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Multiscale analysis of wind-induced responses of plants at tissue and cellular levels in sunflower growth

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Abstract

A number of studies have been conducted on the relationship between plant growth and external stimuli. There has been, however, little research on the effects of wind stimuli that are one of the major stress factors acting on plants in natural environments. Understanding how mechanical properties and morphologies of plants respond to external stimuli is essential for elucidating plant growth mechanisms. This study, therefore, focused on wind-induced changes in mechanical, histological and cellular properties of plants. Mini sunflowers (*Helianthus annuus* L.) were grown in a wind tunnel with wind speeds of 3.0 m/s and no-wind (control), while room temperature and light-dark conditions were kept consistent between the two groups. After approximately one month of growth under each condition, measurements of the length of stem, the Young's modulus of stem, the length of cells, the lignified cell area ratio and the cell cycle were conducted. Compared with the control group, the wind-stimulated group exhibited a 67% decrease in the Young's modulus, a 38% reduction in the stem length, and a 64% reduction in the lignified area ratio, whereas no significant difference in the cell length was observed. In addition, cell cycle progression was inhibited under the wind-stimulated condition. The results indicate that a reduction in cell number contributes to decreased stem length, while a lower ratio of lignified cell area contributes to decreased Young's modulus. These findings suggest that plants adapt to wind stimuli by maintaining shorter and more flexible stems, thereby reducing the risk of mechanical failure.

Keywords : Plant biomechanics, Wind stimulation, Adaptive response, Young's modulus, Flow cytometry, Lignification

1. Introduction

When plants encounter stressful conditions different from suitable growing environment, it is considered that they respond by altering their mechanical, histological and cellular properties to enable sustainable growth. Typical stresses on plants in natural environments include temperature (Chinnusamy et al., 2007; Rymen et al., 2007; Zhao et al., 2014), water (Yamaguchi-Shinozaki and Shinozaki, 1994), light (Blackman and Wilson, 1951; Pedmale et al., 2010), bacteria (Zipfel et al., 2004; van Loon, 2007), salinity (Shi et al., 2000; Yamaguchi-Shinozaki and Shinozaki, 1994; Zhao et al., 2014), metals (Conrad, 2008) and nutrient availability (Gruber et al., 2013; Skirycz et al., 2011) as well as mechanical stimuli such as wind (Coutand et al., 2008; Smith and Ennos, 2003), vibration (Niklas, 1998), touch (Chehab et al., 2009; Jaffe, 1973; Paul-Victor and Rowe, 2011) and water flow (Miler et al., 2012). For example, Hu et al. (2011) have reported that maize grown under cold environment induced the expression of cold-induced genes involved in cold acclimation. Focusing on mechanical stimuli, touch and perturbation cause thigmomorphogenesis to inhibit stem elongation (Chehab et al., 2009; Jaffe, 1973; Paul-Victor and Rowe, 2010). In addition, wind stimulation altered growth patterns while maintaining the total biomass (Coutand et al., 2008) and reduced the stem strength with shorter stem length (Smith and Ennos, 2003). Although some researchers have reported morphological and mechanical responses to mechanical stimuli, the mechanisms underlying tissue- and cellular-level processes remain poorly understood.

Understanding plant responses to wind stimuli is important for controlling plant growth and improving cultivation efficiency, which may contribute to the development of agricultural practices. This study, therefore, aims to elucidate the

mechanisms of plant responses to wind stimuli by quantitatively evaluating changes in morphology and functions of plants at tissue and cellular levels. Plants were grown under controlled wind conditions in a wind tunnel, and their responses were evaluated by tensile testing to assess mechanical properties of stems, microscopic observation to quantify the area ratio of lignified cells and cell length, and flow cytometry to analyze cell cycle distribution based on DNA content. Plants grown under wind stimulation were compared with those grown under no-wind conditions. Mini sunflower ‘Junior’ (Sakata Seed Corporation, Japan), a small-sized plant with a short generation time, was selected as a model species. Wind stimulation experiments were conducted at wind velocities of 2.7 m/s or higher, at which growth suppression has been reported by Wadsworth (1959).

2. Materials and methods

2.1 Plant materials and wind stimulation

The experimental design and analytical workflow are summarized in Fig. 1. As shown in Fig. 1(a), seeds of sunflower were sown in pots after keeping the seeds at 4°C more than 1 week to uniform the germination time. The plants were grown under a 24 h light period and a temperature of 23.5°C and watered once a day. Seven days after germination, the plants were used for experiments. Two experimental conditions were set: a control group grown in a windless environment and a wind stimulation group grown in a custom-built wind tunnel with a wind speed of 3 m/s for up to 3 weeks. After 7, 14 and 21 days, the plants of both groups were harvested for the following measurements and analysis.

2.2 Stem length measurement

The plant samples after harvest were placed on a desk with a ruler and taken photos using iPhone XR (Apple, USA). The stem length (see Fig. 1(b)) was then measured along the stem contour using ImageJ software (NIH, USA) (Schneider et al., 2012).

2.3 Mechanical characterization of stems

The plant stems were cut at 50 mm from the ground level, fixed to brass tubes using adhesive on both sides of stems. After measurement of the stem length and diameter in this region, the specimens were attached to a force gauge (DTG-1N or DTG-100N, Digitech Co., Ltd., Osaka, Japan) and subjected to tensile loading at a speed of 20 mm/min until fracture (Fig. 1(b)). To prevent drying of the specimens, tensile tests were performed within 3 min after stem cutting. Young’s modulus of stems was determined as a linear elastic body because the stress-strain relationship was linear. In addition, flexural rigidity was calculated from the Young’s modulus and stem diameter.

2.4 Histological observation of stem sections

The plant stems were histologically observed in transverse and longitudinal sections using the paraffin sectioning method (Nitta, 2005; Sakai, 1973), as shown in Fig. 1(b). The base of the plant stems was cut into large pieces (approximately 1 cm) and immediately fixed by submerging in FAA solution (formalin-acetic acid-alcohol solution), containing 5% formaldehyde (Kanto Chemical Co., Inc., Japan), 5% acetic acid (Kanto Chemical Co., Inc., Japan) and 45% ethanol (Kanto Chemical Co., Inc., Japan) under degassed environment for one day, followed by dehydration in t-butyl alcohol (Kanto Chemical Co., Inc., Japan): ethanol: water series (0:1:1, 1:1:2, 4:3:3, 2:1:1, 7:2:1, 4:1:0, 1:0:0, 1:0:0 and 1:0:0) for 12 h each at room temperature. The specimens were then infiltrated with molten paraffin at 58°C for 3 days. The final paraffin embedded specimens were sectioned with a microtome (HM325, Thermo Fisher Scientific, USA) to 20 µm thick sections. The slice specimens were stained with 0.05% toluidine blue O (Muto Pure Chemicals Co., Ltd., Japan) for 20-30 min, followed by washing them for 1 min and drying at room temperature (Watanabe, 2011). After staining, the specimens were deparaffinized and cleared by washing twice with xylene (Kanto Chemical Co., Inc., Japan). Lignified cell walls were stained green to light blue, while other sections were stained reddish purple. Transverse and longitudinal cross-sectional images were taken under a 50x magnification using a digital microscope (VHX-600, Keyence, Japan) and analyzed using ImageJ software. In the transverse sections, the area of purple lignified cells was divided by the area of the entire stem to calculate the lignified cell area ratio, while in the longitudinal sections, the length of the cells along the stems was measured at the inner pith regions.

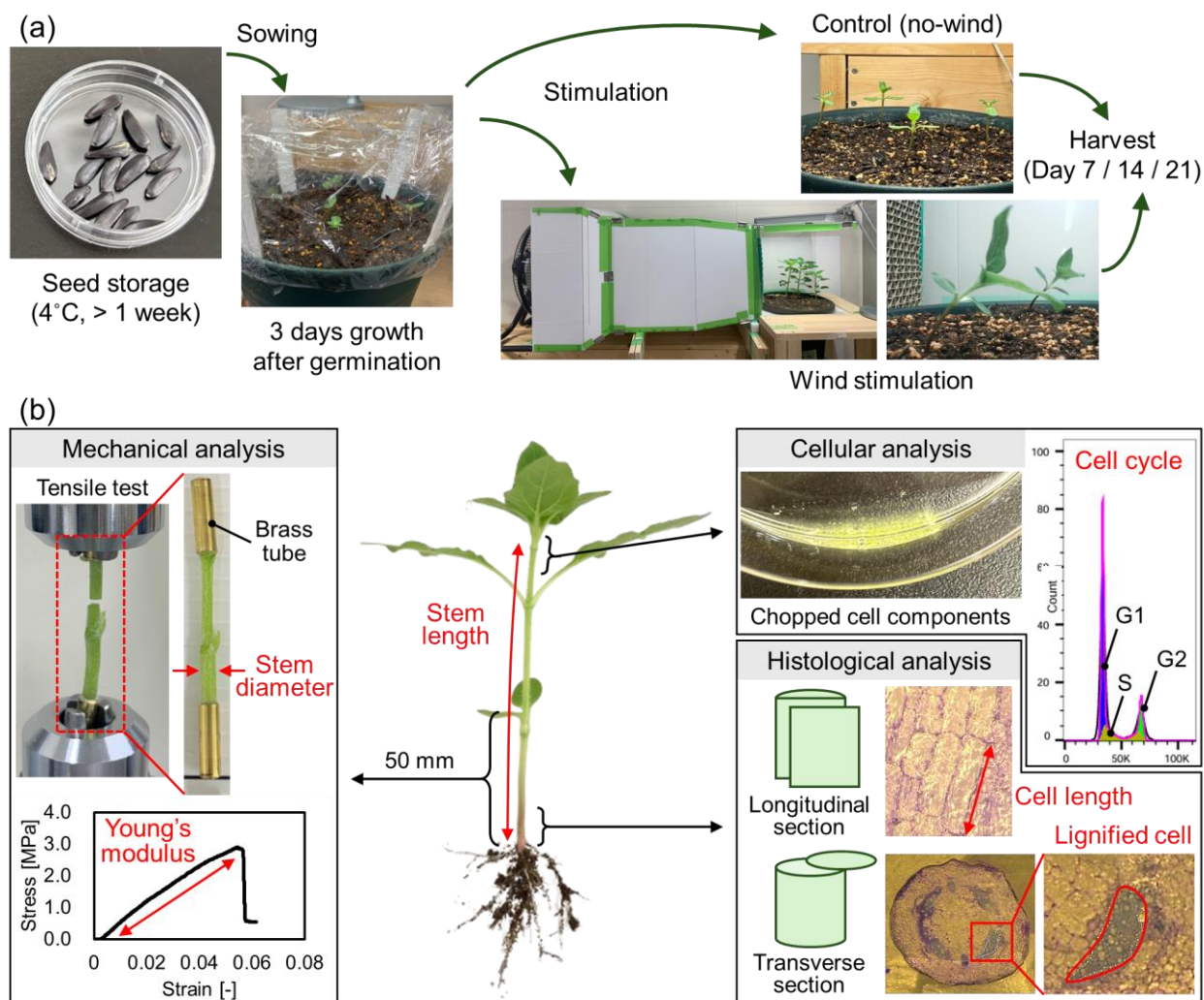


Fig. 1 Experimental design and analytical workflow. (a) Seeds were stored at 4°C more than 1 week. Wind stimulation was applied from 7 days after germination. Plants were harvest at 7, 14 and 21 days. (b) Mechanical, histological and cellular analyses were conducted to evaluate wind-induced changes in stem properties. In mechanical analysis, tensile tests were performed to obtain Young's modulus of plant stems. In histological analysis, cross-sections were observed in transverse and longitudinal sections to measure lignified cell area and cell length, respectively. In cellular analysis, flow cytometry was utilized to determine cell cycle proportion.

2.5 Cell cycle analysis by DNA content measurement

The plant nuclei were released by chopping method and then DNA content was measured using a flow cytometer (Fomicheva and Domblides, 2023), as shown in Fig. 1(b). Chopping buffer was prepared by mixing 50 mM Tris-HCl (Fujifilm Wako Pure Chemical Industries, Ltd., Japan), 1% Triton X-100 (Merck Millipore, USA), 140 mM 2-mercaptoethanol (Bio-Rad Laboratories, USA) and 50 mM sodium hydrogen sulfite (Fujifilm Wako Pure Chemical Industries, Ltd., Japan). Three millimeters sections were cut from the tips of the plant stems and finely chopped in 300 μ L of chopping buffer. After 1 h, the samples were filtered by a cell strainer, added 1.2 ml of the chopping buffer and centrifuged at 1000 $\times$ g for 10 min. The supernatant was discarded and replaced with 1 ml of fresh chopping buffer. To stain DNA, a few drops of PI (propidium iodide 1 mg/ml, Dojindo Laboratories, Japan) were added and mixed. Finally, the nuclear fluorescence intensity was measured using a flow cytometer (FACSCanto, BD Biosciences, USA). The results were analyzed with the Dean-Jett-Fox model to determine the rate of cell cycles in G1, S and G2 phases.

2.6 Statistical analysis

Statistical analysis was performed using Microsoft Excel with a two-tailed Welch's t-test. The significance level was set at $p < 0.05$.

3. Results

3.1 Stem length

Figure 2(a) shows images of the plants grown under windless (control group) and wind-stimulated (wind group) conditions. Figure 2(b) shows changes in the lengths of plant stems at day 0, 7, 14 and 21. The plants of the control group grew straight and gradually elongated over 3 weeks, while the plant stem of the wind group grew curved and shorter. The length of plant stems on the wind group was significantly shorter than control from after 1 week and was less than two-thirds that of control at 3 weeks (138.5 ± 18.2 mm on the control group, 85.7 ± 6.2 mm on the wind group, $p < 0.05$).

3.2 Mechanical properties of stem

As shown in Fig. 3(a), the Young's modulus increased in the control group (8.78 ± 2.45 , 24.09 ± 2.12 and 29.49 ± 13.05 MPa on 1-3 weeks), while slightly increased in the wind group (3.94 ± 0.70 , 9.15 ± 0.37 and 9.95 ± 2.03 MPa on 1-3 weeks) over 3 weeks. The stem diameter increased throughout the 3 weeks in both groups (Fig. 3(b)). Furthermore, the flexural rigidity in the control group was larger than one in the wind group although there was no significant difference at any time point (Fig. 3(c)).

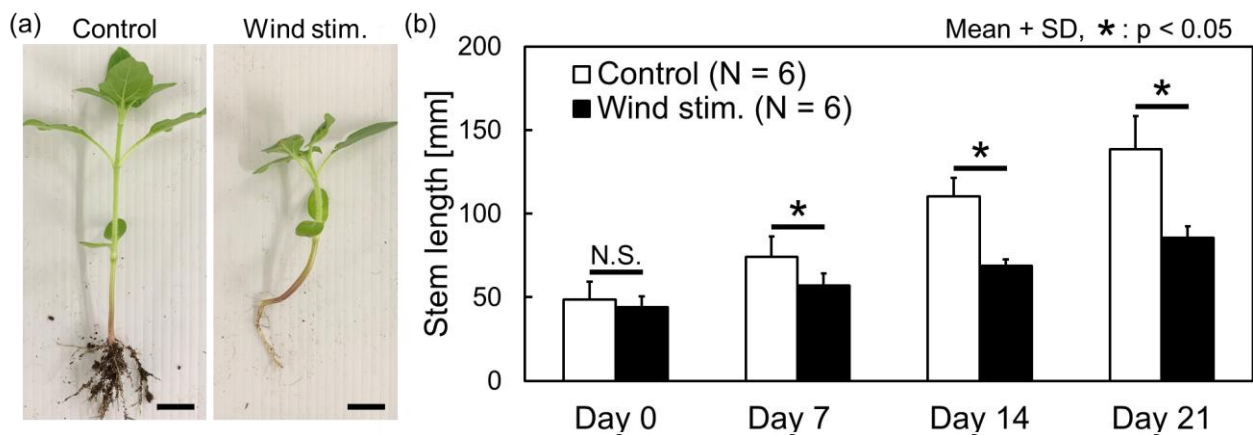


Fig. 2 (a) Representative images of plants grown under the control (left) and wind-stimulated (right) conditions at 3 weeks. Scale bars: 20 mm. (b) Stem length under each condition. N.S.: no significant. *: $p < 0.05$.

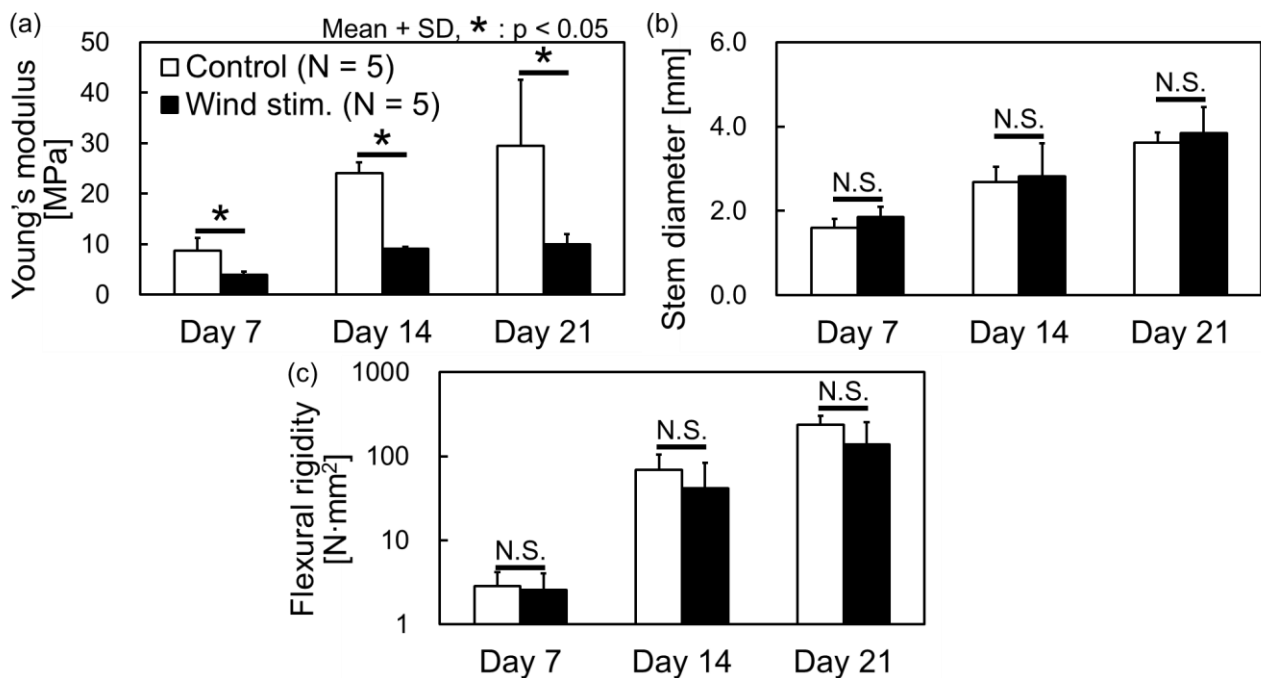


Fig. 3 (a) Young's modulus, (b) diameter and (c) flexural rigidity of plant stems under each condition. N.S.: no significant. *: $p < 0.05$.

3.3 Lignified cell ratio

Figure 4(a) shows microscopic images of cells on the transverse plane for windless (control group) and wind-stimulated (wind group) conditions. The area ratio of lignified cells (Fig. 4(b)) was no significant difference between both groups at 1 week, however, after 2 and 3 weeks, it increased in the control group and was significantly higher than in the wind group. While the control group continued to increase the area ratio of lignified cells, the wind group remained the low area ratio of the cells.

3.4 Cell length

Figure 5(a) shows microscopic images of cells on the longitudinal plane for windless (control group) and wind-stimulated (wind group) conditions. The measurement results of longitudinal cell length were summarized in Fig. 5(b). Although there was no significant difference in both groups, the cells elongated as the days passed.

3.5 Cell cycle distribution

The cell cycle distribution at 3 weeks is shown in Fig. 6. The wind stimulation caused more cells to be blocked in the G1 phase, while fewer cells in the S phase (control vs. wind stimulation: $62.36 \pm 6.75\%$ vs. $73.90 \pm 2.07\%$ for G1 phase; $22.81 \pm 8.57\%$ vs. $9.47 \pm 4.61\%$ for S phase). However, no significant difference was observed in the G2 phase ($P > 0.05$).

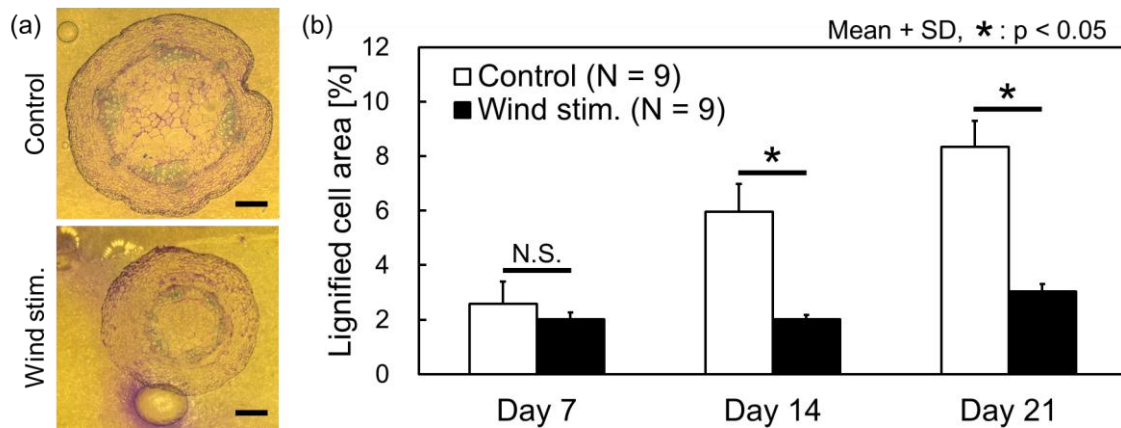


Fig. 4 (a) Representative images of transverse sections grown under the control (top) and wind-stimulated (bottom) conditions at 3 weeks. Scale bars: 500 μm . (b) Ratio of lignified cell area under each condition. N.S.: no significant. *: $p < 0.05$.

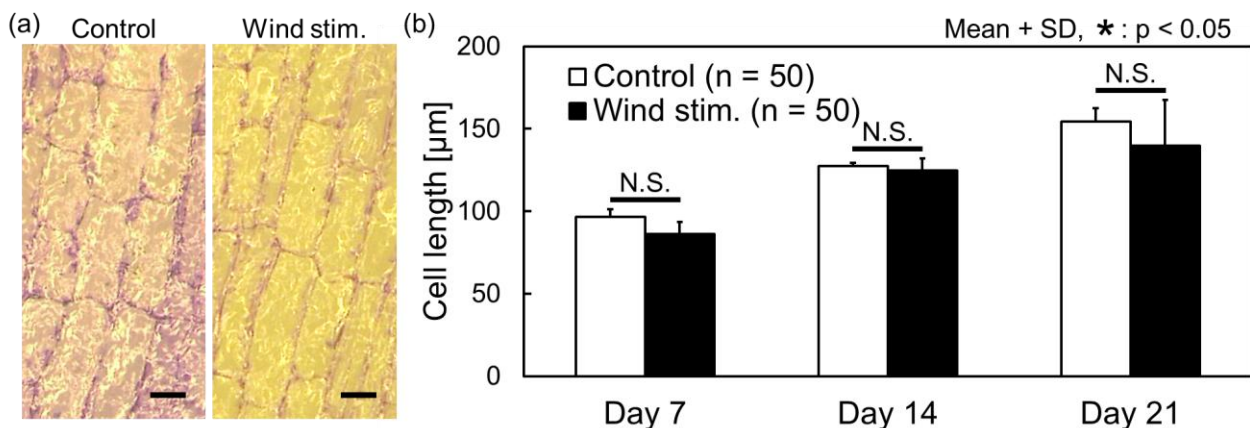


Fig. 5 (a) Representative images of longitudinal sections of cells grown under the control (top) and wind-stimulated (bottom) conditions at 3 weeks. Scale bars: 50 μm . (b) Cell length under each condition. N.S.: no significant. *: $p < 0.05$.

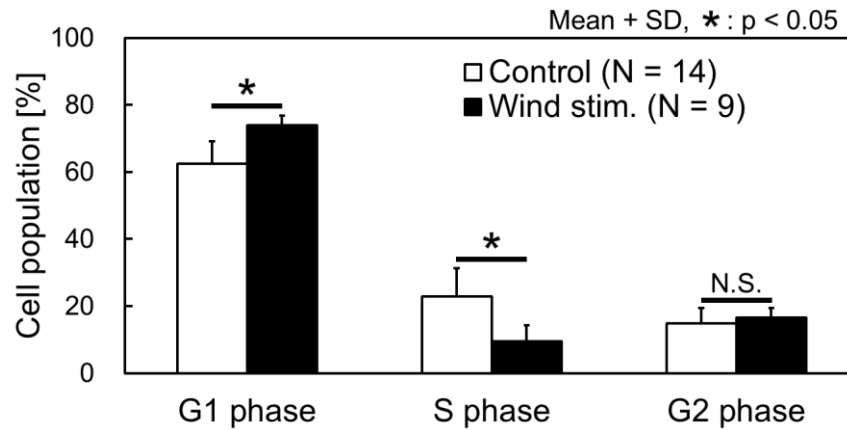


Fig. 6 Cell population of G1, S and G2 phases under each condition. N.S.: no significant. *: $p < 0.05$.

4. Discussion

In this study, tissue and cellular responses of plants grown with/without wind stress stimulation were analyzed. Wind stimuli reduced the stem length and inhibited cell cycle progression, while no significant difference was observed in cell length. These results suggest that wind-induced reduction in stem length may be caused by inhibition of cell proliferation rather than cell elongation. This phenomenon is considered to be an adaptive response that shortens stems and reduces bending moments to deflect wind and reduce the risk of stem failure. Furthermore, the Young's modulus of stems and the lignified cell ratio decreased on the wind-stimulated group. In particular, their time-dependent changes showed similar trends, indicating that the changes are closely related. Lignification is known to strongly influence the mechanical stiffness of plant tissues because lignin possesses a relatively high Young's modulus compared with the other cell wall components (Gibson, 2012). Previous studies have reported that the mechanical properties of plant stems could correlate with lignin content (Hidalgo-Cordero et al., 2023). Therefore, the reduction in lignified cell area observed under wind stimulation may explain the decrease in the Young's modulus measured in this study. These results may reflect a strategy of mechanical acclimation in which the stem increases its flexibility by decreasing its rigidity in a wind-stimulated environment, making it easier to deflect the wind. Wind loading causes stem bending, generating tensile stress on the leeward side and compressive stress on the windward side. Such stress distributions may induce different tissue responses. However, consistent structural differences between these regions were not observed in the present samples. Further studies are required to clarify cellular and tissue-level responses to bending-induced compressive and tensile stresses. In summary, the present study suggests that the plant responses to wind stimuli are a mechanical acclimation that integrates the regulation of cell proliferation with changes in tissue-level mechanical properties. Specifically, reductions in the stem length and the Young's modulus may function to decrease bending moments acting on the stem, thereby reducing the risk of mechanical failure under wind conditions.

Many researchers have reported, to date, that external stimulation inhibits plant growth (Chehab et al., 2009; Jaffe, 1973; Paul-Victor and Rowe, 2011; Coutand et al., 2008; Smith and Ennos, 2003), on the other hand, some researchers have indicated that the stimulation promote plant growth. For instance, Horikoshi (2017) have found that microwave irradiation of *Arabidopsis* increased stem length and doubled growth compared to control. Oikonomou et al. (2023) have shown that electrical stimulation accelerated growth of barley, resulting in root development and increase of dry weight. These reports suggest that plant growth is not necessarily inhibited by all external stimuli, instead, the growth response varies with the type and intensity of the stimuli and plant growth can be either inhibited or promoted. Therefore, whether growth changes induced by stimuli should be interpreted as growth inhibition or as adaptive responses to environmental stress remains an open question.

Based on the presented results, the plant responses to wind stimuli can be interpreted as adaptive responses. This interpretation is supported by two considerations. First, plants are known to adapt their tissues and structures to mechanical environments. Previous studies by Mattheck (1990) and Nogata (1996) demonstrated that trees growing on flat and inclined ground develop the trunks and branches to minimize stress concentrations on the outer surfaces. Their stress analyses based on the size and geometries of trees revealed that trees grow toward mechanically optimized

structures with nearly uniform strength, indicating that plants can adapt their tissues and structures to mechanical environments. Second, this study did not show significant differences on the stem diameter and the cell length. The results of the stem length, the Young's modulus and the lignified area ratio were significantly lower under wind stimulation than control. Supposing that growth changes by wind stimulation considered as growth inhibition, the stimulation should reduce the stem diameter and the cell length. In fact, however, the values remained unchanged, indicating that plant growth may selectively adjust specific mechanical and/or morphological properties. Based on the two considerations, this study suggests that wind-induced changes of plant growth is an adaptive response to the mechanical environment.

This study has several potential limitations. First, cell cycle analysis based solely on flow cytometry could not demonstrate inhibition of cell cycle progression. Although the results imply that wind stimulation inhibits cell cycle progression at the G1-S transition, flow cytometry does not provide information on regulatory subunits controlling the cell cycle. A previous study combined flow cytometry and measurements of the subunits, such as cyclins, to demonstrate cell cycle inhibition (Zhao et al., 2014). An additional analysis of cyclin expression, therefore, would be required to confirm this mechanism. Next, while there were significant differences in the Young's modulus and lignified area ratio between the two groups, flexural rigidity did not show significant differences. This is likely caused by measurement methods of stem diameter as bending rigidity is more sensitive to diameter than to Young's modulus. Although mechanically stimulated plant stems can become elliptical in cross-section (Goodman and Ennos, 1998), in this study, the diameters were measured only in one direction, resulting in that flexural rigidity of wind-stimulated plants may have been overestimated and may not have shown significant differences.

5. Conclusions

In this study, plants were grown under wind-stimulated conditions, and their growth characteristics were compared with those of control plants through a multiscale analysis of stem mechanical properties, tissue structure and cellular characteristics. The results demonstrated that wind-stimulated plants exhibited adaptive responses of suppressed growth due to a reduction in cell number caused by inhibition of cell cycle progression. In addition, the reduced ratio of lignified area was accompanied by a decrease in the Young's modulus of the plant stems. The findings suggest that plants adjust their mechanical properties under wind-stimulated environments to enhance flexibility to deflect wind and to reduce the risk of stem break. The study provides insights into the mechanism of plant growth regulation and contributes to optimizing growth conditions and to improve cultivation efficiency.

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