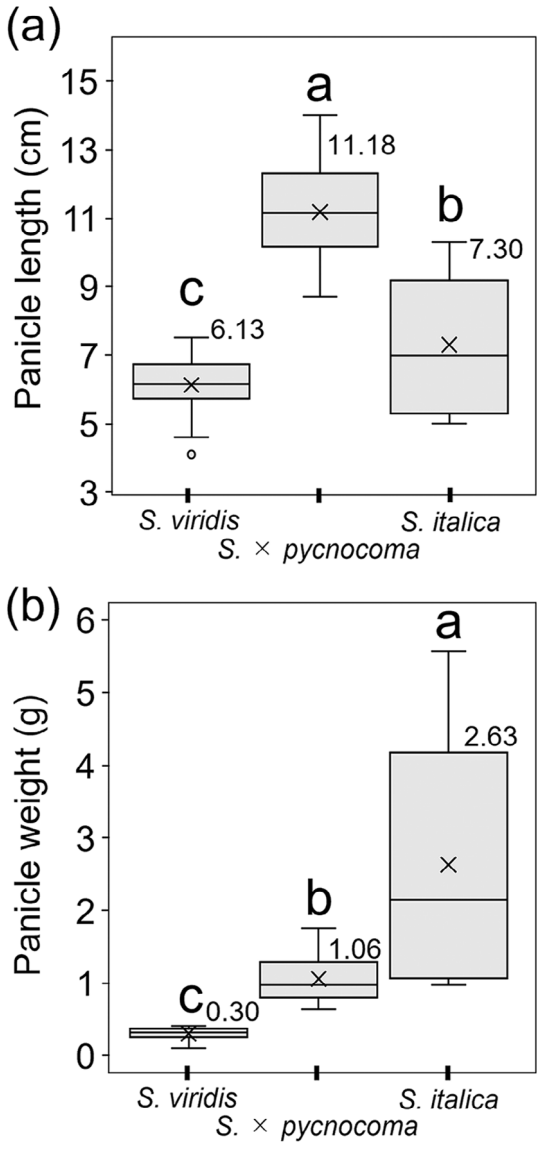


FIGURE 3 (a) Comparison of panicle length of *Setaria viridis* var. *minor* (left), *Setaria* × *pycnocoma* (center), and *Setaria italica* (right). (b) Comparison of panicle weight of *S. viridis* var. *minor* (left), *S.* × *pycnocoma* (center), and *S. italica* (right). × and values indicate mean plots and mean values within the box-and-whisker diagram. Columns marked by different letters differ significantly according to the Tukey–Kramer test ($p < 0.05$).

4 | DISCUSSION

Our results indicated that *S. viridis* var. *minor*, which has a lower panicle position, tends to have higher bending strength and Young's modulus, which indicate the strength of culms, than *S.* × *pycnocoma*, which has a higher panicle position. Thus, *S. viridis* var. *minor* may have higher lodging resistance than *S.* × *pycnocoma*. Xue et al. (2020) indicated that stalk breakage was primarily affected by the dry weight per unit volume in maize, and stalks with a high dry weight per unit volume were difficult to break, leading to increased stalk lodging resistance. Our results showed that the dry weight per unit culm volume was significantly higher in *S. viridis* var. *minor* than in *S.* × *pycnocoma* (Figure 4), indicating that *S. viridis* var. *minor* has higher lodging resistance of the culms from a biomass perspective. Our results of *S. viridis* var. *minor* and *S.* × *pycnocoma* supported the findings of Xue et al. (2020) that culm lodging resistance is related to dry weight per unit culm volume. We considered that these species could increase their resistance to external forces by increasing the amount of cell wall when subjected to external forces.

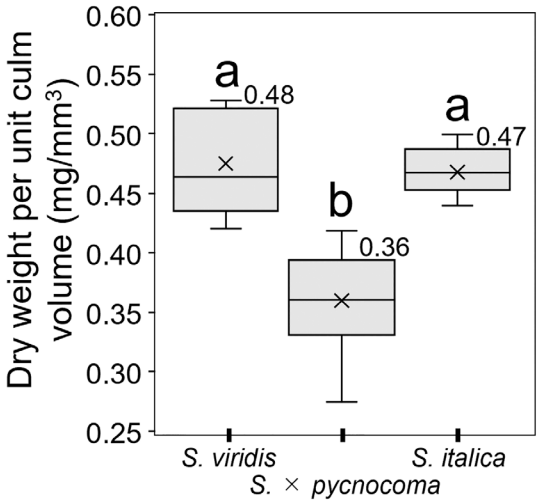


FIGURE 4 Comparison of the dry weight per unit culm volume of *Setaria viridis* var. *minor* (left), *Setaria* × *pycnocoma* (center), and *Setaria italica* (right). × and values indicate mean plots and mean values within the box-and-whisker diagram. Columns marked by different letters differ significantly according to the Tukey–Kramer test ($p < 0.05$).

In contrast, *S. italica* showed lower bending strength and Young's modulus of culms despite a similar dry weight per unit culm volume as *S. viridis* var. *minor* (Figures 4 and 5a,c). The relationship between dry weight per unit culm volume and lodging resistance of *S. italica* culms is still unknown. However, it has been reported that the cellulose microfibril angle, the orientation along the fiber axis of the crystalline cellulose in the secondary cell wall material, has a predominant effect on the mechanical properties of plant stems (Cave, 1966, 1968; Donaldson, 2008; Downes et al., 2002; Walker & Butterfield, 1995). In addition, it has been reported that an increase in the angle of cellulose microfibrils leads to a decrease in the mechanical properties of stems (Barnett & Bonham, 2004), and Huang et al. (2018) have demonstrated the involvement of the angle of cellulose microfibrils in culm lodging resistance in rice. This suggests that, despite having the same dry weight per unit culm volume as *S. viridis* var. *minor*, *S. italica* has lower bending strength and Young's modulus than *S. viridis* var. *minor* due to the larger cellulose microfibril angle than that of *S. viridis* var. *minor*. The significantly higher breaking strain in *S. italica* than in *S. viridis* var. *minor* (Figure 5b) may be due to a larger cellulose microfibril angle, extending the range to the break point at the cellular level. However, the relationship between cellulose microfibril angle and culm organ mobility in dynamic behavior is unknown. Also, the cellulose microfibril angle is correlated with lignin content (Hori et al., 2003; Jungnikl et al., 2008), and therefore it will be interesting to compare the cellulose microfibril angle and lignin content of these species based on our results.

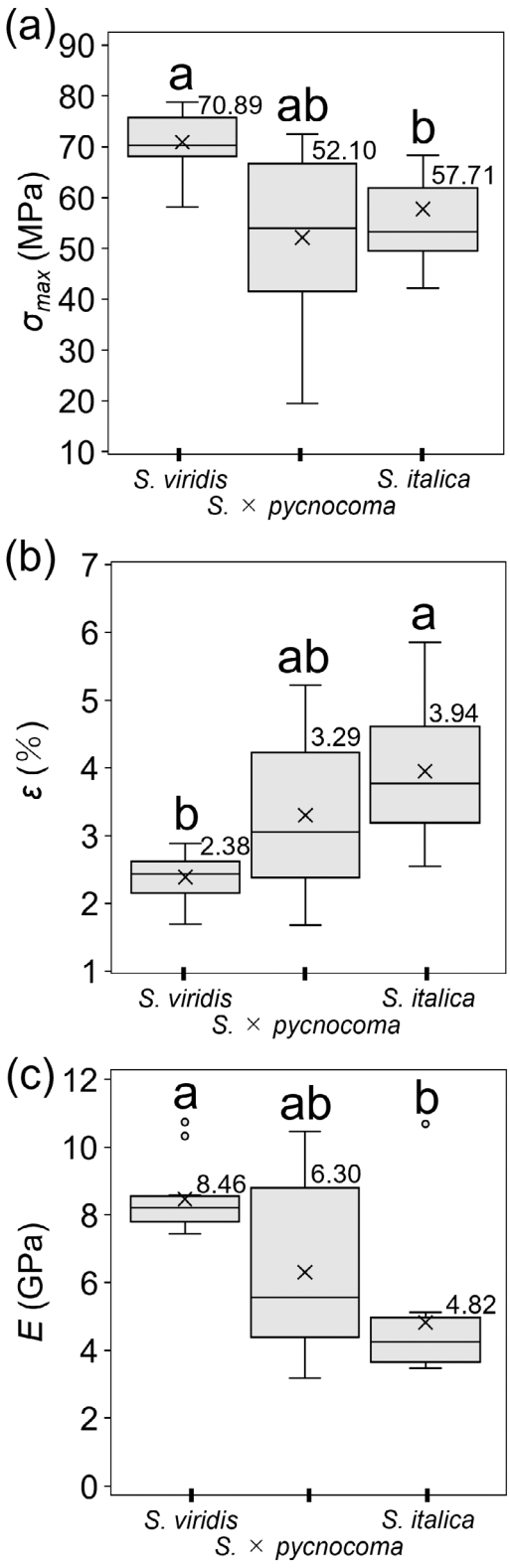


FIGURE 5 Comparison of the culm: (a) bending strength σ, (b) breaking strain ε, and (c) Young's modulus E of *Setaria viridis* var. *minor* (left), *Setaria* × *pycnocoma* (center), and *Setaria italica* (right). × and values indicate mean plots and mean values within the box-and-whisker diagram. Columns marked by different letters differ significantly according to the Tukey–Kramer test ($p < 0.05$).

In addition, Xue et al. (2020) reported that the higher the panicle position, the higher the mechanical strength with respect to lodging resistance in maize. But *S. italica* with lower bending strength was shown to have a higher panicle position than *S. viridis* var. *minor*, and *S. italica* had heavier panicles than *S. viridis* var. *minor*. These results differ from those of Xue et al. (2020), suggesting that the mechanical strength of *S. italica* was lower than that of *S. viridis* var. *minor* and that it had a more unstable body position. However, *S. italica* has increased the breaking strain and acquired a body position to hang down the panicle. We conclude that *S. italica* culms have gained mechanical properties that make them easily deformable and difficult to break, thereby avoiding culm breakage from external forces such as strong wind.

Interestingly, the bending strength, breaking strain, and Young's modulus of *S.* × *pycnocoma* culms were in a range that included the mechanical properties of *S. italica* and *S. viridis* var. *minor* (Figure 5). These results suggest that the mechanical properties of *S.* × *pycnocoma* are of hybrid origin. However, it was surprising that *S.* × *pycnocoma* had no significant difference in mechanical properties from the other two species. One possible explanation is that *S.* × *pycnocoma* showed a wide variation in mechanical properties upon repeated backcrossing with *S. italica* or *S. viridis* var. *minor*. Kim et al. (2015) reported that *S.* × *pycnocoma* need not be a fixed narrow group as numerous weedy forms may originate through natural crossing between *S. viridis* var. *minor* and cultivated *S. italica*. A few studies have indicated that genetic variations in *S. viridis* var. *minor* could be introgressed directly into cultivated *S. italica* through interspecific crosses (Mauro-Herrera et al., 2013; Mauro-Herrera & Doust, 2016; Qie et al., 2014). Considering these reports, we hypothesized that *S.* × *pycnocoma* gained a wide range of mechanical properties by repeated introgression within themselves and readily adapted in various areas. For example, Rieseberg et al. (2003) showed that the genomic composition of hybrids matches that of the subset of synthesized hybrids with high fitness in sunflowers and Hovick et al. (2012) reported that radish hybrids could enhance colonization success in a novel region and that the life-history traits enhancing hybrid success could differ across regions, even for lineages originating from the same hybridization event. These results indicated that hybridization was one of the significant processes in environmental adaptation, and our result that *S.* × *pycnocoma* had wide ranges of bending strength, Young's modulus, and breaking strain suggests that this species has a much broader arena for success than the ancestral species *S. viridis* var. *minor* and *S. italica*.

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CONFLICT OF INTEREST STATEMENT

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

ORCID

Masayuki Shiba https://orcid.org/0000-0002-8699-942X
Tatsuya Fukuda https://orcid.org/0009-0005-5873-0019

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