

ORIGINAL ARTICLE

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Stem gravitropism and tension wood formation in three tropical woody species with different wood densities

Widyanto Dwi Nugroho^{1,2,4}, Gita Dwi Anjayani¹, Arisandy Fernando Tampubolon¹, Adhitya Wisnu Pradhana¹, Hairi Cipta¹, Novena Puteri Tiyasa^{1,2}, Yusuke Yamagishi², Kayo Kudo³, Md Hasnat Rahman^{2,3,4}, Satoshi Nakaba^{2,4} and Ryo Funada^{2*} 

Abstract

Angiosperm trees develop tension wood on the upper side of leaning stems to reorient the direction of stems towards their normal positions in response to a gravitational stimulus. The development of gelatinous fibers with thick inner gelatinous layers (G-layers) might elevate tensile stress required for such reorientation in many angiosperm species. This study aims to investigate negative gravitropism and tension wood formation in response to a gravitational stimulus in tree species with different respective wood densities. Seedlings of three tropical trees, namely, *Diospyros celebica*, *Artocarpus heterophyllus*, and *Falcataria moluccana* were artificially inclined at 45° from the vertical and harvested three months later for analysis of plant gravitropism and tension wood formation. Inclined seedlings of the three species exhibited different rates of stem recovery and movement towards the vertical. The widths of region of tension wood in the thickness of G-layers were positively correlated with the negative gravitropism of stems. However, such relationships differed significantly among the three species. The differences in patterns of negative gravitropism of stems, widths of tension wood and thicknesses of G-layers in inclined seedlings of *F. moluccana*, *A. heterophyllus*, and *D. celebica* were due to differences among species rather than to differences in the wood density of the respective species. Larger amounts of gelatinous fibers and/or thicker G-layers were essential for the negative gravitropism of inclined stems. However, each tree species exhibited different features during stem recovery.

Keywords *Artocarpus heterophyllus*, *Diospyros celebica*, *Falcataria moluccana*, G-layer, Gravitropism, Stem recovery degree, Tension wood

Introduction

When woody plants have been perturbed by abiotic or biotic factors such as wind, landslide, snow, volcanic eruption, or grazing, they reorient their stems and branches towards the normal direction. Reaction wood allows woody plants to adjust the orientation of stems and branches when they are displaced from the upright or normal position [1–7]. Reaction wood in angiosperm trees is referred to as tension wood. To pull an inclined stem into a favorable position, tension wood generates a strong tensile force along the grain of the upper side of the leaning stem [7–15].

*Correspondence:

Ryo Funada
funada@cc.tuat.ac.jp

¹ Faculty of Forestry, Universitas Gadjah Mada, Jalan Agro No. 1
Bulaksumur, Yogyakarta 55281, Indonesia

² Faculty of Agriculture, Tokyo University of Agriculture and Technology,
Fuchu, Tokyo 183-8509, Japan

³ Institute of Wood Technology, Akita Prefectural University, Noshiro, Akita
016-0876, Japan

⁴ Institute of Global Innovation Research, Tokyo University of Agriculture
and Technology, Fuchu, Tokyo 183-8538, Japan

The formation of tension wood is generally associated with increased cambial growth, modified wood anatomy and xylem cell morphology, and a change in the ultrastructure and chemistry of the secondary cell walls of wood fibers [4, 16–21]. Tension wood is usually characterized by the presence of gelatinous fibers with thick inner gelatinous layers (G-layers), on the upper side of the leaning stem, for reorientation towards the normal position in response to a gravitational stimulus [4, 5, 11–14, 22–26]. Thick inner G-layers contain elevated levels of cellulose and low levels of lignin [2, 27–30]. In the G-layer, the cellulose microfibrils are oriented parallel or nearly parallel to the longitudinal axis of the fibers [31–34]. However, in some angiosperm species, typical gelatinous fibers are not found in the tension wood region [1, 35–38].

A gravitational stimulus also induces modifications in the anatomical characteristics of other elements of wood, such as vessel elements and ray parenchyma cells [16, 23, 36]. The modifications in the anatomical characteristics of tension wood and in the chemical properties and wall structure of fibers differ among species [4, 11, 13, 39, 40]. The anatomical characteristics of wood are closely related to the wood density itself. Thus, wood density might be associated with the responses of angiosperm species to a gravitational stimulus. However, limited information is available about the way in which tree species with different wood densities generate tension wood and exhibit negative gravitropism.

This study was designed to investigate how trees species with different respective wood densities respond to a gravitational stimulus and form tension wood. Seedlings of three tropical trees, namely, *Diospyros celebica* (Family: Ebenaceae), *Artocarpus heterophyllus* (Family: Moraceae) and, *Falcataria moluccana* (Family: Fabaceae) were used for experiments, representing woody species with high, medium, and low wood densities, respectively. These density classifications are based on wood density categories reported in previous studies [41, 42]. Our results revealed that larger amounts of gelatinous fibers and/or thicker G-layers were important for the negative gravitropism and stem-recovery movement of inclined stems in all three species. However, three species exhibited different patterns of stem gravitropism in response to a gravitational stimulus, with differences in widths of tension wood areas and the thickness of G-layers. These differences were not correlated with wood density.

Materials and methods

Plant materials

Five healthy seedlings of *Diospyros celebica*, *Artocarpus heterophyllus*, and *Falcataria moluccana* (approximately

1.5 years old), grown from seeds and selected for uniformity in age, stem straightness, single-stem structure, minimal basal foliage, and absence of visible damage, were used in the experiments.

The wood density value of each species is based on wood density near the pith and base of the tree, as this region is expected to have a density value closest to those of seedlings. Accordingly, we used density values reported in previous studies [43–45] for the pith area and basal section. Each species is categorized into wood density classes [41, 42]: low density (≤ 0.50 g/cm³) for *F. moluccana* (0.28 g/cm³ [43]), medium density (0.50–0.72 g/cm³) for *A. heterophyllus* (0.516 g/cm³ [44]), and high density (> 0.72 g/cm³) for *D. celebica* (0.8 g/cm³ [45]).

Five seedlings of each species, which were approximately 100 cm tall, were planted in 20-cm-diameter pots. Pots were filled with regosol soil and kept in a greenhouse at the nursery of the Faculty of Forestry, Universitas Gadjah Mada, Yogyakarta, Indonesia. Pots were tilted to approximately 45° from the vertical and the soil in each pot was moistened with approximately 200 ml of water daily. Inclined seedlings were harvested three months after the start of inclination for detailed analysis of wood anatomy.

Determination of stem recovery degree (R°)

During the first month after the start of inclination, seedlings were photographed every three days. After 30 days, photographs of seedlings were taken weekly for the remaining two months. Photographs were analyzed with image-analysis software (Image-J; National Institutes of Health, MD, USA) [46]. The stem recovery degree (R°) was measured as an index of negative gravitropism, as described by Nugroho et al. [22].

Preparation and analysis of transverse sections

Two-cm segments of stems, 10 cm above soil level, were obtained from each seedling for analysis. The segments were fixed in 4% glutaraldehyde in 0.1 M phosphate buffer (pH 7.3). Transverse sections of 15-μm in thickness were cut from the fixed segments on a sliding microtome (NS-31; Yamato Kohki, Saitama, Japan). Sections were stained with a 0.1% solution of safranin (WAKO Pure Chemical Industries, Osaka, Japan) and then with a 1% solution of Astra blue (Sigma-Aldrich, Steinheim, Germany). They were dehydrated in a graded ethanol series, mounted on glass slides, fixed in resin (Entellan new; Merck, Darmstadt, Germany) and secured with coverslips [22–24]. Images were recorded under a light microscope (BX51; Olympus Corporation, Japan) with a digital camera (DP70; Olympus Corporation) as described by Nugroho et al. [47].

Digital images of transverse sections were captured for measurements of the width of the region of tension wood in the outermost xylem in the upper part of each inclined stem. The width of the region of tension wood was determined by measuring the width of the region that consisted of gelatinous fibers with inner G-layers that had been stained blue by the combination of Astra blue and safranin [22–24]. For measurement of the apparent thickness of G-layers, digital images of transverse-sectional areas of $35.3 \times 10^3 \mu\text{m}^2$ were recorded from regions of the tension wood and “opposite” wood of inclined stems. Fifty wood fibers were measured in each sample. The width of the region of tension wood and the thickness of the G-layers were determined with image-analysis software (Image-J).

Statistical analysis

Data were analyzed with the statistical software Prism5 for Mac OS X (GraphPad Software Inc., USA). The effects of wood density on gravitropism, on the width of the tension wood region and on the thickness of G-layers were analyzed by one-way analysis of variance (ANOVA), which was followed by Tukey’s post hoc test. Significance of differences was recognized at $P < 0.05$. Linear regression analysis was performed to examine the relationship between the width of the region of tension wood and R° . The relationship between the thickness of G-layers and R° was examined similarly.

Results

Negative gravitropism of inclined seedlings

Figure 1 shows typical positions of stems of *D. celebica*, *A. heterophyllum* and *F. moluccana* seedlings at the start of the experiment (day zero) and after three months of inclined growth. All the inclined seedlings had reoriented towards the vertical three months after the start of inclination. Figure 2 shows the changes in stem recovery degrees (R°) for the artificially inclined stems of *D. celebica*, *A. heterophyllum* and *F. moluccana* from day zero to three months after the start of inclination. *A. heterophyllum* seedlings, typical of a species with medium wood density, were associated with the greatest recovery in terms of R° , with rapid movement towards the vertical. The seedlings of lower wood density, represented by *F. moluccana*, responded rapidly to the gravitational stimulus initially but then remained stable, from 21 days after the start of inclination, with limited stem recovery. The seedlings of *D. celebica*, representing high wood density, did not recover during the early stage of inclination. However, recovery progressed rapidly after 15 days. The value of R° , the stem recovery degree, of *D. celebica* seedlings was approximately 30° three months after the start of inclination and the recovery overtook

that of *F. moluccana* seedlings approximately 40 days after the start of inclination.

Width of tension wood regions

The inclination of stem seedlings at 45° induced the formation of tension wood in all of the inclined seedlings examined. Tension wood was observed in the upper part of the stems (Figs. 3A–3C). While no tension wood was detected on the opposite in *D. celebica* (Fig. 3C), narrow bands of tension wood were present in the opposite part of *F. moluccana* (Fig. 3A) and *A. heterophyllum* (Fig. 3B). This tension wood in the opposite part of *F. moluccana* and *A. heterophyllum* may have developed prior to the inclination treatment.

Three months after the initial tilting of pots, the widths of regions of tension wood in the upper parts of inclined stems differed significantly among the three-woody species ($P < 0.0001$; Fig. 4). The widths of tension wood areas ($\pm$ s.e.) were approximately 0.59 ± 0.10 mm in *F. moluccana*, 1.20 ± 0.03 mm in *A. heterophyllum* and 0.92 ± 0.01 mm in *D. celebica*. Seedlings of *A. heterophyllum*, representing medium wood density, had significantly wider regions of tension wood than those of *F. moluccana* and *D. celebica*.

Thickness of G-layers

Microscopic investigation of $15 \mu\text{m}$ thick transverse sections revealed that gelatinous fibers with an inner G-layer that had been stained blue by combination of safranin and Astra blue were present in the tension wood regions of *F. moluccana*, *A. heterophyllum* and *D. celebica* (Fig. 5A–C). By contrast, no gelatinous fibers were found in the opposite regions of the inclined seedlings (Fig. 5D–F). The thicknesses of G-layers differed significantly among the woody species examined ($P < 0.0001$). The mean values ($\pm$ s.e.) of thicknesses of G-layers in inclined seedlings were approximately $1.7 \pm 0.1 \mu\text{m}$ in *F. moluccana*, $4.0 \pm 0.2 \mu\text{m}$ in *A. heterophyllum* and $2.8 \pm 0.1 \mu\text{m}$ in *D. celebica* (Figs. 5 and 6). The inclined seedlings of *A. heterophyllum* formed thicker G-layers than those of *D. celebica* and *F. moluccana*.

Figure 7 shows relationships among widths of regions of tension wood in the upper portions of stems of inclined seedlings of *F. moluccana*, *A. heterophyllum* and *D. celebica* seedlings and stem recovery degrees (R°). In general, there was a strong correlation between the width of the region of tension wood and R° . However, linear regression analysis of results from each tree species demonstrated that the respective relationships between the width of the region of tension wood and R° differed among trees species. Only in *F. moluccana*, the width of

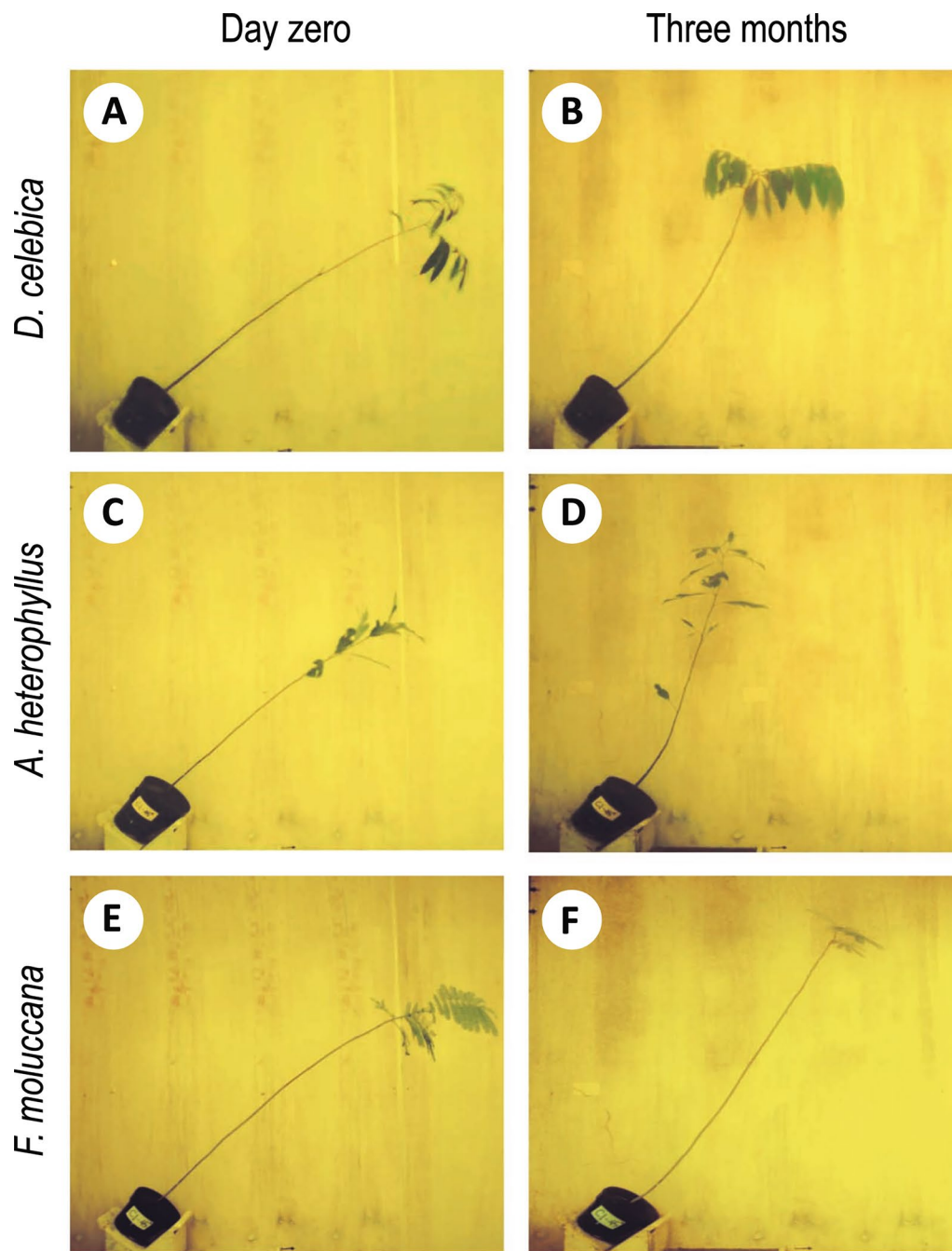


Fig. 1 Photographs showing the typical positions of stems of seedlings on day zero and three months after the start of inclination at 45°: **A, B** *D. celebica*; **C, D** *A. heterophyllus*; **E, F** *F. moluccana*. Scale bar = 20 cm

the regions of tension wood was positively correlated with R° .

When we examined relationships between the thickness of G-layers in the tension wood and R° , we found a positive correlation in all three species

examined (Fig. 8). However, separate linear regression analysis for each of the three species revealed that the thickness of G-layers was positively correlated with R° in *A. heterophyllus* and *D. celebica* but not in *F. moluccana*.

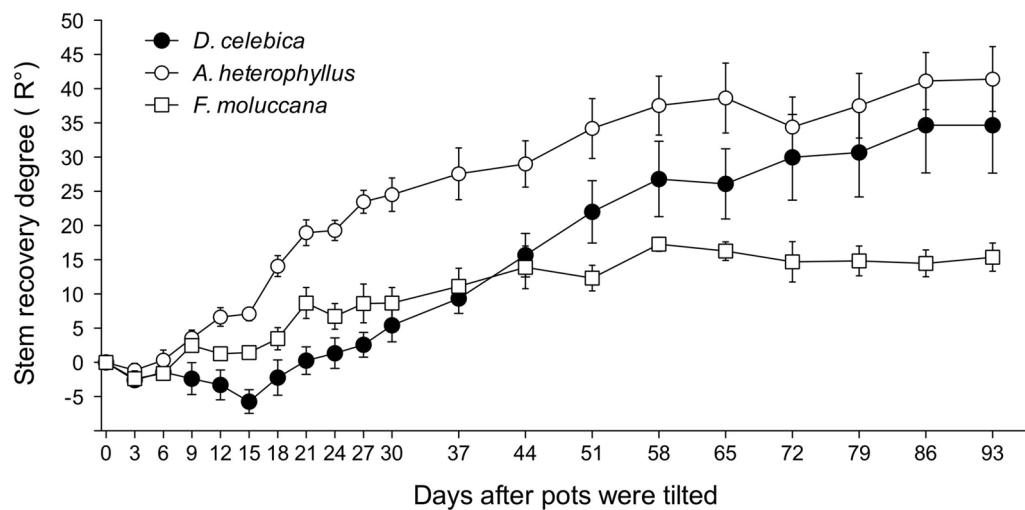


Fig. 2 Time courses, in term of average stem-recovery degrees (R° 's), of changes in orientation of artificially inclined seedlings of *D. celebica*, *A. heterophyllum* and *F. moluccana*. All seedlings returned towards the vertical but the degrees of recovery (R°), the timing of the recovery and speed of recovery differed among species. Bars indicate standard errors ($n=5$ seedlings per species)

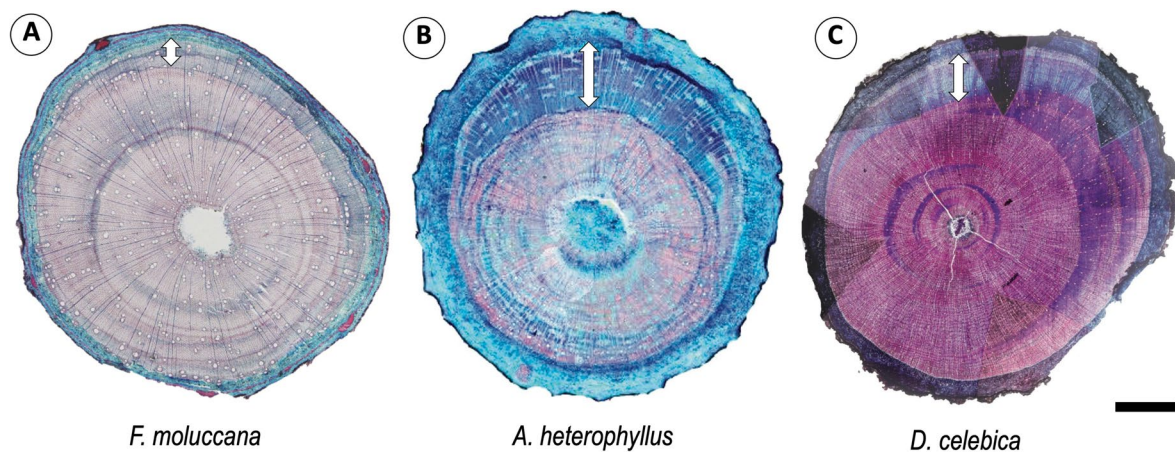


Fig. 3 Light micrographs of cross sections of inclined stems, stained with safranin and Astra blue, three months after pots had been inclined: **A** *F. moluccana*; **B** *A. heterophyllum*; **C** *D. celebica*. Double-sided arrows indicate the presence of gelatinous fibers in the upper regions of the inclined stems. These fibers were colored blue after staining with safranin and Astra blue. Scale bar = 1 mm

Discussion

The results described above show clearly that seedlings of woody species with different wood densities exhibit different patterns of stem gravitropism in response to a gravitational stimulus, with development of tension wood and G-layers of varying thickness in the upper parts of inclined stems (Figs. 3 and 5). In the present study, we found that inclined seedlings of *F. moluccana*, *A. heterophyllum* and *D. celebica* returned to the vertical or near vertical position and formed tension wood with typical inner G-layers, which were stained blue by a solution of safranin and Astra blue, in the upper parts of the inclined stems. Aiso et al. [48] also observed that

seedlings of *F. moluccana* formed G-layers, which were stained by a solution of zinc chloride-iodine, in the upper parts of inclined stems.

Our experiments revealed that *F. moluccana* seedlings, with low wood density, responded rapidly to the gravitational stimulus during the early period of inclination but ultimately the extent of stem recovery (R°) was low (Figs. 1E, F and 2). *A. heterophyllum* seedlings, with medium wood density, yielded the highest values of R° , with rapid movement towards the vertical direction (Figs. 1C, D and 2). In *D. celebica* seedlings, with high wood density, recovery movement in response to the gravitational stimulus was delayed at the early stage of

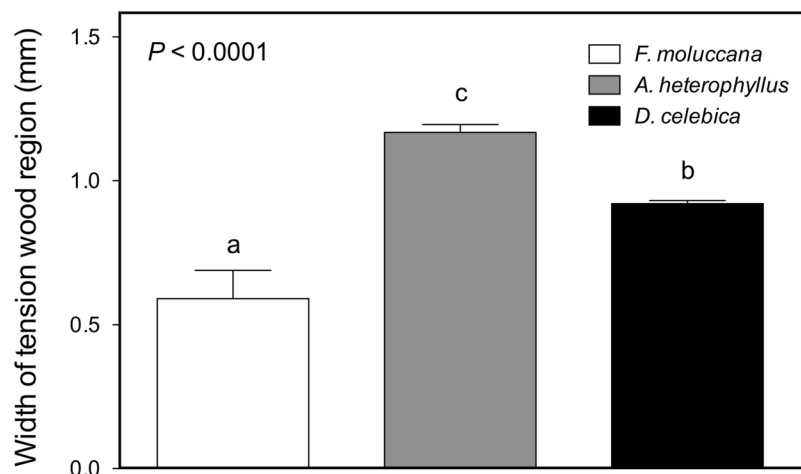


Fig. 4 Quantitative analysis of the widths of regions of tension wood in the upper portions of stem of inclined seedlings of *F. moluccana*, *A. heterophyllum* and *D. celebica*, three months after the start of inclination. The widths differed significantly among species ($P < 0.001$). Error bars indicate standard errors ($n = 5$ seedlings per species). Different letters above bars indicate significant differences, as determined by Tukey's post hoc test at $P < 0.05$

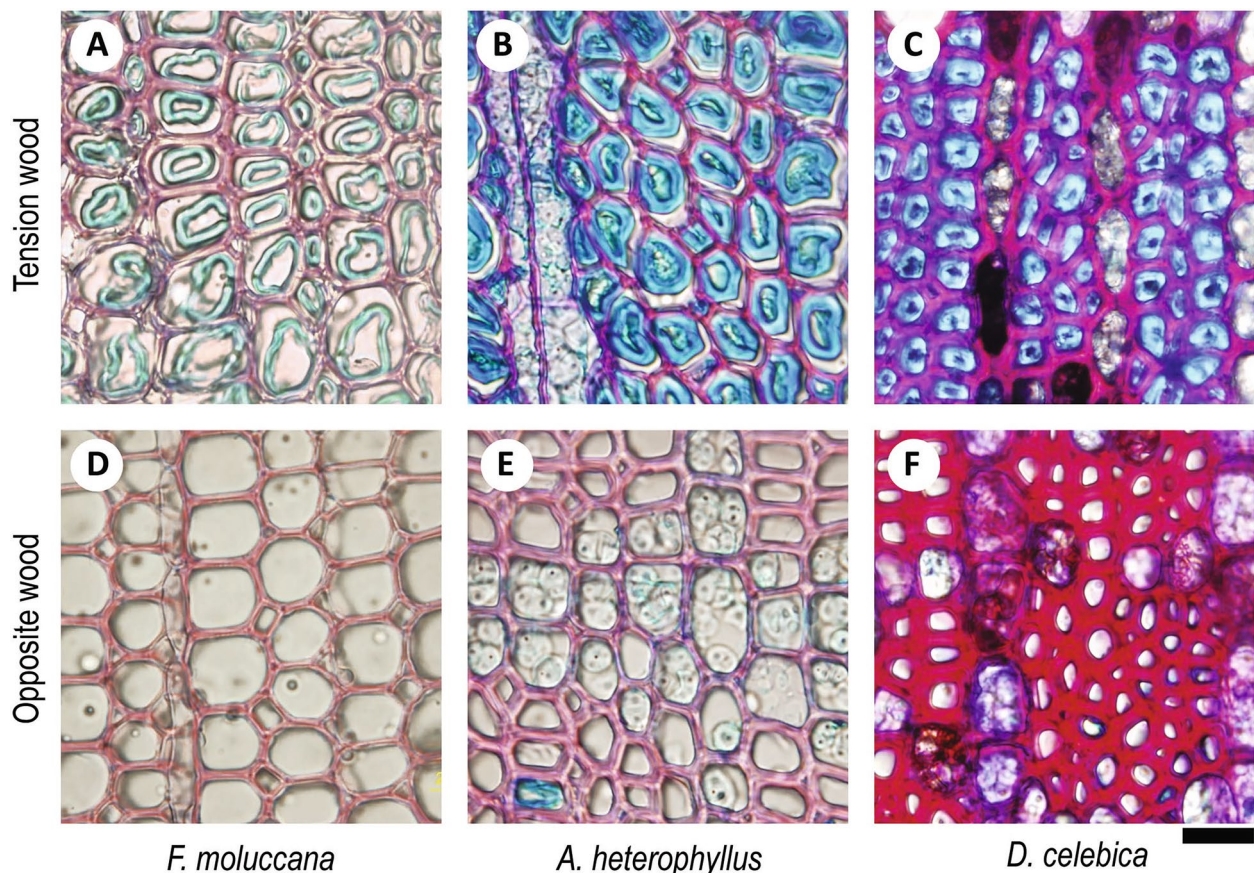


Fig. 5 Light micrographs of transverse sections of tension wood in the upper portions of inclined stems and in the opposite wood, after staining with safranin and Astra blue: **A, D** *F. moluccana*; **B, E** *A. heterophyllum*; **C, F** *D. celebica*, three months after the start of inclination. Seedling of *A. heterophyllum* formed the thickest G-layers. Blue coloration indicates the presence of G-layers. Scale bar = 20 μ m

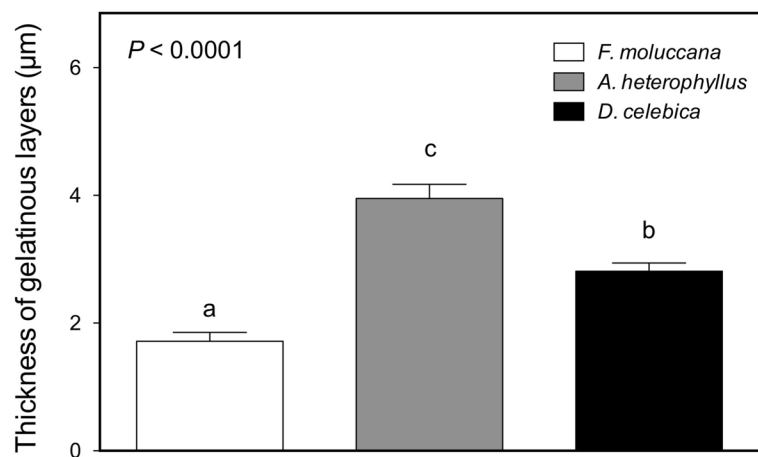


Fig. 6 Quantitative analysis of the thickness of G-layers in the upper portions of inclined seedlings of *F. moluccana*, *A. heterophyllus* and *D. celebica*, three months after the start of inclination. Thicknesses differed significantly among species ($P < 0.0001$). Error bars indicate standard errors ($n = 5$ seedlings per species). Different letters above bars indicate significant differences, as determined by Tukey's post hoc test, at $P < 0.05$

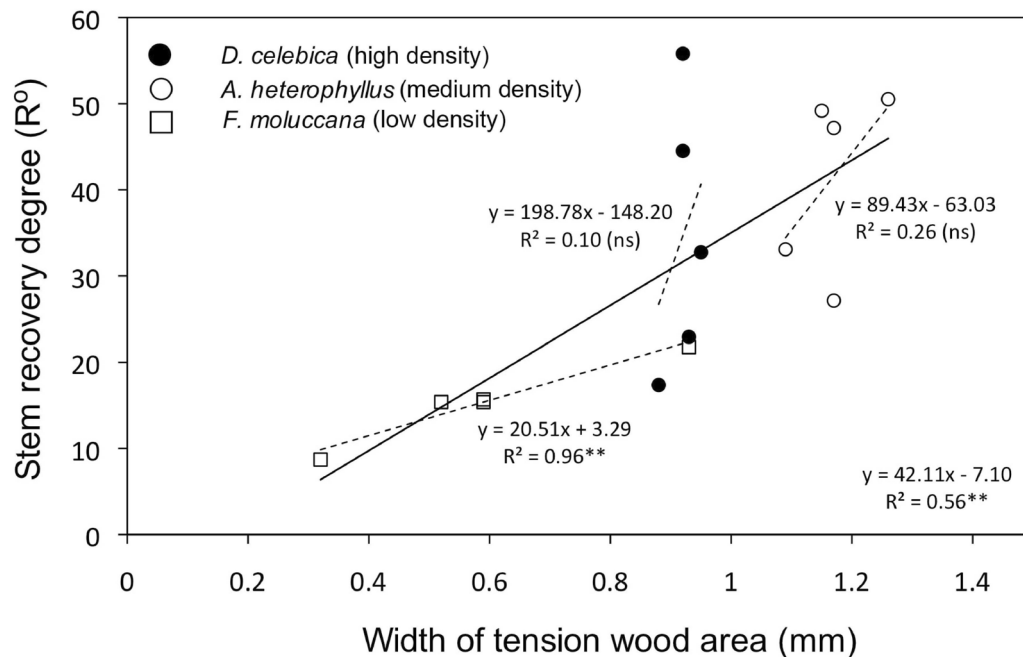


Fig. 7 Relationships between widths of regions of tension wood in the upper portions of stems of inclined seedlings of *F. moluccana*, *A. heterophyllus* and *D. celebica* and stem recovery degrees (R° s) three months after the start of inclination. The straight solid line shows that the widths of regions of tension wood were positively correlated with R° s in all three species examined. The straight dashed lines show the relationships between widths of regions of tension wood and R° s in each species examined. In *F. moluccana*, the widths of regions of tension wood were positively correlated with R° s. Each symbol represents a single set of measurements from a single seedling. **, Significantly different at $P < 0.01$; (ns), not significantly different

inclination but recovery proceeded rapidly after 15 days (Figs. 1A, B and 2). Seedlings with medium wood density exhibited the greatest stem-recovery movement towards the vertical, followed by seedlings with higher wood density and those with lower wood density. Therefore, the negative gravitropism of stems was not related to

the wood density. Negative gravitropism of stems might depend on characteristics of individual tree species rather than on the wood density.

The widths of regions of tension wood in the upper parts of inclined stems and the thicknesses of G-layers differed significantly among the tree species examined.

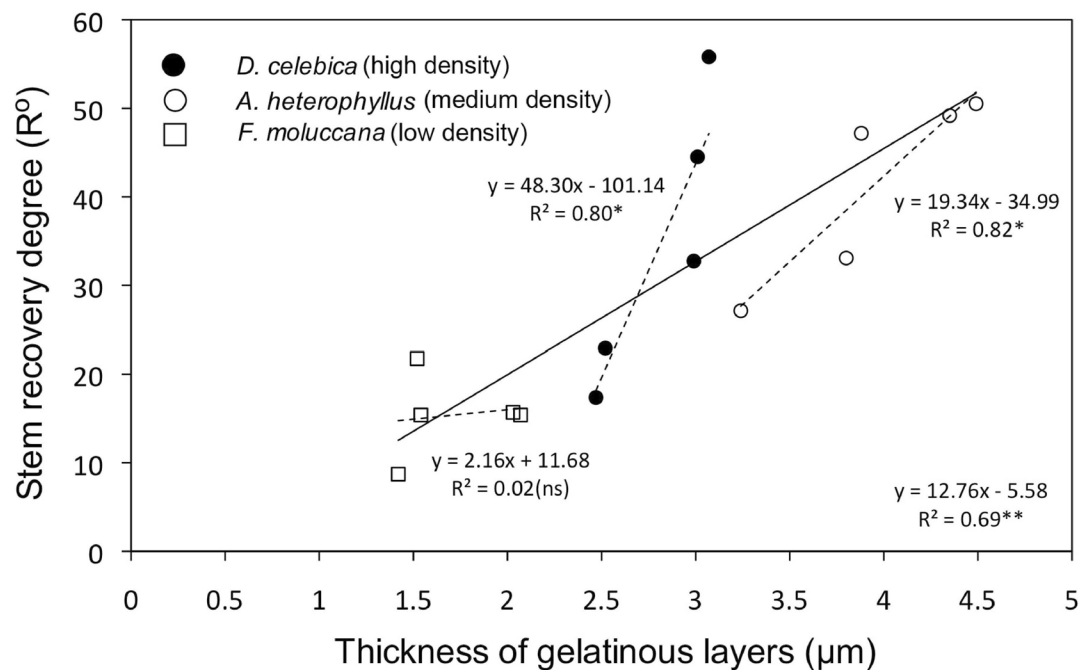


Fig. 8 Relationships between thicknesses of G-layers in tension wood of stems of inclined seedlings of *F. moluccana*, *A. heterophyllum* and *D. celebica* and stem recovery degrees (R° s) three months after pots had been inclined. The straight solid line shows that the thicknesses of G-layers were positively correlated with R° s in all three species examined. The straight dashed lines show the relationships between widths of regions of tension wood and R° s in each species examined. The thicknesses of G-layers were positively correlated with R° s in *A. heterophyllum* and *D. celebica*. Each symbol represents a single set of measurements from a single seedling. *, Significantly different at $P < 0.05$; **, significantly different at $P < 0.01$; (ns), not significantly different

Seedlings of *A. heterophyllum*, with medium wood density, had significantly wider regions of tension wood and formed thicker G-layers than seedlings of *F. moluccana* and *D. celebica* (Figs. 4 and 6). In tropical rain forests, there is wide variability in the structure of tension wood among tree species [11, 13]. Our results suggest that variations in the width of tension wood regions and the thickness of G-layers are due to differences among species rather than to differences in the wood density.

As shown in Fig. 3, tension wood formation induces eccentric growth in tree stems. This structural adaptation may increase the second moment of area compared to normal wood [49]. The second moment of area, a critical geometric property quantifying the distribution of material around a bending axis, directly influences a structure's stiffness and capacity to resist deformation under mechanical stress [50]. In a previous study [22], stems that lacked tension wood formation due to hormonal treatment are unable to recover from tilting and likely exhibit a lower second moment of area. These findings show the importance of incorporating precise measurements of the second moment of area in future experiments to quantify better the biomechanical role of tension wood in stem reorientation.

Differences in recovery degrees of stems and in the timing of stem recovery (Fig. 2) were closely related to the formation of tension wood in all three species examined. Wider regions of tension wood and thicker G-layers in the tension wood of inclined stems might generate stronger tensile forces that bend leaning stems upward more efficiently. *A. heterophyllum* seedlings had significantly wider regions of tension wood and formed thicker G-layers than seedlings of *F. moluccana* and *D. celebica* (Figs. 3–6). This difference might explain why *A. heterophyllum* seedlings yielded higher recovery degrees and more rapid reorientation towards the vertical. *F. moluccana* seedlings had the narrowest regions of tension wood and the thinnest G-layers. As a probable consequence, inclined *F. moluccana* seedlings yielded the lowest stem recovery degrees. We found that, in general, the width of the region of gelatinous fibers and the thickness of the G-layers were strongly correlated with the negative gravitropism of inclined seedlings of all tree species examined (Figs. 7 and 8). In previous studies, we showed that the width of the region of gelatinous fibers and the thickness of G-layers were strongly correlated with the negative gravitropism of inclined seedlings of *Acacia mangium* [22–24]. In poplar (*Populus* 14551), larger numbers of gelatinous fibers per unit area of tissue

and thicker G-layers generated elevated longitudinal growth stress [51]. The formation of fibers with thick G-layers induces strong tensile stress through the lateral swelling of the G-layer, which is sufficient to bend a leaning shoot upward and it is, thus, responsible for the negative gravitropic movement of inclined woody stems [7–11, 13, 15, 51–53]. Our results also show that the development of wood fibers with thick inner G-layers is important for generation of the tensile force required for the negative gravitropism of seedlings.

Development of larger amounts of gelatinous fibers and thicker G-layers might be strategies whereby inclined stems of angiosperms generate the tensile forces required for stem-recovery movement [22–24]. In the present study, while there was a strong correlation between the width of the region of tension wood or the thickness of G-layers, and stem recovery degree (R°) in all examined species, such relationships differed among tree species (Figs. 7 and 8). The widths of regions of tension wood were positively correlated with stem recovery degrees (R°) in *F. moluccana*. Furthermore, the thicknesses of G-layers in inclined seedlings of *A. heterophyllum* and *D. celebica* were positively correlated with stem recovery degrees (R°) (Fig. 8). Our results suggest that, in *F. moluccana*, the development of wider regions of tension wood was more important than the thicker G-layers for stem-recovery movement (Fig. 7). In contrast, the stem-recovery movement of inclined seedlings of *A. heterophyllum* and *D. celebica* might be due to the development of thick G-layers rather than to the width of the tension wood. Therefore, anatomical factors that generate the tensile force required for negative gravitropism of seedlings differ among species.

We found that *D. celebica* seedlings, with high wood density, exhibited delayed recovery movement at the early stages of inclination but recovery was rapid after 15 days (Fig. 2). The delayed recovery might be related to the timing of generation of tensile force during the maturation of cell walls. Wood maturation occurs with the thickening of cell walls [7, 51, 54]. *D. celebica* is categorized as a slow-growing species with high wood density [55]. Therefore, *D. celebica* might require a longer time for generation of the higher tensile forces required for negative gravitropism.

Conclusions

In summary, the differences among patterns of stem negative gravitropism, widths of tension wood regions and thicknesses of G-layers in inclined seedlings of *F. moluccana*, *A. heterophyllum* and *D. celebica* were due to differences among species rather than to differences in wood density. Our results suggest that the appropriate

width of the region of gelatinous fibers and the appropriate thickness of G-layers are essential for the negative gravitropism of inclined stems and are species-specific. Thus, the factors associated with the generation of tensile force for the negative gravitropism of seedlings differ among species.

Abbreviations

R°	Stem recovery degree
G-layer	Gelatinous layer

Acknowledgements

Widyanto Dwi Nugroho thanks the Japan Student Services Organization (JASSO) program, Japan, and Institute of Global Innovation Research (GIR), Tokyo University of Agriculture and Technology for supporting this work.

Author contributions

W.D.N. and R.F. designed the experiment, data analysis and wrote the manuscript. G.D.A., A.F.T., A.W.P., H.C., N.P.T., Y.Y., K.K., M.H.R. and S.N. performed the experiments and data analysis.

Funding

This work was supported, in part, by Grants-in-Aids for Scientific Research from the Japan Society for the Promotion of Science (JSPS) (nos. 15H04527, 16 K14954, 18H02251, 21H02253 and 24 K01822), the Hitachi Scholarship Foundation, and the Yanmar Environmental Sustainability Support Association, Japan.

Availability of data and materials

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests

The authors declare they have no competing interest.

Received: 5 December 2024 Accepted: 9 April 2025

Published online: 07 May 2025

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