

吉野川水系における溪流沿い植物群の形態学的解析



東京都市大学理工学部

自然科学科生物多様性研究室

福田達哉

溪流沿い植物とは

水位が増減する地帯に自生する植物

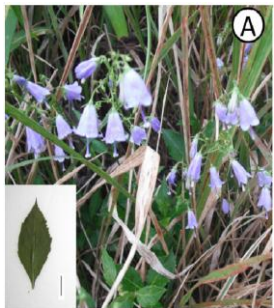


陸上型植物
と
住み分け

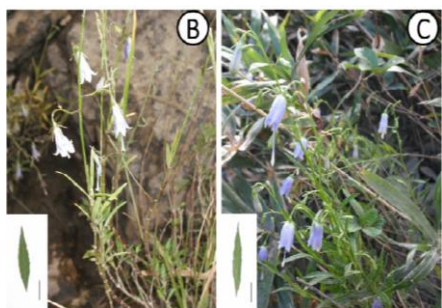
葉を細くするetc...
溪流環境に適応した形態をしている

背景～水流ストレス環境における葉身の適応例～

ツリガネニンジンの**溪流種**と**内陸種**



溪流型

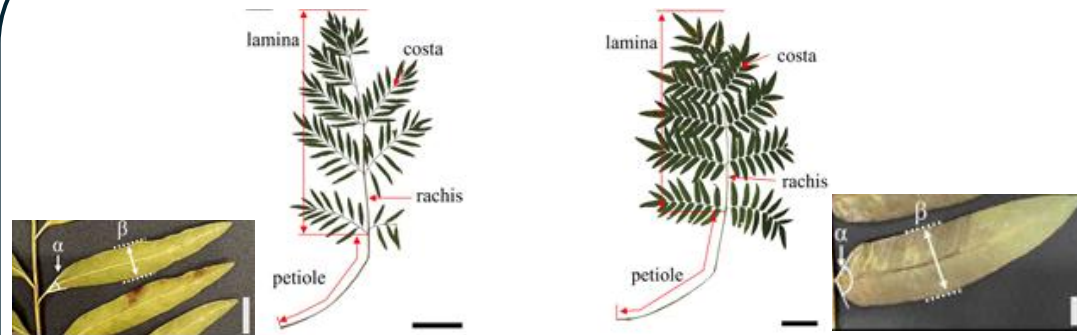


内陸型

狭葉化

(Ohga et al., 2012)

ヤシャゼンマイと**ゼンマイ**



bar=10mm

bar=10cm

ヤシャゼンマイ

ゼンマイ

狭葉化

(Imaichi and Kato, 1992)

ヒサカキの**溪流型**と**内陸型**

溪流型



bar=1cm

内陸型



小型化

(Shiba et al., 2021)

地上部全体が水流ストレスを受ける



葉身と支持器官による適応を**統合的に**評価

実際に研究例は？

なぜ吉野川水系？

Journal of Phytogeography and Taxonomy 59: 35-42, 2011
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Yurika Yamada¹, Hiroshi Hayakawa^{2, 3}, Yukio Minamiya¹, Katsura Ito¹, Zenichiro Shibayama¹, Ryo Arakawa¹ and Tatsuya Fukuda^{1*}:
Comparative morphology and anatomy of rheophytic *Aster microcephalus* var. *ripensis* (Asteraceae)

¹Faculty of Agriculture, Kochi University, Munakata 783-8502, Kochi, Japan; ²The National Graduate School of Agricultural Sciences, Ehime University, Muroto 790-8502, Japan; ³Ukudatei kochi.ac.jp (*Corresponding author)

Systematic investigation of various plants has shown that extreme and rapid divergence in morphological characteristics in association environments an entire shifts in

December 2011 J. Phytogeogr. Taxon. Vol. 50, No. 1

index (leaf length per leaf width). Measurements were obtained using a digital caliper. Leaf measurements were taken from five fully expanded stem leaves per plant (Figs. 2 A-C, E).

Anatomical analysis
For anatomical analysis, fully expanded leaves were collected from each individual. To count the number of cells on the blade, the surface of each leaf was peeled off by using Suzuki Universal Micro-Printing (SUMP) method.

Results
We measured the epidermal cell size, guard cell size, and stomatal density among four different sites of the leaf (Fig. 2 (D) I-IV). Then, the central part of the leaf (Fig. 2 (D) I) was analyzed to determine the number and size of the epidermal cells and the size of the guard cells. Replicas of each leaf (1 cm²) were made for measuring the density and size of the stomata. We analyzed 10 cells per SUMP image for each leaf by using a light microscope.

Statistical analysis
We compared differences between the two

of selective pressures such as flash floods after heavy rain differs for each river, and the morphological characteristics of rheophytic species

varieties by using a t-test. To compare leafy differences for *A. microcephalus* var. *ripensis*, we used Tukey's Honestly Significant Difference (HSD) test ($p < 0.05$). Because the leaf index in either population was not normally distributed, nonparametric pairwise comparison was conducted (Sidak-Steel test, Dwass 1960; Steel 1960).

Materials and Methods
A. microcephalus var. *ripensis* generally had a shorter leaf length than did *A. microcephalus* var. *ooutae* (52.7 ± 12.2 mm and 17.1 ± 11.5 mm, respectively) (Table 2). However, the size difference was more conspicuous for the leaf width (7.4 ± 3.6 mm in *A. microcephalus* var. *ripensis* and 21.2 ± 5.7 mm in *A. microcephalus* var. *ooutae*) (Fig. 3). The leaf area was estimated as 140 ± 124 mm² for *A. microcephalus* var. *ripensis* and 525 ± 240 mm² for *A. microcephalus* var. *ooutae*. These traits were signif-

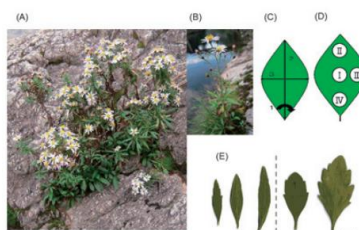


Fig. 2. The plants of *Aster microcephalus* var. *ripensis*. (A) *A. microcephalus* var. *ripensis* in the Yoshida River. (B) *A. microcephalus* var. *ripensis* in the Yoshida River. (C) Diagram of leaf measurements. I: angle of leaf base; 2: leaf length; 3: leaf width. (D) Measured parts of leaf for epidermal cells. I: central part; II: distal part; III: marginal part; IV: proximal part. (E) Leaf shape of *A. microcephalus* var. *ripensis* and var. *ooutae*. Bar = 1 cm.

American Journal of Plant Sciences, 2012, 3, 805-809
http://dx.doi.org/10.3390/ajps2012030805

Comparative Morphology and Anatomy of Non-Rheophytic and Rheophytic Types of *Adenophora triphylla* var. *japonica* (Campanulaceae)

Kyoko Ohga¹, Miwako Murai¹, Hiroshi Hayakawa², Jun Yokoyama³, Katsura Ito¹, Shin-Ichi Takayama¹, Ryo Arakawa¹, and Tatsuya Fukuda^{1*}

¹Faculty of Agriculture, Kochi University, Kochi, Japan; ²Faculty of Science, Yamagata University, Yamagata, Japan; ³Faculty of Science, Yamagata University, Yamagata, Japan; Email: tkohga@koch-u.jp

Received April 10th, 2012; revised April 30th, 2012; accepted May 10th, 2012

ABSTRACT

The morphology and anatomy of leaves of rheophytic and non-rheophytic types of *Adenophora triphylla* (Thunb.) A.D.C. var. *japonica* (Rydb.) H. Hara were compared in order to clarify how leaf characteristics differ. Our results revealed that the leaf of the rheophytic type of *A. triphylla* var. *japonica* was narrower than the leaf of the non-rheophytic type because of fewer cells that were also smaller. Moreover, surprisingly, the rheophytic ecotype of *A. triphylla* var. *japonica* was thicker than that of the non-rheophytic type, although the general tendency is that the rheophytic leaf is thicker than the closely related non-rheophytic species, suggesting that the rheophytic type of *A. triphylla* var. *japonica* adapts differently, as compared to other rheophytic plants, to solar radiation and evaporation.

Keywords: Rheophytic; Leaf; Ecotype; *Adenophora triphylla* var. *japonica*

1. Introduction

Morphological diversity is a species, and a key challenge is to how the extraordinary morphological leaves on the main phenotypic plants, and they show a strong variation in shape, making them a studying the evolution of form. It is not clear how morphological diversification and whether it arose in situ. Rheophytic plants, which have narrow lanceolate or ovate leaves, are subject to flash floods and thus act as strong selective pressure. Rheophytic plants, which have narrow lanceolate or ovate leaves, are subject to flash floods and thus act as strong selective pressure. Rheophytic plants, which have narrow lanceolate or ovate leaves, are subject to flash floods and thus act as strong selective pressure. Rheophytic plants, which have narrow lanceolate or ovate leaves, are subject to flash floods and thus act as strong selective pressure.

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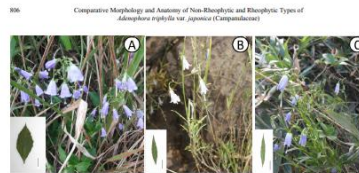


Figure 1. Plants of *Adenophora triphylla* var. *japonica*. (A) Non-rheophytic type in Higashiboku. (B) Rheophytic type in Shimano River. (C) Magnified view of stomata. (D) Magnified view of epidermal cells. Bar = 1 cm.

2. Materials and Methods

All specimens of non-rheophytic and rheophytic types of *Adenophora triphylla* var. *japonica* examined in this study were collected from the fields. A total of 60 individuals of the non-rheophytic type of *A. triphylla* var. *japonica* (Higashiboku: 35; Higashiboku: 30) were analyzed. A total of 60 individuals of the non-rheophytic type of *A. triphylla* var. *japonica*, representing 2 populations of the var. *ripensis* (31 individuals) and the Yoshida river (29 individuals) were analyzed. Collecting locations are indicated in Figure 2 and Table 1.

For morphological analysis, individual specimens were measured for the following continuous macro-morphological variables of leaves: length and width of the leaf blade and angle of the leaf base. Measurements were made using a pair of digital calipers. Three fully expanded leaves per specimen were measured. We calculated the mean leaf length, width, and thickness of each specimen. For anatomical analysis, the fully expanded leaves from each specimen were collected. The leaves were fixed overnight in a solution of formaldehyde, ethanol, and acetic acid (FAA). To count the number of cells on the blade, the surface of the leaf leaves were peeled off using the Suzuki's Universal Micro-Printing (SUMP) method. The middle part of the blade along the midrib was examined to determine the number and size of the epidermal cells. Replicas of each leaf (1 cm²) were made to measure the density of the stomata. These copies SUMP images were examined twice for each leaf by using a light microscope.

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NOTES AND COMMENTS Morphological and anatomical analyses of rheophytic *Rhododendron ripense* Makino (Ericaceae)

KYOKUSU UEDA¹, YUKIO MINAMIYA¹, AVA HIRATA¹, HIROSHI HAYAKAWA², YUKIO MURAMATSU¹, MICHIBIKI SAITO¹ and TATSUYA FUKUDA^{1*}
¹Faculty of Agriculture, Kochi University, Munakata 783-8502, Kochi, Japan; ²National Graduate School of Agricultural Sciences, Ehime University, Muroto 790-8502, Japan; ³Ukudatei kochi.ac.jp (*Corresponding author)

Abstract

The non-rheophytic leaf of *R. ripense* is wider than the leaf of the rheophytic type because of fewer cells that were also smaller. Moreover, surprisingly, the rheophytic ecotype of *R. ripense* was thicker than that of the non-rheophytic type, although the general tendency is that the rheophytic leaf is thicker than the closely related non-rheophytic species, suggesting that the rheophytic type of *R. ripense* adapts differently, as compared to other rheophytic plants, to solar radiation and evaporation.

Introduction

Plants adapt to survive in surrounding environments. The leaf is one of the most important organs along rivers. The leaf is one of the most important organs along rivers. The leaf is one of the most important organs along rivers. The leaf is one of the most important organs along rivers.

A number of ecotypes and morphological forms of *R. ripense* are known from various environments. The leaf is one of the most important organs along rivers. The leaf is one of the most important organs along rivers.

Correspondence:

Tatsuya Fukuda (tkohga@koch-u.jp)

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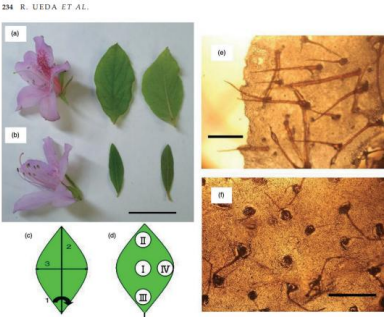


Fig. 3. Flowers and leaves of (a) *Rhododendron ripense* and (b) *Rhododendron ripense*. Bar = 1 cm. (c) Diagram of the leaf measurements. I: angle of the leaf base; II: distal part; III: marginal part; IV: proximal part.

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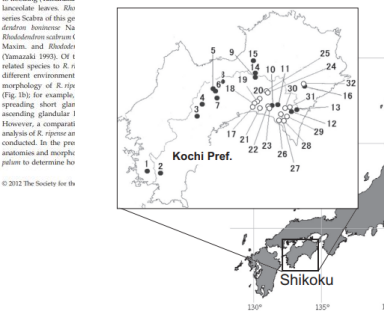


Fig. 4. Sampling localities used in the present study. See Table 1 for the names of the numbered sites. Black circles indicate sampling localities of *Rhododendron ripense*. White circles indicate sampling localities of *Rhododendron macrocarpum*.

6.53 ± 3.00 cm² for *R. macrocarpum* when the leaf length is multiplied by leaf width. These traits were significantly different between the two species ($P < 0.01$). The leaf thickness of *R. ripense* and *R. macrocarpum* was 135 ± 9.58 and 101 ± 15.0 μm, respectively. We also calculated the leaf index value as the ratio of leaf length to leaf width, as specified by Tsukada (2002). Data plots show significant variation ($P < 0.01$) in the leaf index (2.92 in *R. ripense* and 1.91 in *R. macrocarpum*). The average angle of the leaf base was 41 ± 10° for *R. ripense* and 79 ± 17° for *R. macrocarpum*. In most cases the values for *R. ripense* were less than 80°.

Epidermal cells of *R. ripense* and *R. macrocarpum*

We confirmed that there were no significant differences in the epidermal cell size between *R. ripense* and *R. macrocarpum* at four sites on a leaf (Table 2). In addition, we could not find any significant differences in the epider-

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Ueda et al. (2012) Plant Species Biology 27: 233-240

吉野川水系の 特徴的な植物を 多数報告

Ohga et al. (2012) American Journal of Plant Sciences 3: 805-809

Yamada et al. (2011) Journal of Phytogeography and Taxonomy 59: 35-42

吉野川水系の植物の面白さ

吉野川

吉野川水系の遺伝的に 変化した植物を報告

Yajima et al. (2025)
Ecology and Evolution 15: e72222

Is Genetic Differentiation Involved in the Morphological Adaptation of *Adenophora triphylla* var. *japonica* (Campanulaceae) to Water Flow Stress Along Rivers?

Iori Yajima¹ | Masayuki Shiba¹ | Kyohet Ohga² | Yoshimasa Kumekawa³ | Tatsuya Fukuda¹

¹Graduate School of Integrative Science and Engineering, Tokyo City University, Tokyo, Japan | ²Miyoshi City Hall, Tokushima, Japan | ³The United Graduate School of Agricultural Sciences, Ehime University, Nankoku, Kochi, Japan

Correspondence: Masayuki Shiba (msy.kshiba4@gmail.com)

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Keywords: *Adenophora triphylla* | genetic differentiation | morphological adaptation | phenotypic plasticity | rheophyte | riverside habitat | water flow stress

ABSTRACT

Plants along rivers have narrow lanceolate leaves, flexible stems, and petioles to avoid the water flow stress caused by flooding. This study aimed to determine whether the adaptation of *Adenophora triphylla* (Thunb.) A. DC. var. *japonica* (Regel) H. Hara (Campanulaceae) with narrow leaves in riverside habitats was achieved through phenotypic plasticity or genetic morphological changes, where we conducted comparative morphological analyses through cultivation experiments. Our cultivation experiments revealed that the morphology of radical leaves in the riverside population had significantly smaller and narrower lamina and shorter and thicker petioles than those in the inland population, and that the former had significantly more radical leaves than the latter, suggesting that the former brings the total leaf area closer to that of the latter by increasing the number of radical leaves. The cauline leaves were significantly thinner and smaller in the riverside population than in the inland population, and the stems of the former were significantly shorter and thicker than those of the latter. In addition, a significant difference was observed between the riverside and inland populations in the number of rosette leaf branches from the rhizome, with the former having significantly more rosette leaf branches. Our results reveal that populations of *Ad. triphylla* var. *japonica* with genetically distinct leaf and stem morphologies have become established along rivers, where flooded water imposes strong selective pressure. In these riverside populations, thicker and shorter petioles and stems appear to reduce bending moments without breaking, while narrower and smaller laminae of both radical and cauline leaves further contribute to this reduction.

1 | Introduction

Various plant traits are observable characteristics that reflect adaptive responses to environmental conditions (Pootier et al. 2009). In particular, the morphological characteristics of leaves have often been used for species identification for several years (Foster and Gifford 1989; Cope et al. 2012), but they also change depending on the environment (Givnish

and Vermeij 1976; Royer and Wilf 2006; Nicotra et al. 2011; Schermer et al. 2012). Leaf traits reflect the growing environment (Johnson 1975; Ellenberg 1985; Yeats and Rose 2013; Goldsmith et al. 2017; Grace 2019), and recent studies have documented variations in the morphology and anatomy of leaf traits along environmental gradients (Hayakawa et al. 2012; Tunala et al. 2012; Ohga, Muroi, Hayakawa, Yokoyama, et al. 2012; Ohga et al. 2013; Sunami et al. 2012;

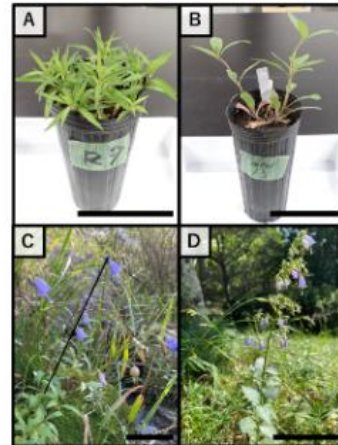


FIGURE 1 | *Adenophora triphylla* var. *japonica*. Cultivation of (A) riverside and (B) inland. Wild of (C) riverside and (D) inland. Scale bar = 10 cm.

and the racemes form at the apex of the stem. The pale purple to white, 1.5–2 cm long, bell-shaped flowers grow in whorls slightly downwards, with fused sepals that are five-lobed, and the sepal lobes are linear and 3–5 mm long (Okazaki 1993). Yamanka and Takezaki (1959) reported that populations with narrow lanceolate leaves of *Ad. triphylla* var. *japonica* are found along several rivers in Japan. Ohga, Muroi, Hayakawa, Ito, et al. (2012) reported that the riverside population of *Ad. triphylla* var. *japonica* adapts to riverside environments as a rheophytic ecotype by forming narrow lanceolate leaves and decreasing both the size and number of leaf cells. The question then arises as to whether the narrow lanceolate leaves of the riverside populations of *Ad. triphylla* var. *japonica* are phenotypic plasticity, influenced by water flow stress during leaf growth, or whether this group has genetically narrow lanceolate leaves. Therefore, this study aimed to clarify the adaptive morphological characteristics of *Ad. triphylla* var. *japonica* associated with riverside adaptation, using wild population data from Ohga, Muroi, Hayakawa, Ito, et al. (2012) and cultivated populations from this study.

2 | Materials and Methods

2.1 | Seed Collection and Cultivation Conditions

The seeds of the rheophytic ecotype of *Adenophora triphylla* var. *japonica* used in this study were collected from a population along the Yoshino River in Molyoama, Molyoama-cho,

Nagaoka-gun, Kochi Prefecture (33°76'N, 133°60'E), the same site as the population used by Ohga, Muroi, Hayakawa, Ito, et al. (2012). The seeds of the inland population were collected from a population in Shtōriodot, Minamitawaji City, Hyogo Prefecture (34°20'N, 134°48'E).

On April 6, 2023, a cultivation experiment was conducted at Tokyo City University. Seeds from both groups were sown in vertically oriented pots with a capacity of 1,600 ml, filled with black soil. The study was conducted until the second year, when stem and cauline leaf formation occurred. The total number of samples used in this study was 35 individuals from the riverside population and 92 individuals from the inland population.

2.2 | Morphological Measurements

Morphological measurements were conducted in September 2024. Radical and cauline leaves were photographed using a digital camera (Tough TG-6; OM Digital Solutions Corporation, Tokyo, Japan). Lamina length (mm), lamina width (mm), angle at lamina base (°), and lamina area (mm²) were analyzed using the image analysis software ImageJ. The leaf index was calculated as the ratio of lamina length to lamina width. Petiole length (mm) was measured three times using a 15 cm ruler (model 14,001; Shtnwa Rules Co. Ltd., Niigata, Japan), and the average value was calculated. The basal diameter of the petiole (mm) was measured three times using a digital caliper (CD-15APX; Mitutoyo Corporation, Kanagawa, Japan), and the average value was calculated. The number of leaves per individual was also counted. Stem length (cm) was measured using a 60 cm ruler (model 14,036; Shtnwa Rules Co. Ltd., Niigata, Japan). The basal stem diameter (mm) was measured using a digital caliper (CD-15APX; Mitutoyo Corporation, Kanagawa, Japan). In addition, the number of rosette-leaf branches per individual was also counted.

To determine whether the morphological phenotypes of cauline leaves and stems are genetically fixed, a comparison was made with the values from the field populations of Ohga, Muroi, Hayakawa, et al. (2012).

2.3 | Statistical Analysis

Statistical comparisons between two samples were conducted using Microsoft Excel. An *F*-test was first used to assess the homogeneity of variances between the two samples. Based on the results of the *F*-test, a *t*-test was performed under the assumption of either equal or unequal variances. Relationships between two continuous variables were analyzed using the statistical software R. The coefficient of determination (*R*²) and the regression equation were calculated, followed by regression analysis. To evaluate the applicability of ANCOVA between two groups, the normality of the data was tested.

3 | Results

In the relationship between the two variables, a natural logarithmic transformation was applied to improve normality. After

背景 ~ 水流ストレス環境における木本植物の適応例 ~

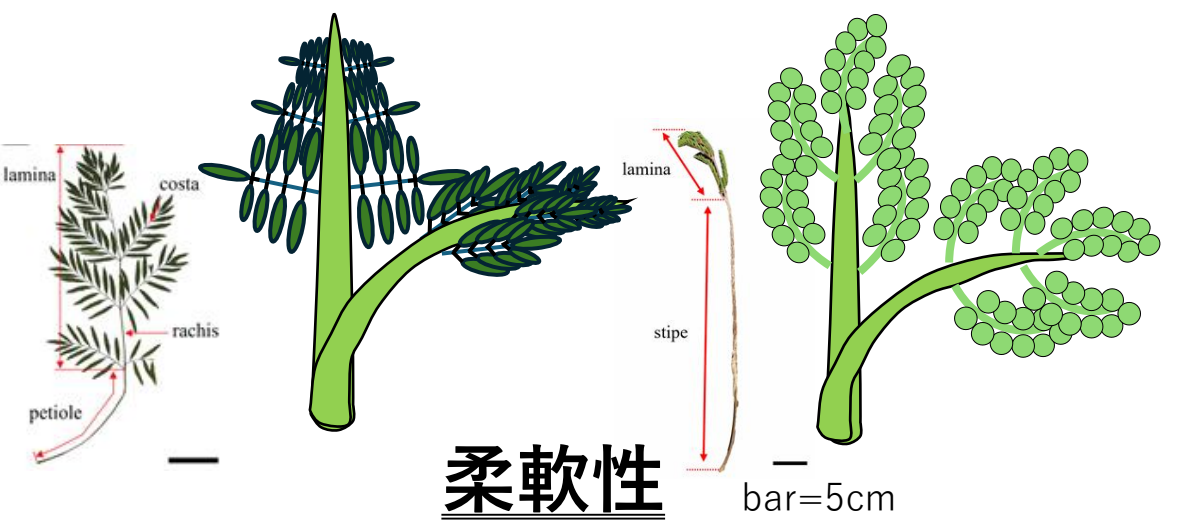
雑種を形成するほど近縁
(Yatabe et al., 1999 ; Kato, 2007)

溪流沿い

ヤシャゼンマイ (*Osmunda lancea*)

葉柄(栄養葉)

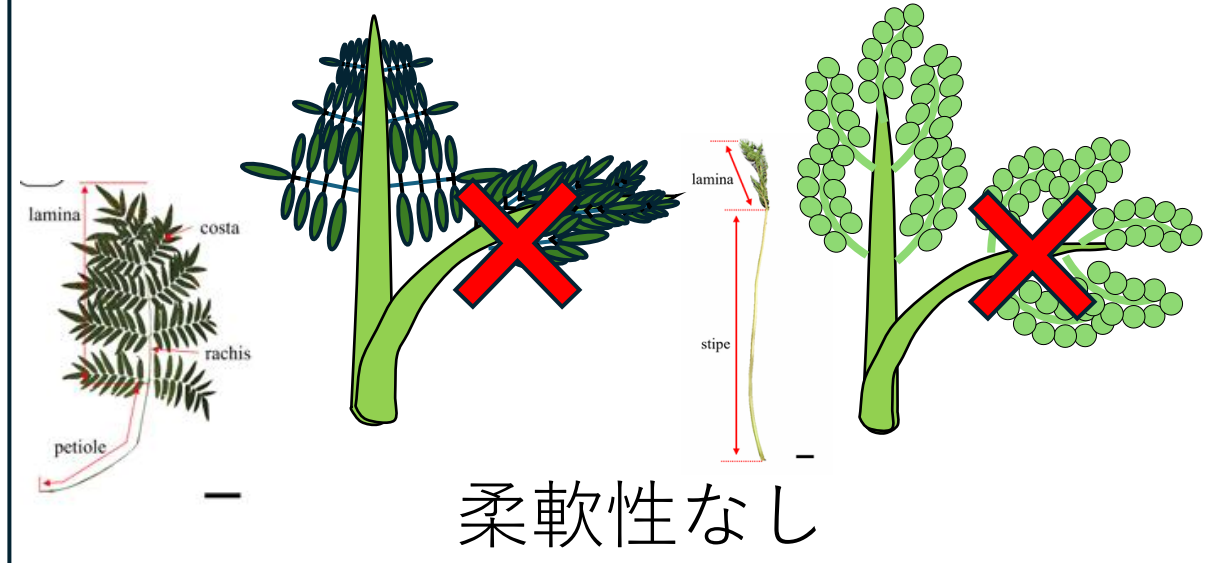
花茎(孢子葉)



ヤシャゼンマイ (*O. japonica*)

葉柄(栄養葉)

花茎(孢子葉)



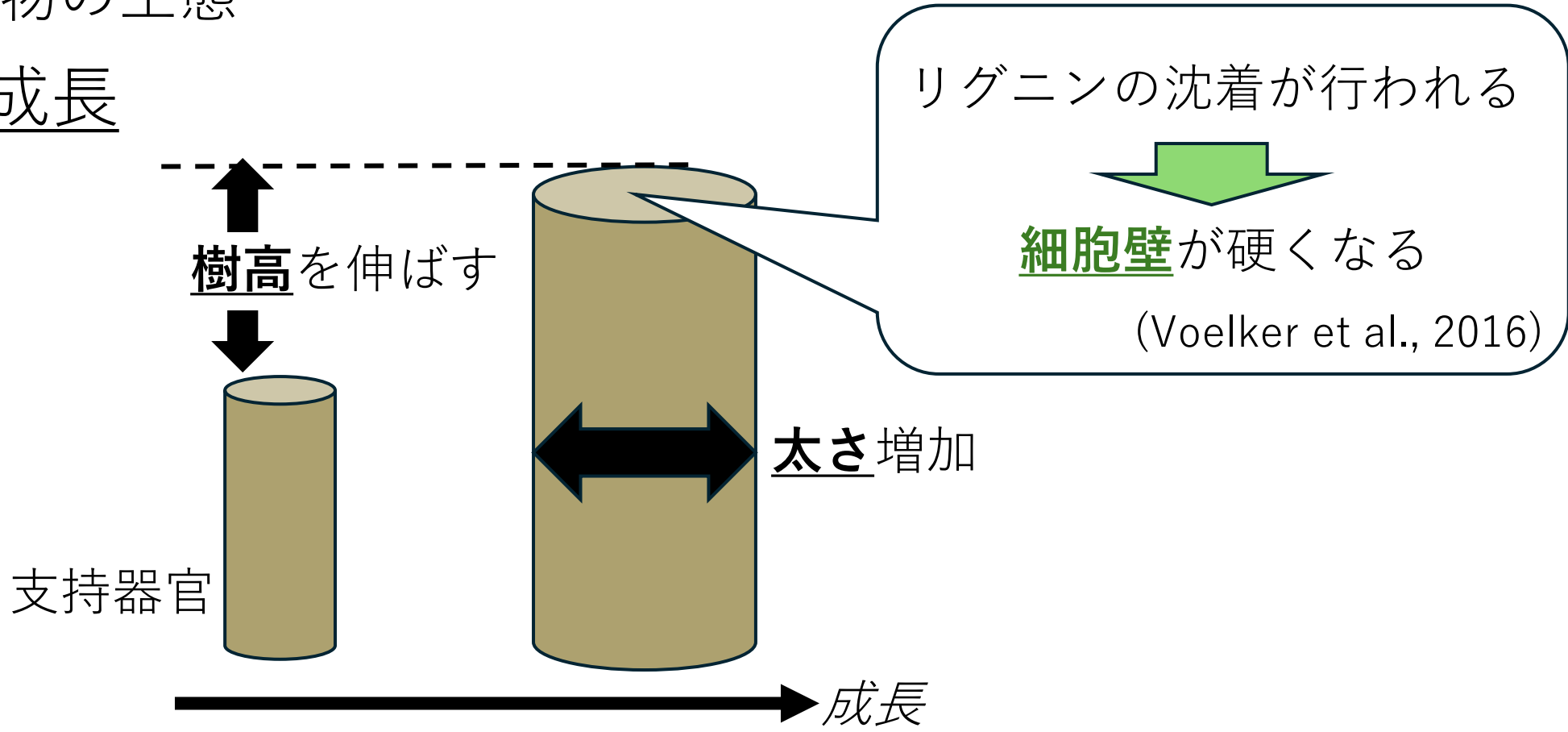
支持器官で柔軟性を獲得して地上部全体でストレス低減



木本植物にもあてはまる？

背景～木本植物の生態～

・ 木本植物の成長



成長とともに太さを増加、樹高を伸ばす

(Franceschini et al., 2016)

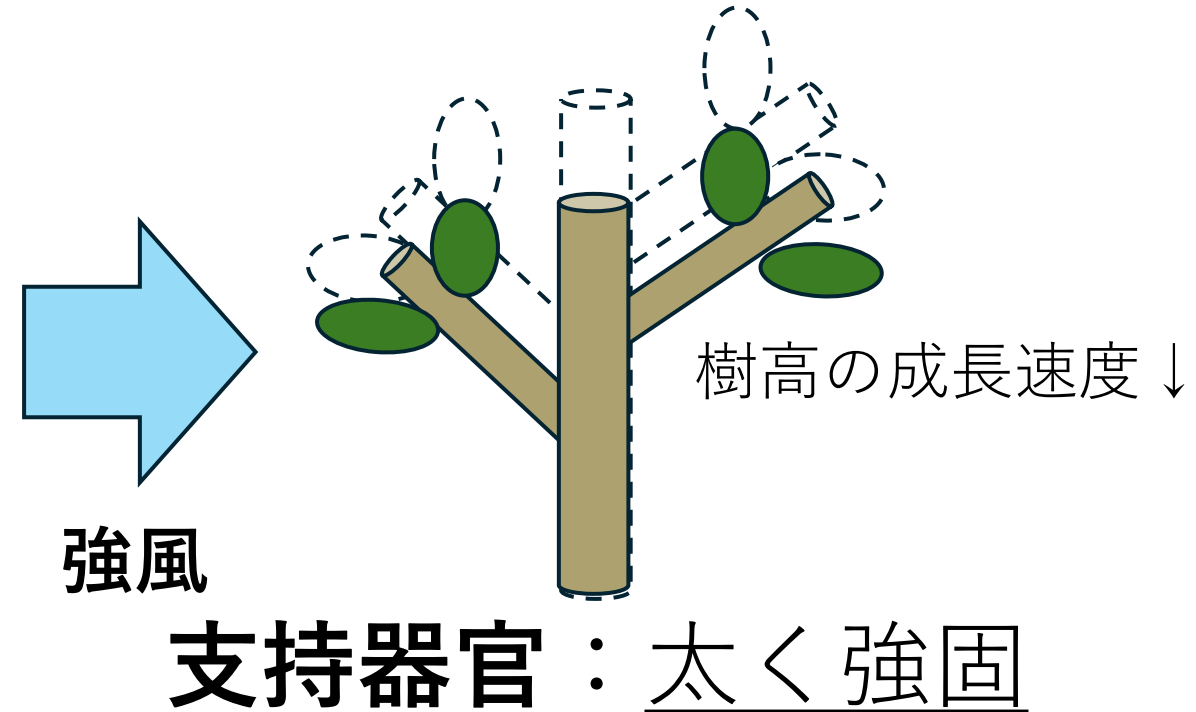
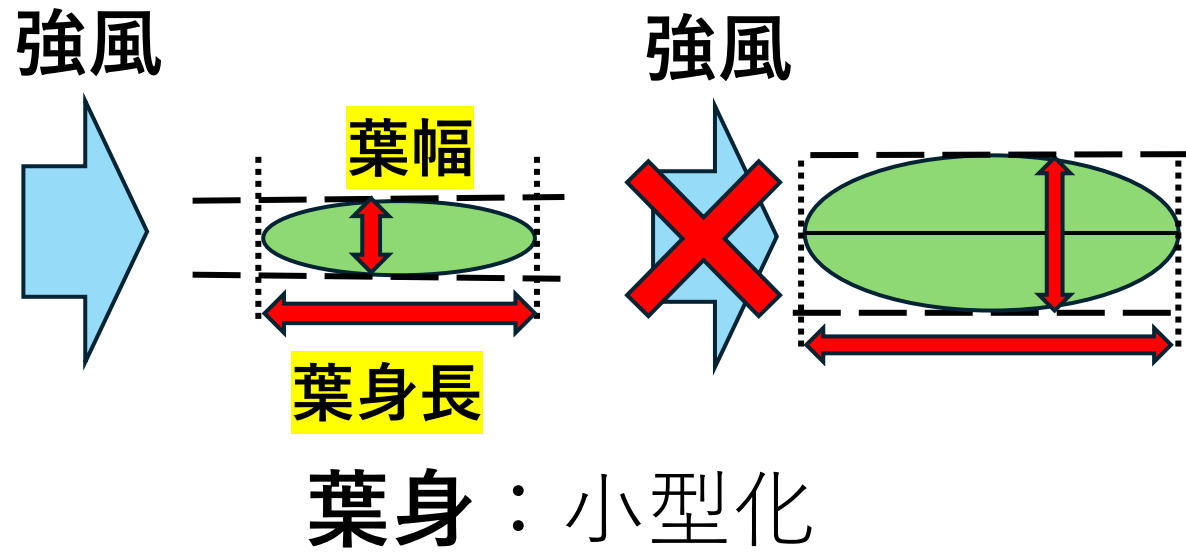
強度に特化するよう成長

背景～木本植物の強風ストレス環境における適応～

(Wu et al., 2016)

- ・ 強風ストレス環境（海岸地）

8種のナラ属(*Quercus*)



樹高を維持しながら太く強固にする **強風耐性**

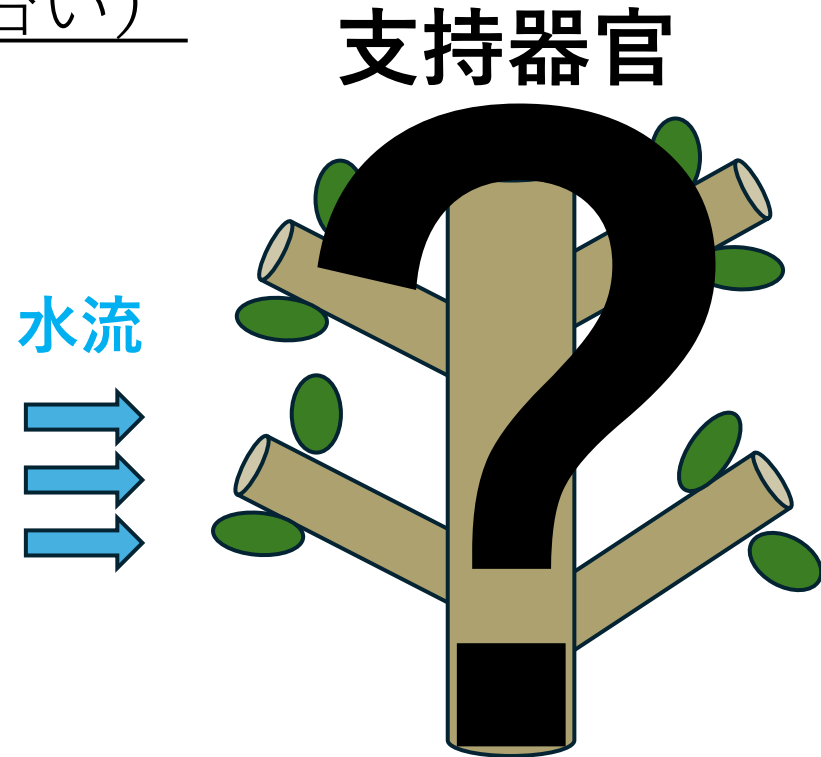
水流ストレス環境下ではどう考えられる？

背景 ～木本植物の水流ストレス環境における適応～

- ・ 増水による水流ストレス環境（溪流沿い）



葉身における適応



仮説：溪流沿いでも**強固**にしている？
(耐性)

今回どのような植物を用いて行うべき？

背景～水流ストレス環境における葉身の狭葉化例(木本植物)～

ヒサカキの**溪流型**と**内陸型**

溪流型



bar=1cm



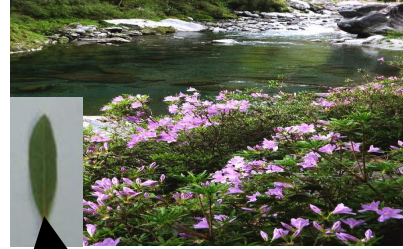
内陸型



小型化

(Shiba et al., 2021)

キシツツジと**モチツツジ**

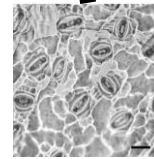


キシツツジ



モチツツジ

bar = 1cm



狭葉化

気孔数の増加

(Ueda et al., 2012)

雑種を形成するほど近縁

(Yokoyama et al., 2012)

オタクミツツジと**サツキ**



オタクミツツジ



サツキ



bar = 1cm

狭葉化

(Setoguchi and Kajimaru, 2004)

葉身における適応が明らか



近縁種間での比較

研究材料

溪流

キシツツジ (*Rhododendron ripense*)

・中国、四国、九州の一部（大分県）
の**河川**の上・中流域に分布



雄しべ10本以上

内陸

モチツツジ (*R. macrosepalum*)

・本州（静岡県・山梨県～岡山県）
と四国の**内陸**に分布



雄しべ5本

目的

吉野川水系のキシツツジを用いて
支持器官の水流ストレス適応メカニズムを明らかにする

採集地

キシツツジ

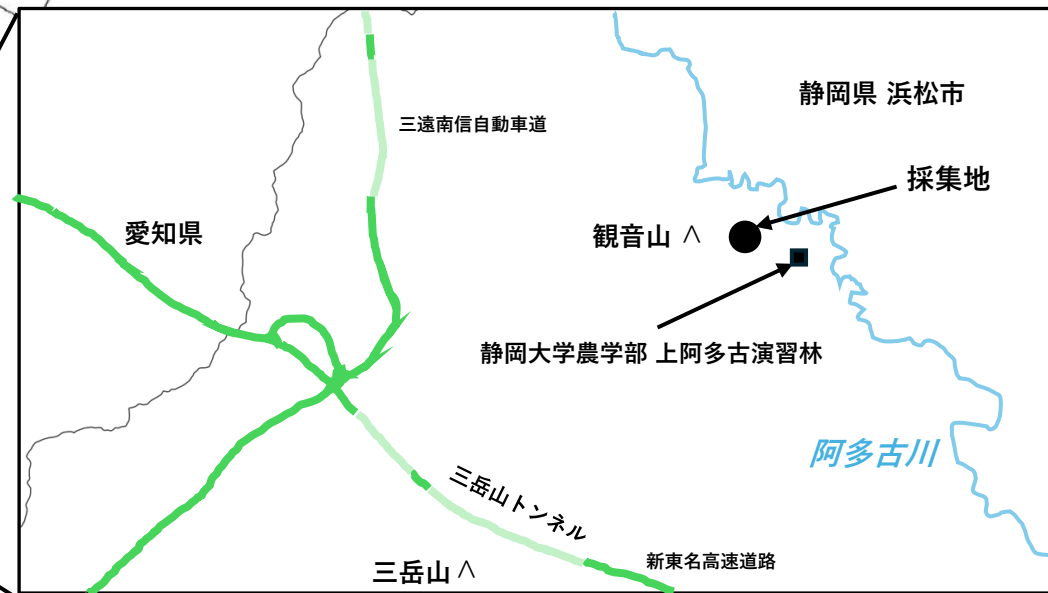


徳島県三好市山城町

33°52'51.6N 133°45'38.2E

109本の枝(支持器官)を採集

モチツツジ



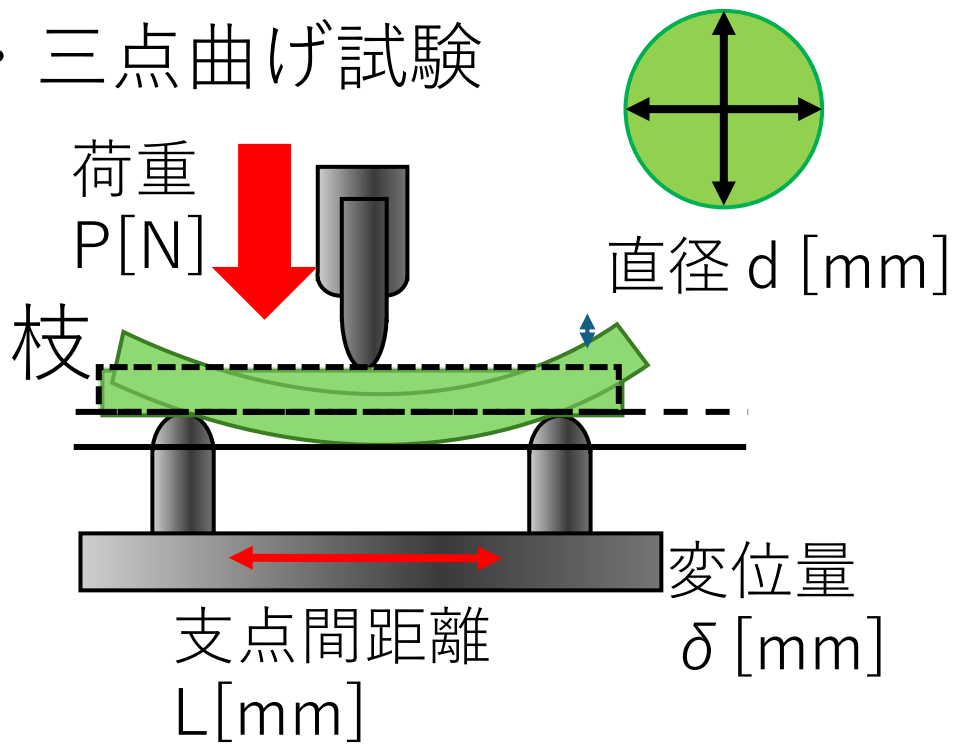
静岡県浜松市天竜区

34°54'22.2N 137°44'39.7E

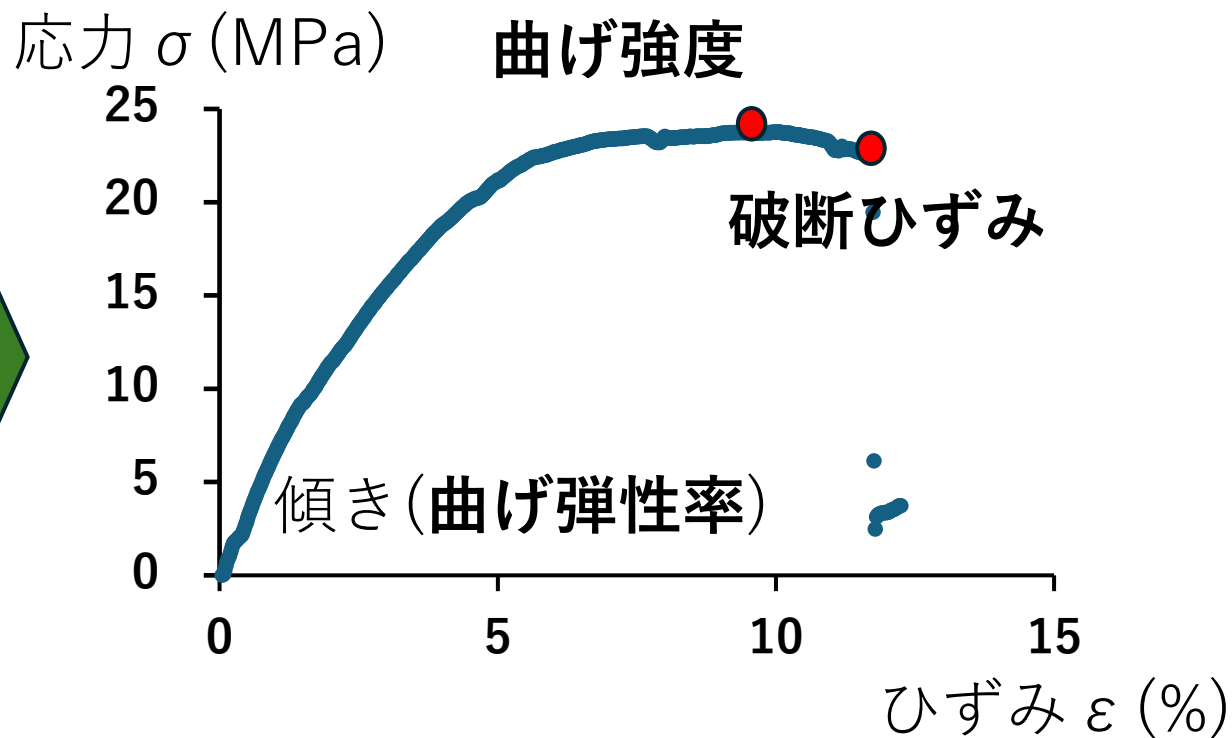
80本の枝(支持器官)を採集

方法 ～力学的解析～

• 三点曲げ試験



応力ひずみ曲線



• 条件

$\frac{L^3}{I}$...太さに対してどれくらい長い距離で曲げているか

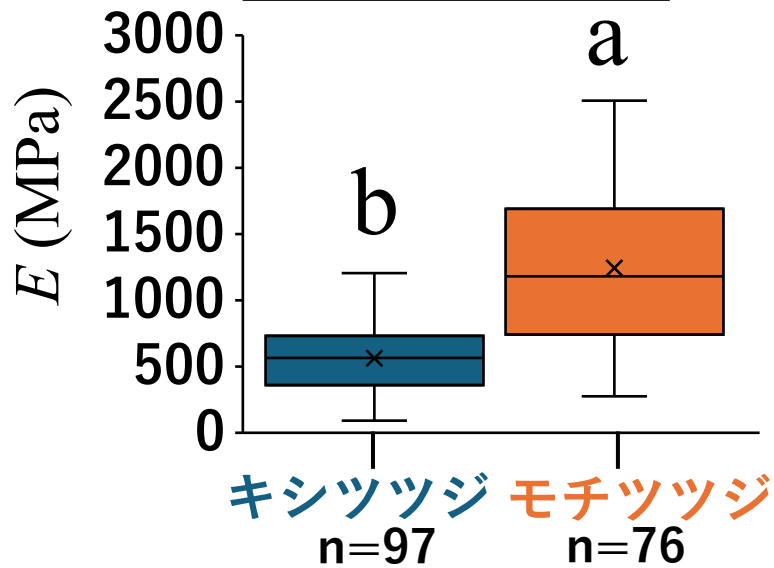
$$\frac{L^3}{I} = 20000$$

$I = \frac{\pi d^4}{64}$...どれだけ曲がりにくい形状か
(断面二次モーメント)

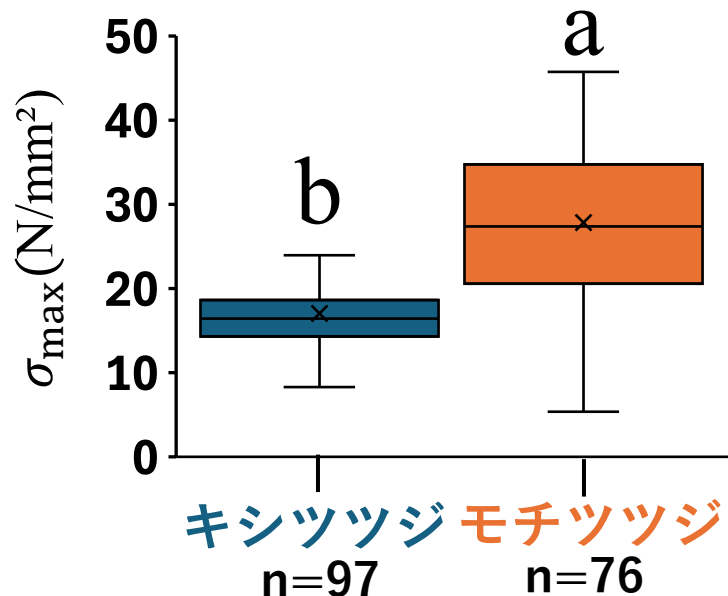
結果～力学的解析～

($p < 0.05$)

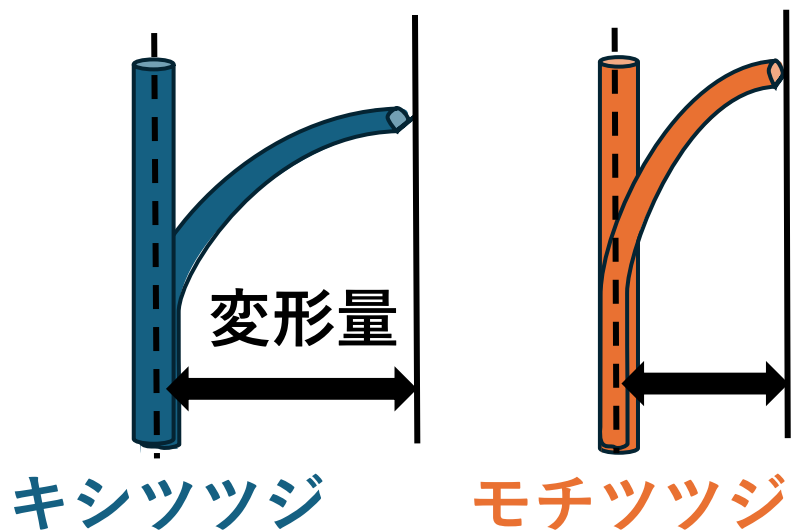
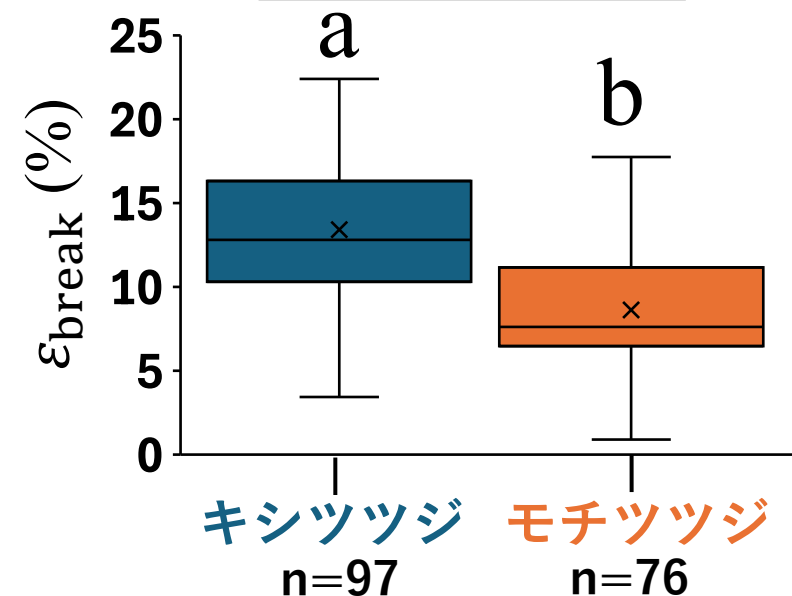
曲げ弾性率



曲げ強度



破断ひずみ

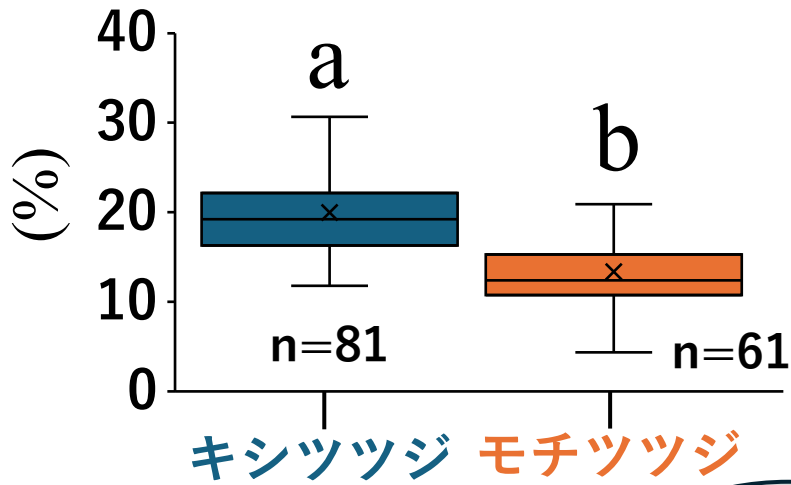


- 小さな力で変形
- 受けられる力は小さい
- 外力に対して柔軟な変形

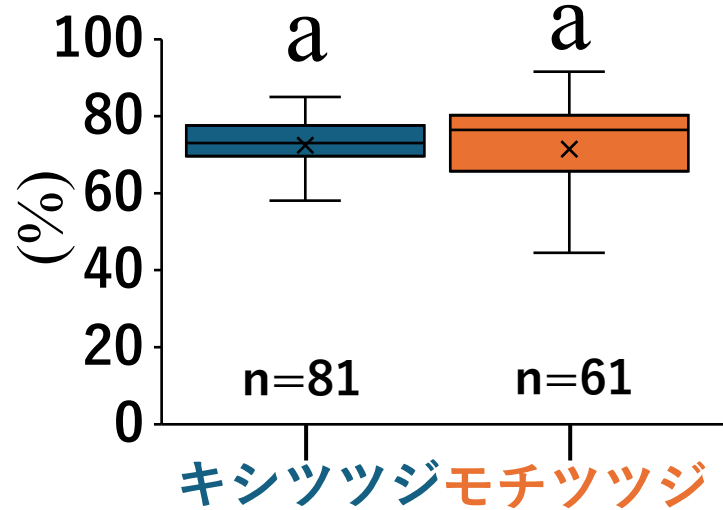
結果 ~解剖学的解析結果~

($p < 0.05$)

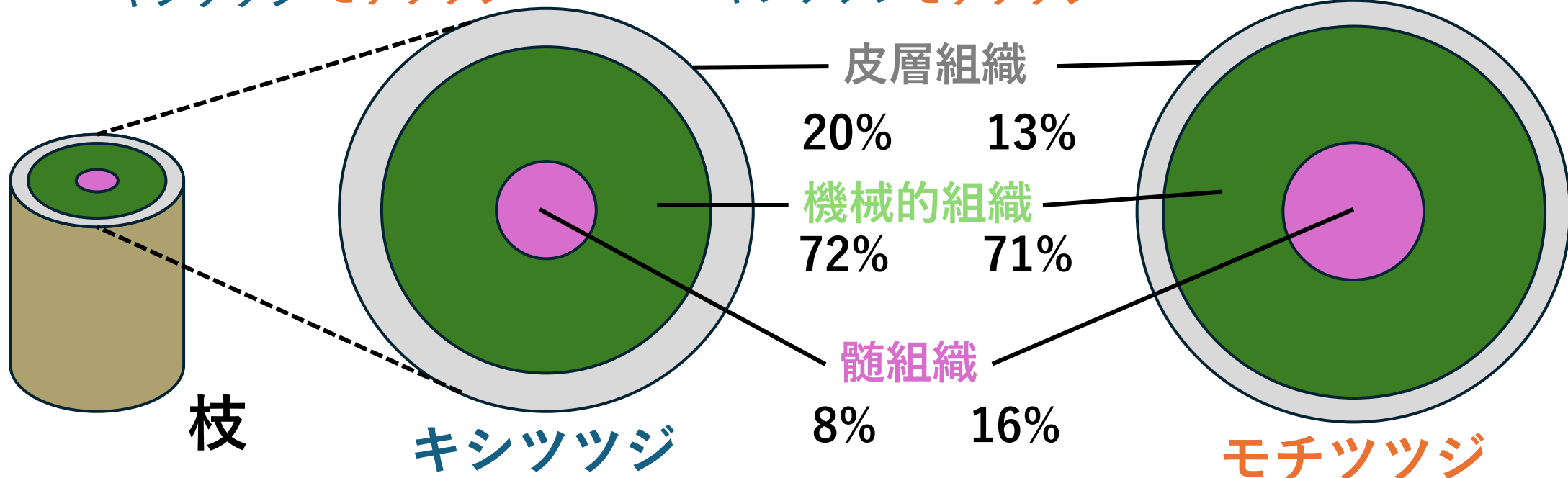
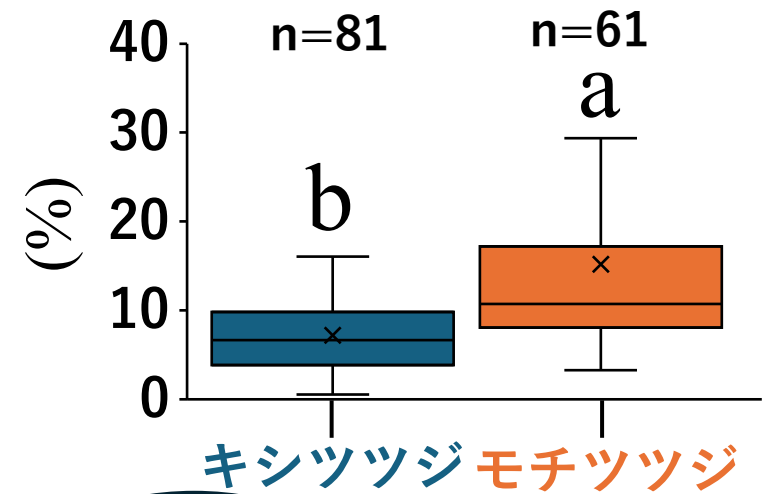
皮層面積率



機械的組織面積率

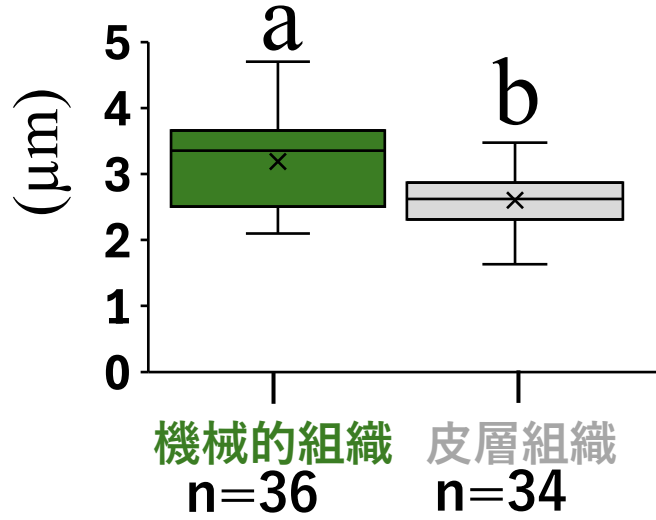


髓組織面積率

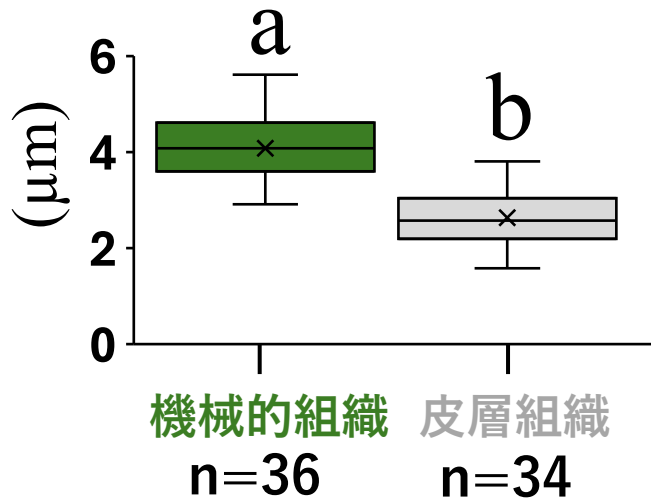


結果～解剖学的解析～

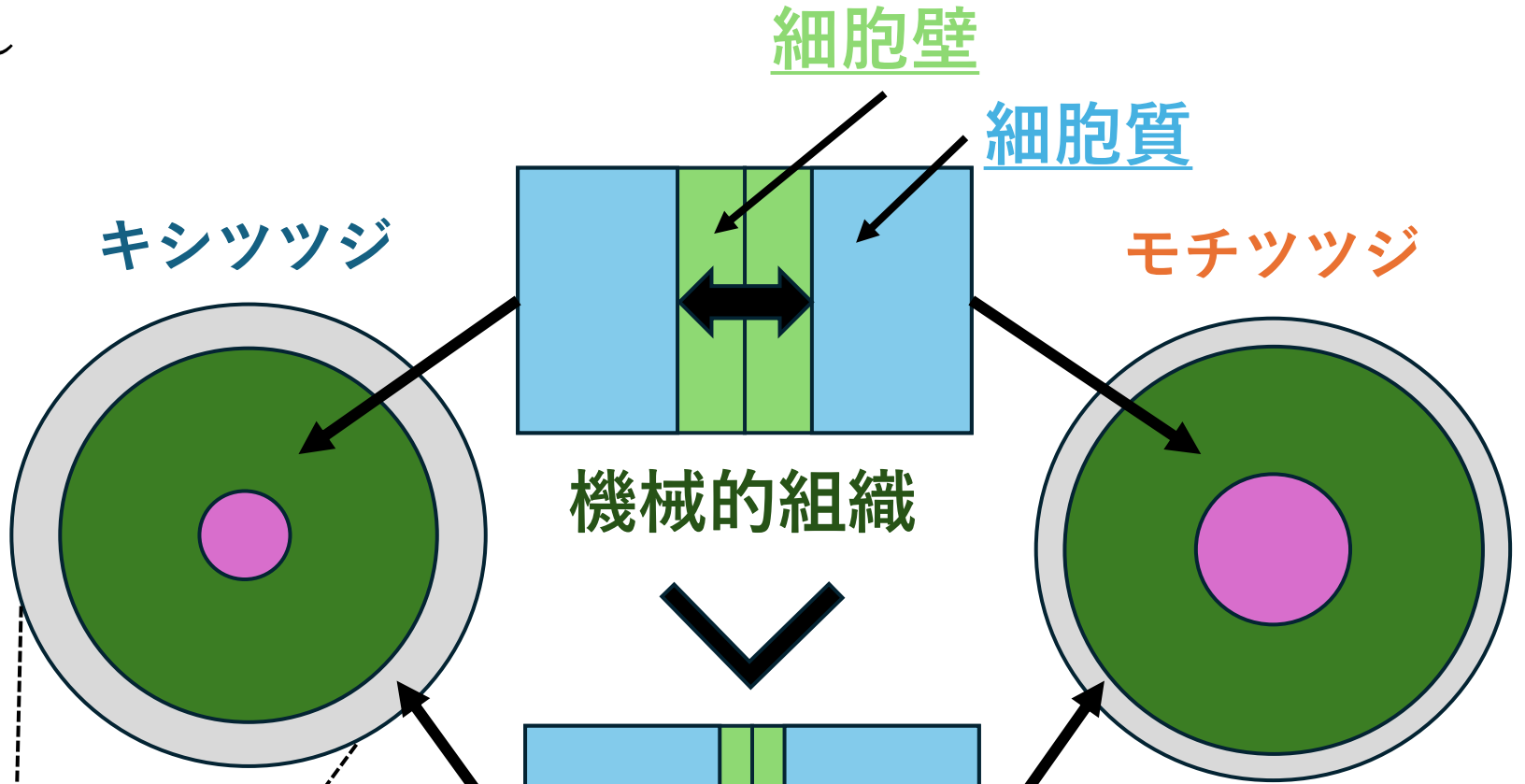
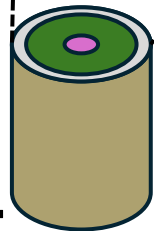
二細胞壁間距離(キシツツジ)



二細胞壁間距離(モチツツジ)



枝

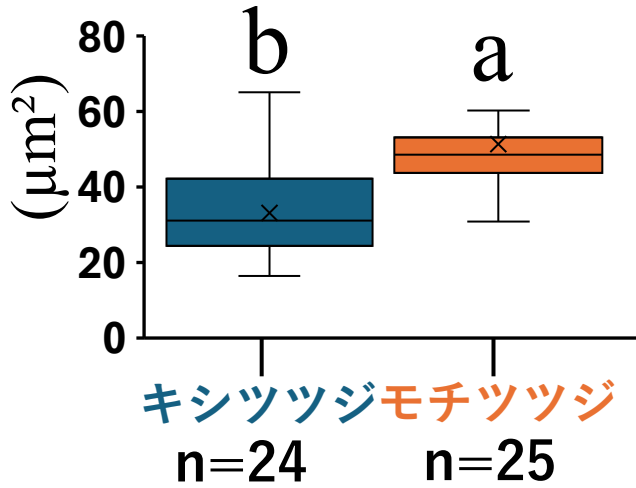


両種とも機械的組織の細胞壁が厚い

結果～解剖学的解析(機械的組織)～

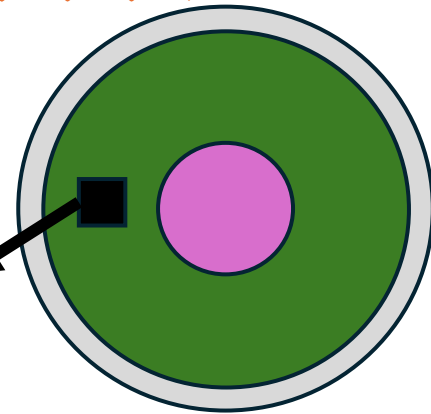
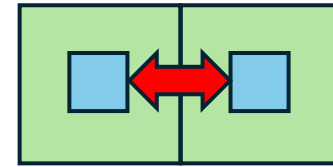
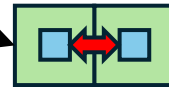
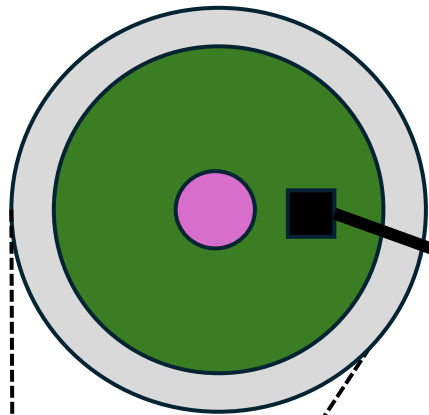
■ 細胞質
■ 細胞壁

細胞質面積



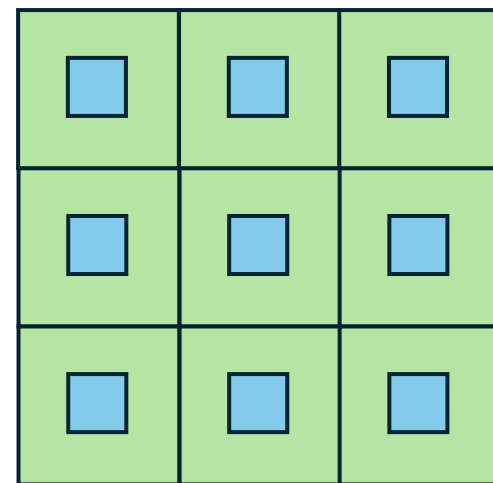
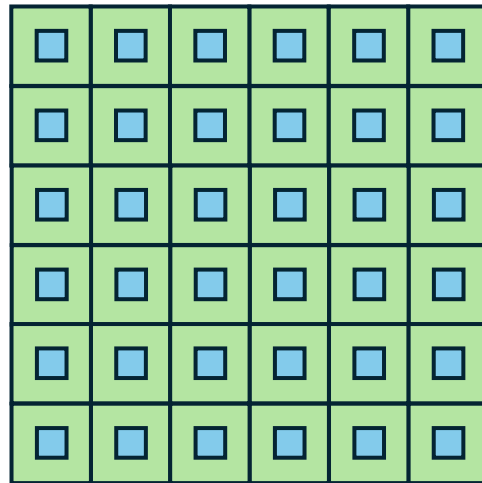
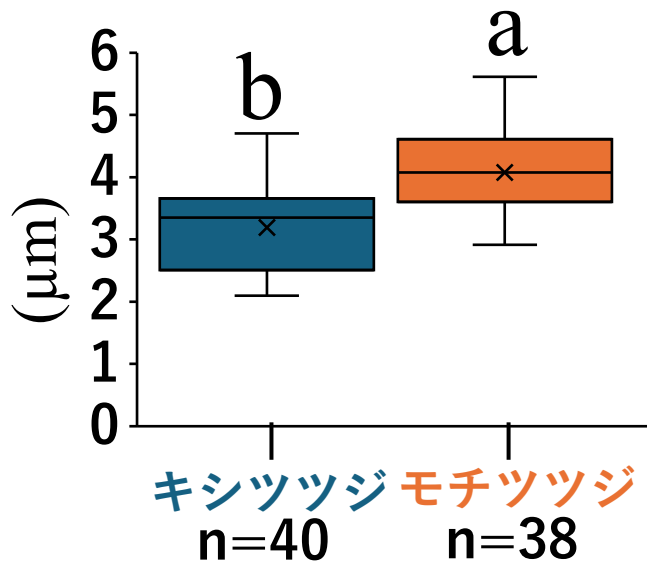
キシツツジ

モチツツジ



細胞サイズが大きい

二細胞壁間距離(機械的組織)



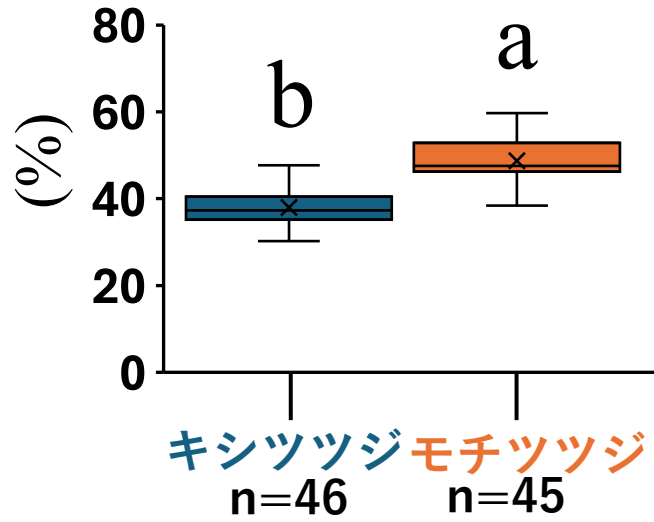
キシツツジ

モチツツジ

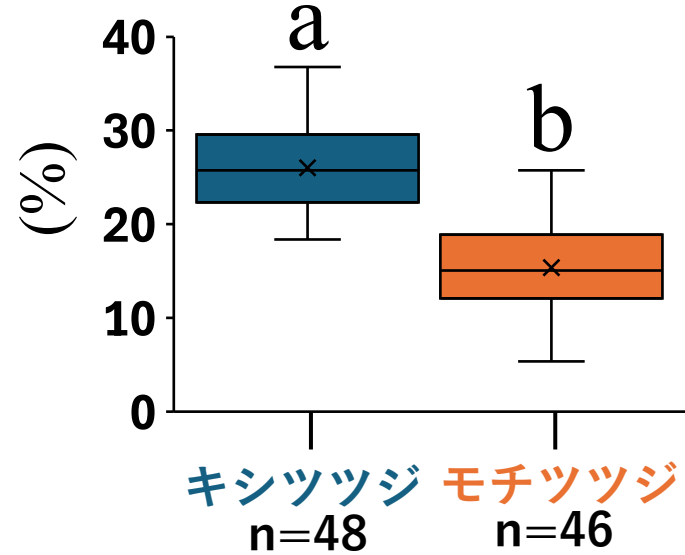
結果～解剖学的解析(機械的組織)～

($p < 0.05$)

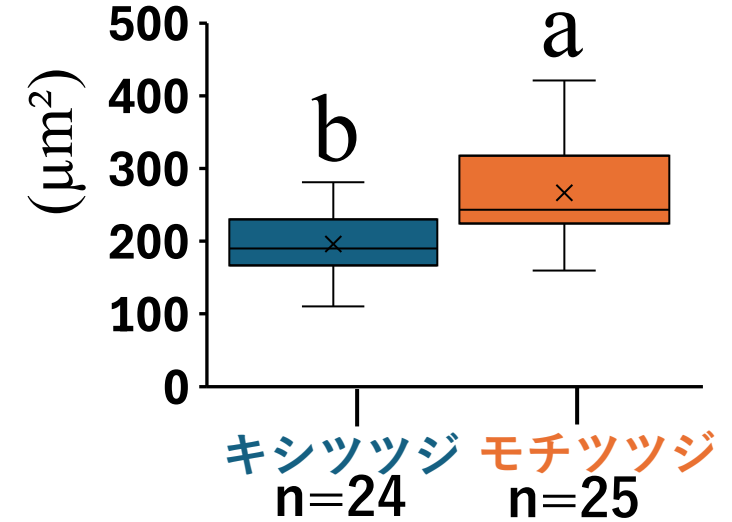
単位面積あたりの細胞壁面積率



単位面積あたりの道管細胞質面積率



道管細胞質面積

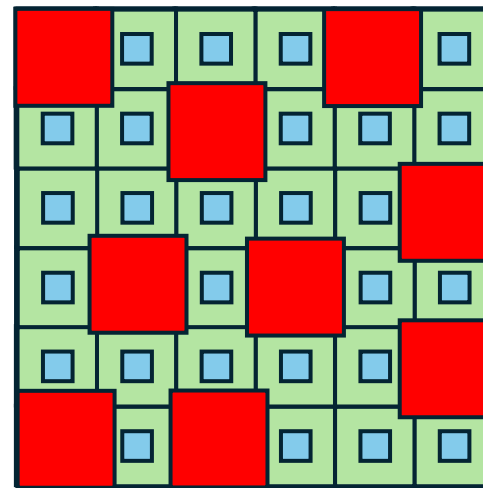


・キシツツジ

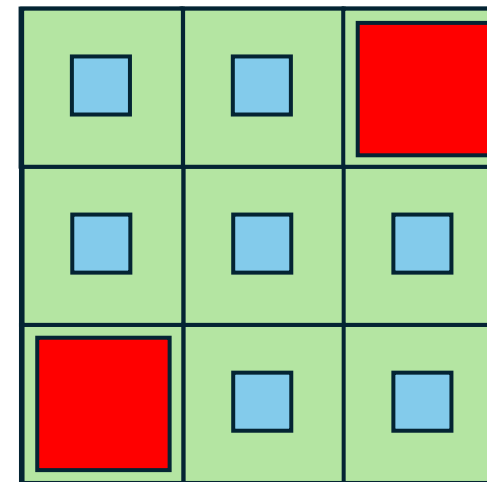
道管細胞を増加



細胞壁量が減少



キシツツジ

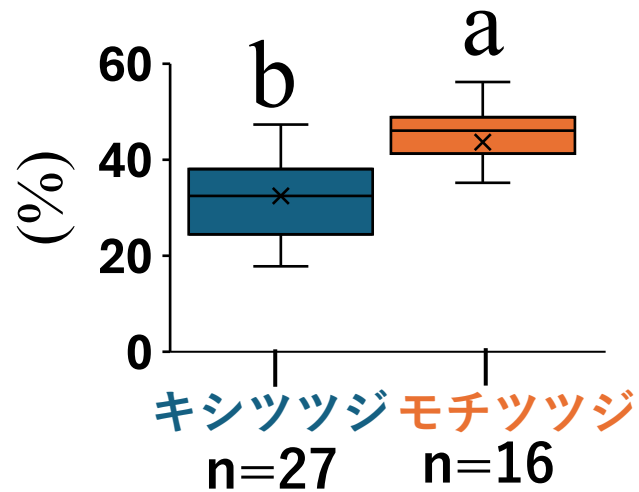


モチツツジ

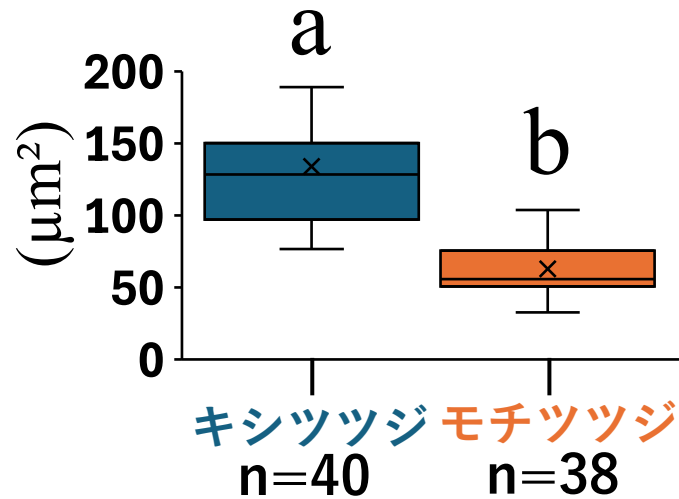
- 細胞質
- 細胞壁
- 道管細胞

結果～解剖学的解析結果(皮層組織)～

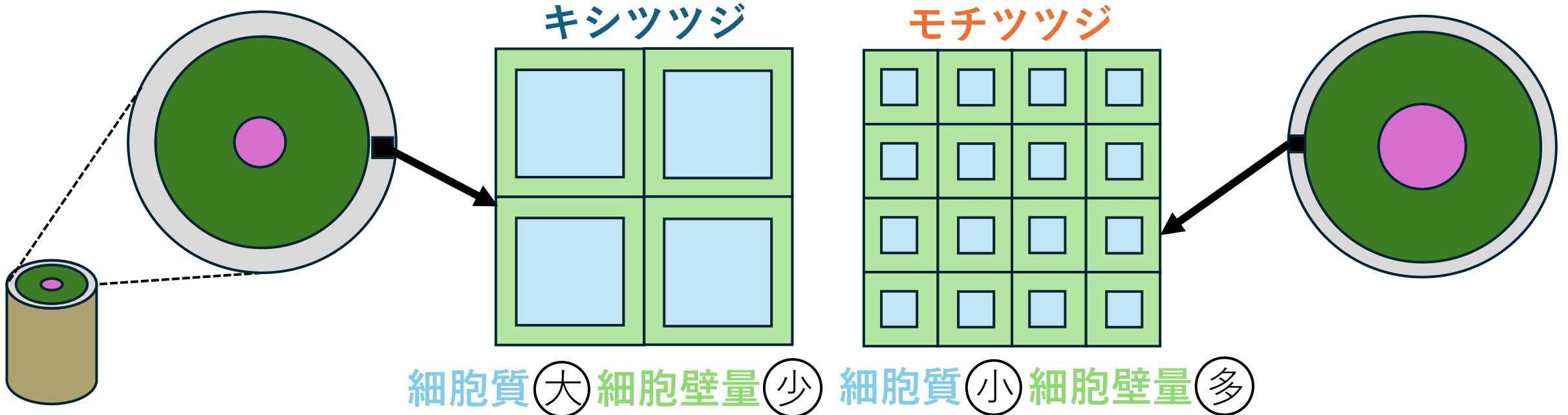
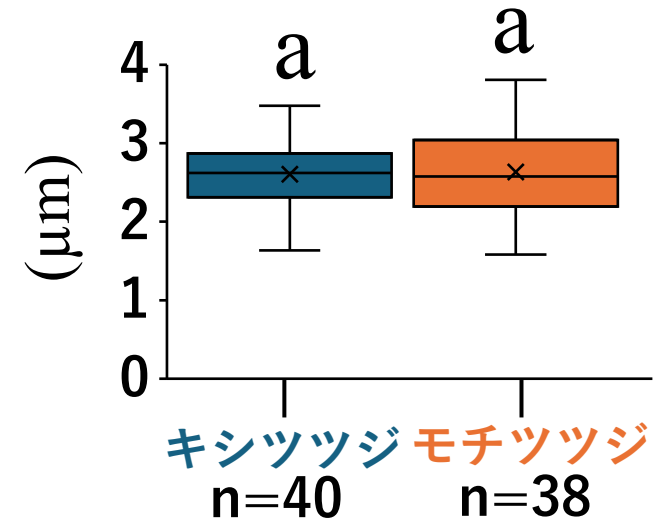
単位面積あたりの細胞壁面積率



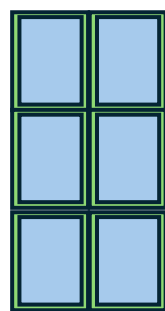
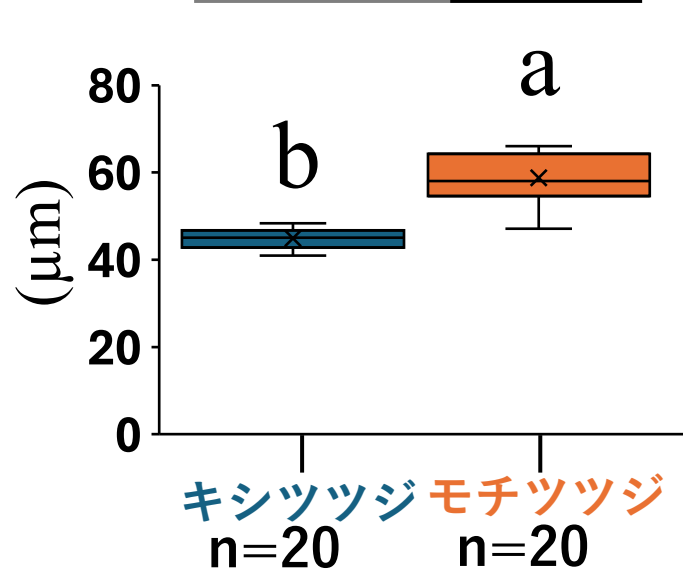
細胞質面積



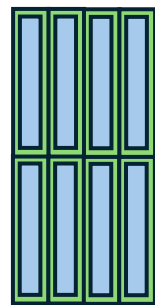
二細胞壁間距離



皮層組織細胞長

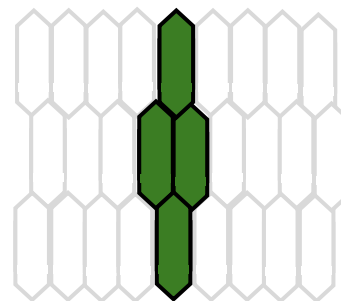
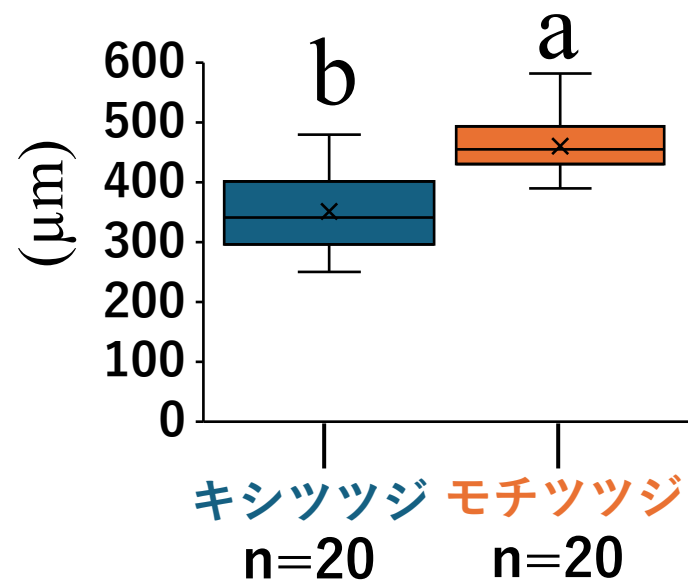


キシツツジ

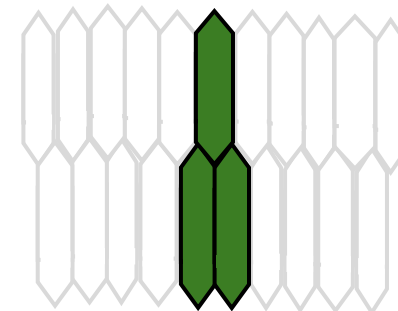


モチツツジ

機械的組織細胞長



キシツツジ



モチツツジ

考察 ～木本植物の水流ストレス環境における適応～

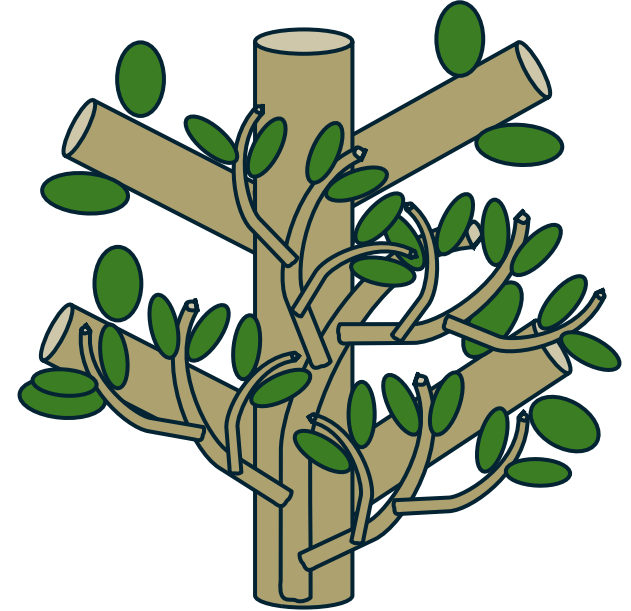
- ・ 増水による水流ストレス環境（溪流沿い）



葉身における適応

水流

支持器官



仮説：溪流沿いの木は強固に支持されている？

(耐性)

柔軟性を獲得

仮説は支持されなかった

考察 ～力学的特性の獲得～

仮説：支持されなかった



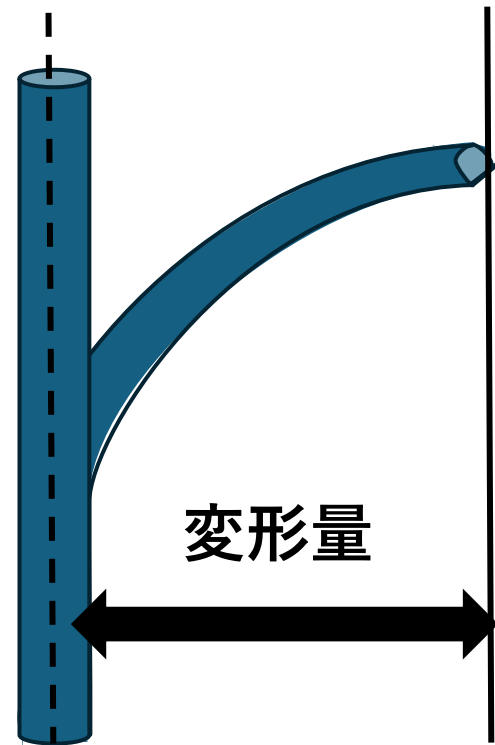
曲げ弾性率・曲げ強度
(変形しやすさ) (耐荷重性)

キシ < モチ

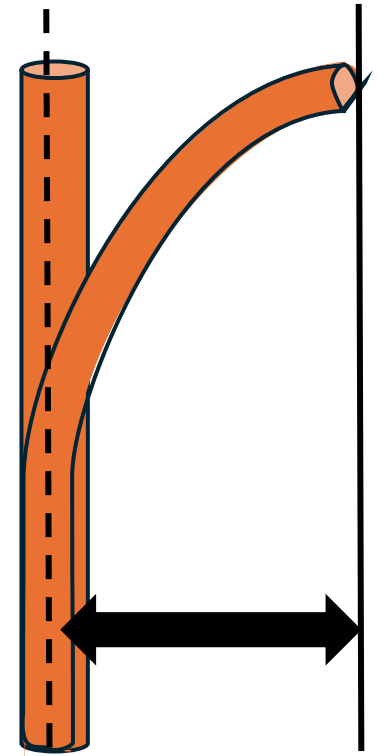
破断ひずみ
(変形割合)

キシ > モチ

キシツツジ



モチツツジ



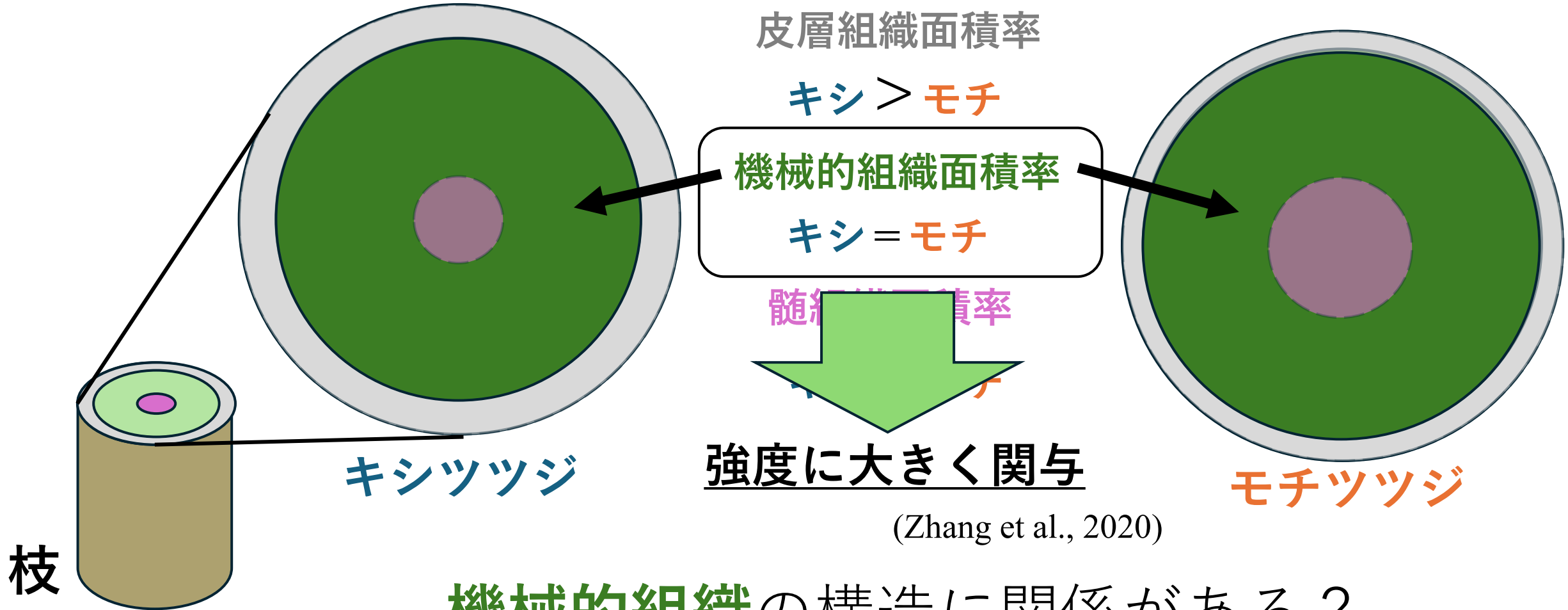
キシツツジは変形しやすい柔軟な枝を獲得

➡ **なぜこのような結果が得られた？**

考察 ～力学的特性の獲得～

曲げ弾性率・曲げ強度 **キシ < モチ**

破断ひずみ **キシ > モチ**



機械的組織の構造に関する関係がある？

考察 ～機械的組織の構造～

曲げ弾性率・曲げ強度

キシ < モチ

破断ひずみ

キシ > モチ

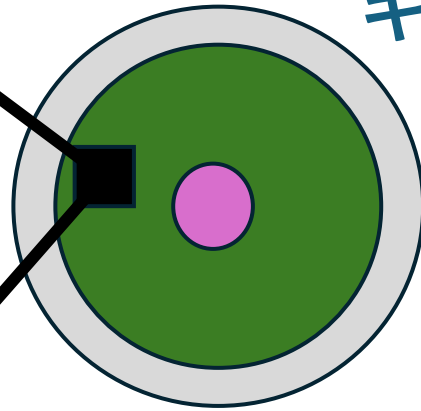
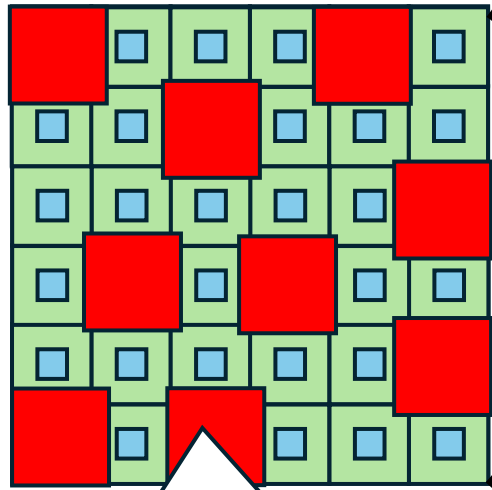
■ 細胞質

■ 細胞壁

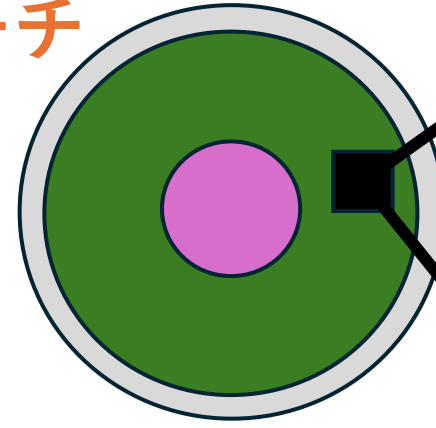
■ 道管細胞

機械的組織面積割合

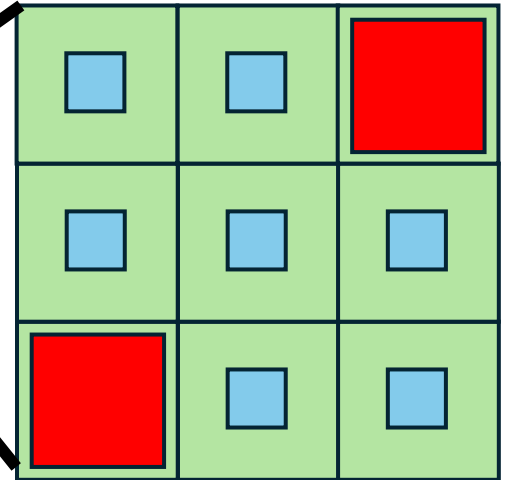
キシ = モチ



キシツツジ



モチツツジ



道管細胞

細胞壁の薄い細胞



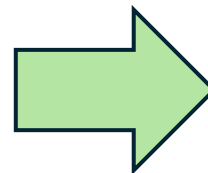
壁が内側にたわみ、形状が崩れる

(Jacobsen et al., 2005)

道管細胞数



細胞壁量



変形しやすさに寄与

なぜ道管を増加？

考察 ～なぜキシツツジは道管を増やす？～

道管

水分輸送

(Bonetti et al., 2020)

大量の水利用可能

キシツツジ

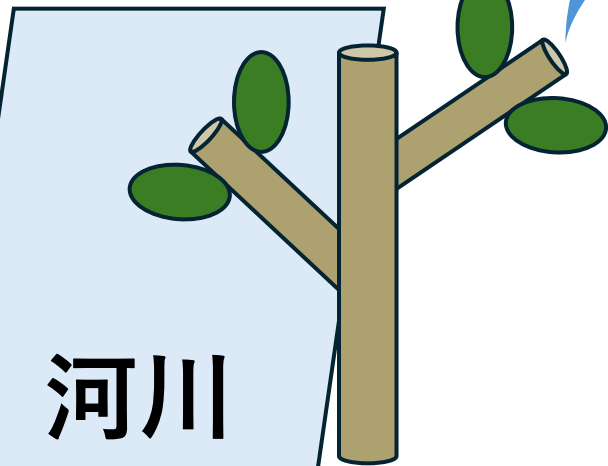
枝：道管数(多) → 光合成効率(高)

葉：気孔数(多) (Ueda et al., 2012)
(Brodrigg et al., 2006; Tanaka et al., 2013)

水利用特性変化 → 成長促進

→ 機械的組織の支持性を犠牲

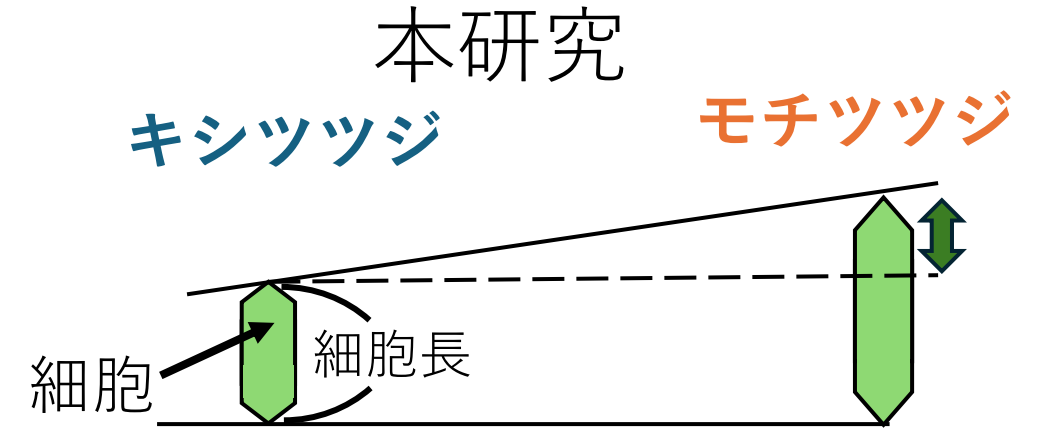
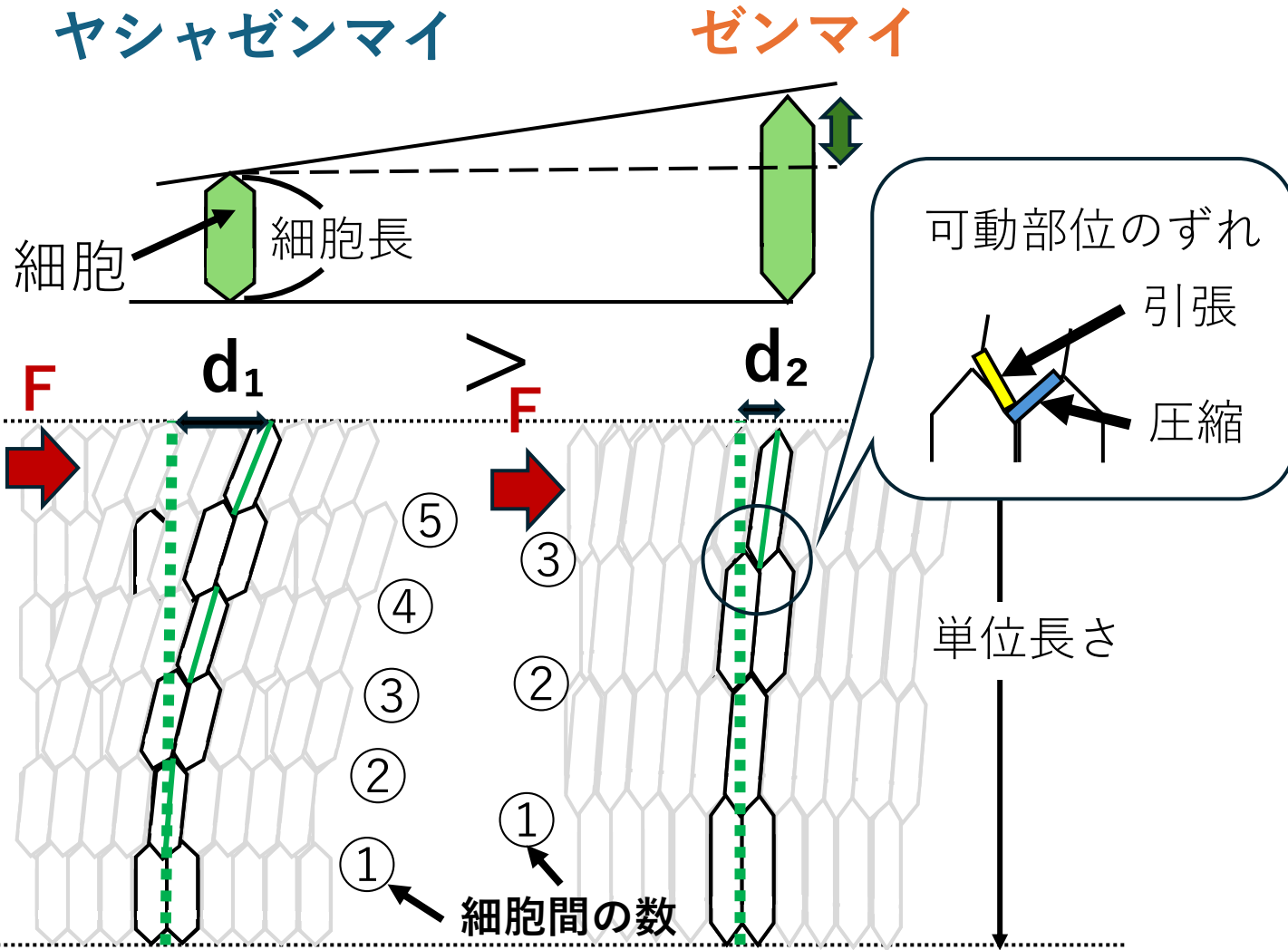
柔軟性は？



キシツツジ

考察 ～外力に対する変形仮説(機械的組織)～

細胞間のずれ仮説 (Shiba and Fukuda, 2025)



同様のメカニズムを適応



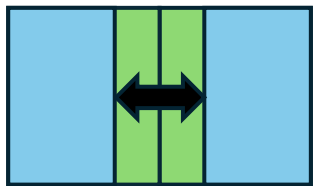
細胞長の短小化が柔軟性獲得を示唆

細胞長の短小化が柔軟性獲得を示唆

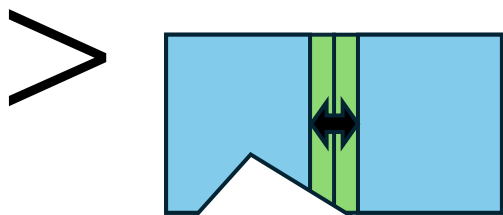
考察 ～皮層組織の変形仮説モデル～

二細胞壁間距離（細胞壁の厚さ）

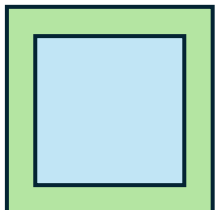
機械的組織



皮層組織

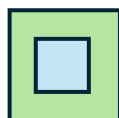


キシツツジ



大きな細胞質

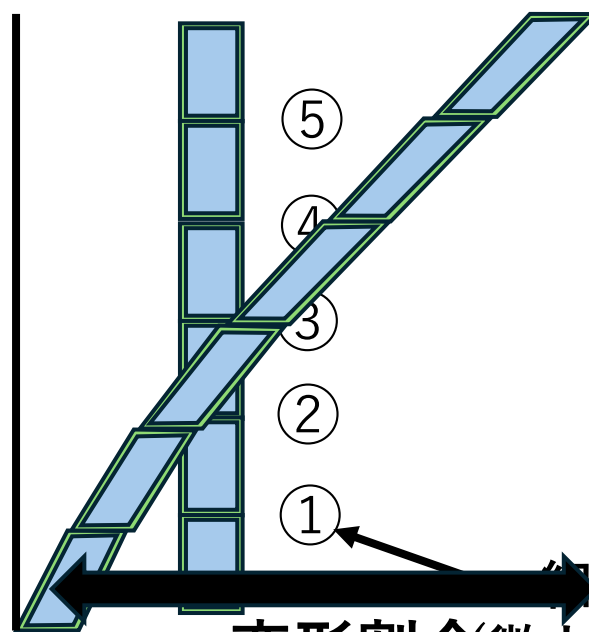
モチツツジ



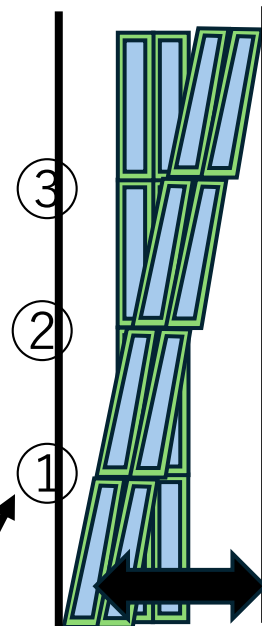
→ 大きな変形を許容

(Niklas, 1992; Gibson and Ashby, 1997)

キシツツジ



モチツツジ



- 短い縦細胞
 - 大きな細胞質
- **大きな変形**

キシツツジの皮層組織は機械的組織の柔軟な変形を支持

考察 ～組織面積率の解析結果～

キシツツジ

モチツツジ

皮層組織面積率

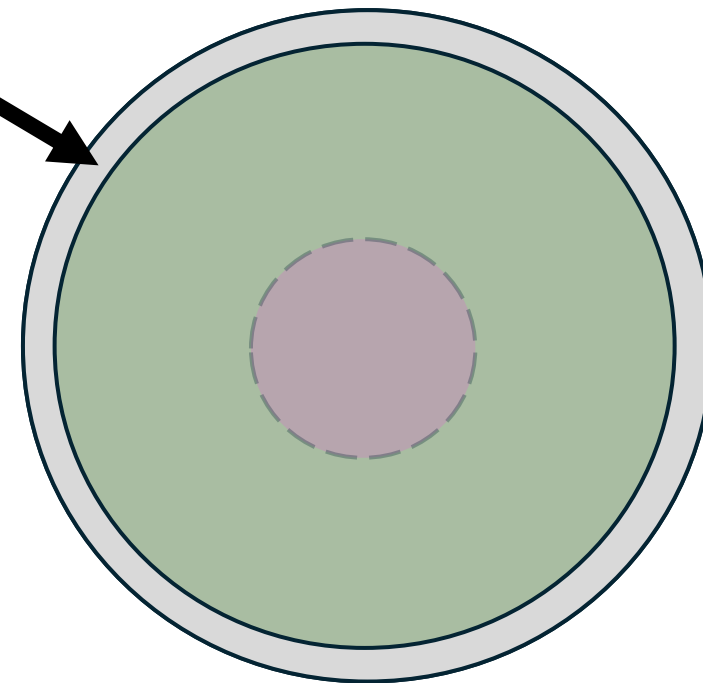
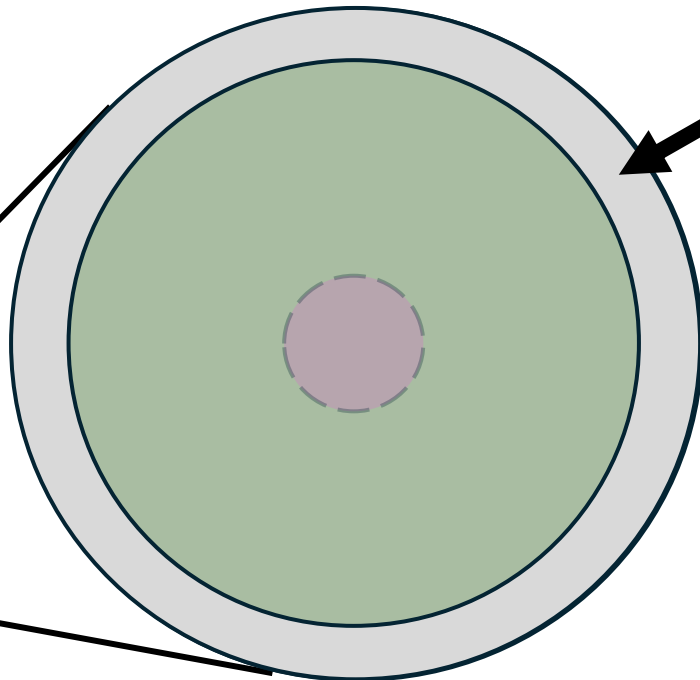
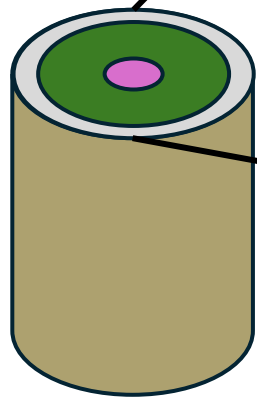
キシ > モチ

機械的組織面積率

キシ = モチ

髓組織面積率

キシ < モチ

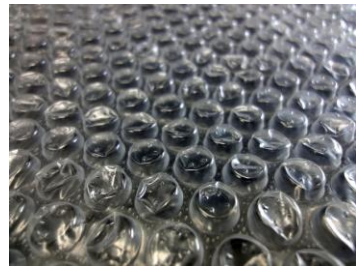


なぜ厚くしている？

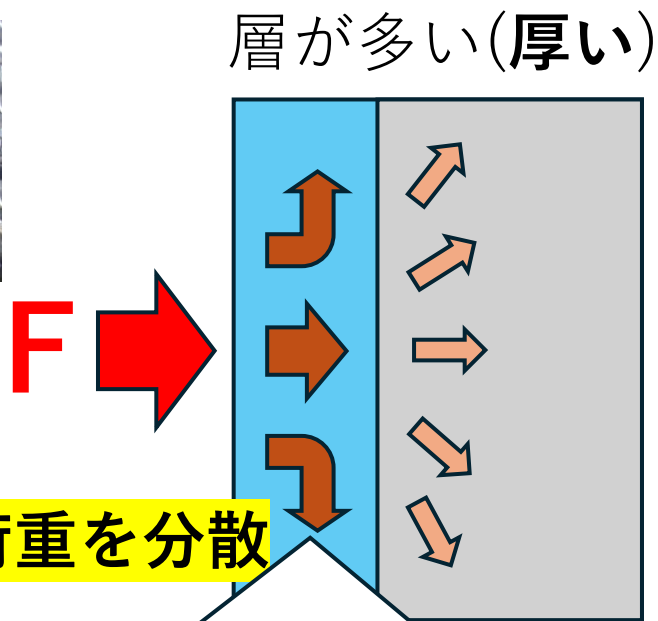
枝

考察 ~なぜキシツツジは皮層組織を厚くしている?~

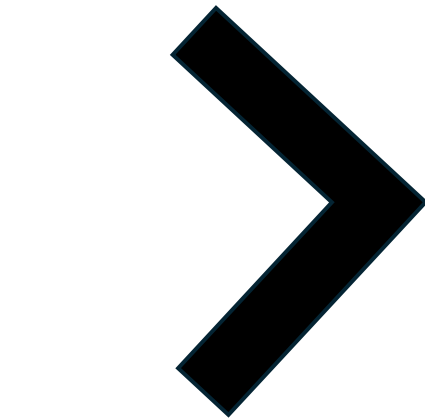
工学分野(Malasri, 2013a)



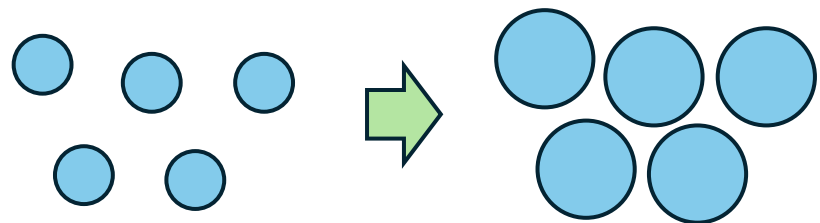
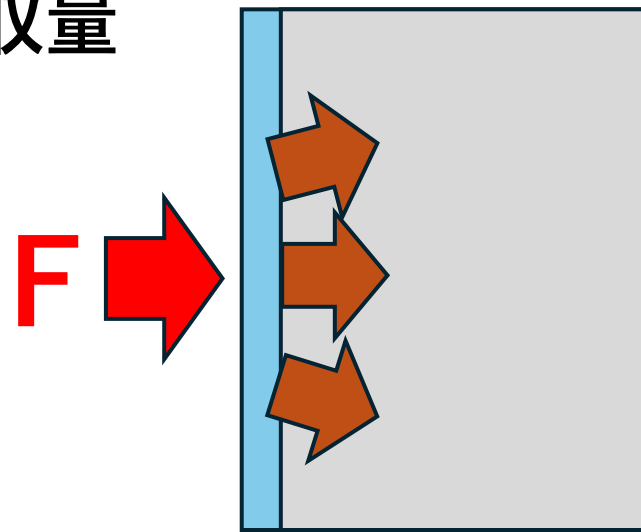
気泡緩衝材



エネルギー吸収量



層が少ない(薄い)



泡サイズが大きい

エネルギー吸収量が多い

(Malasri, 2013b)

キシツツジの皮層組織：厚く、大きな細胞質

外力を分散

外力による植物の内側からの破損を抑制

考察 ～木本植物の水流ストレス環境適応～

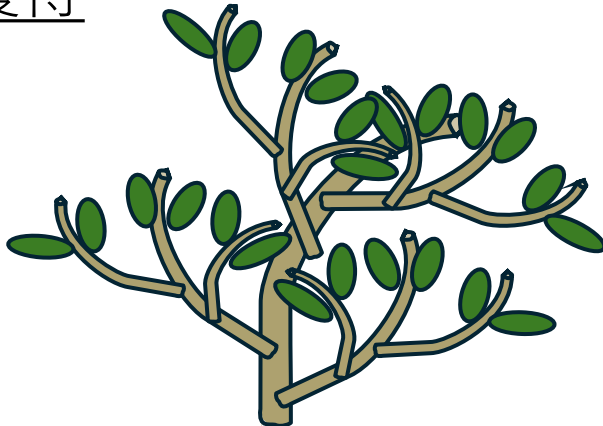
葉

- ・ 狭葉化
- ・ 水利用特性の獲得

+

支持器官(枝)

- ・ 低い樹高
- ・ 柔軟性の獲得
- ・ 水利用特性の獲得



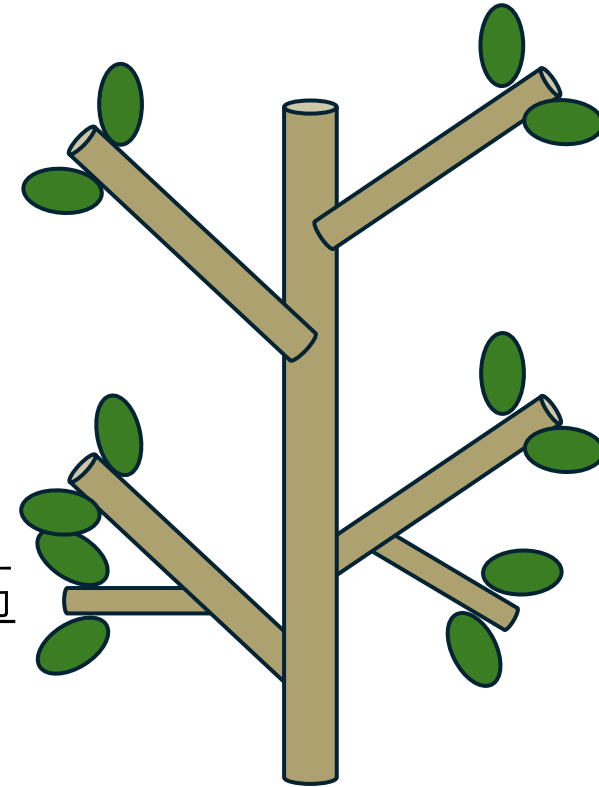
キシツツジ



水流ストレス環境に適応

支持器官(枝)

- ・ 強度を維持した 高い樹高



モチツツジ

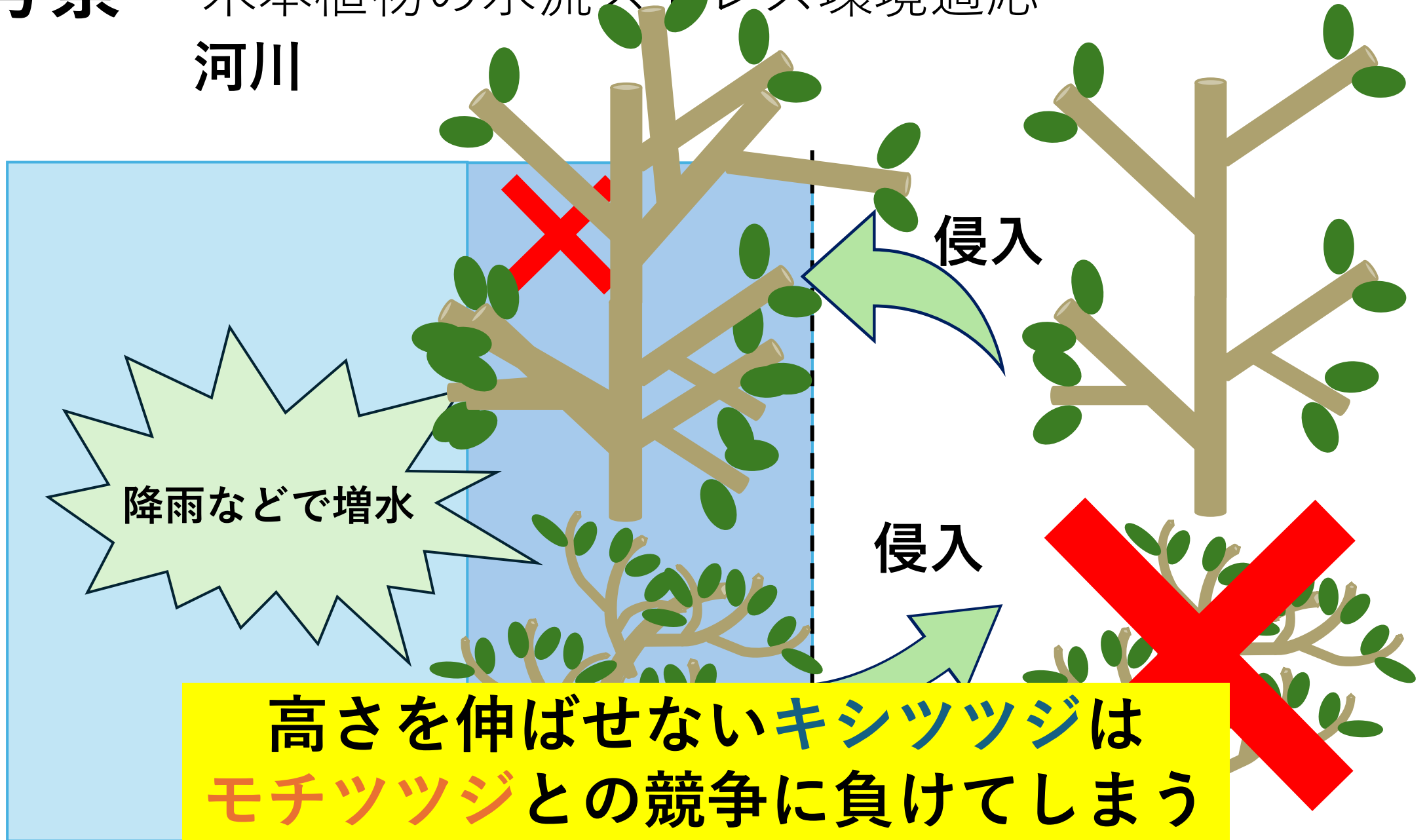


高さで 資源獲得能力 を確保

実際の溪流沿い環境で考えると？

考察 ～木本植物の水流ストレス環境適応～

河川



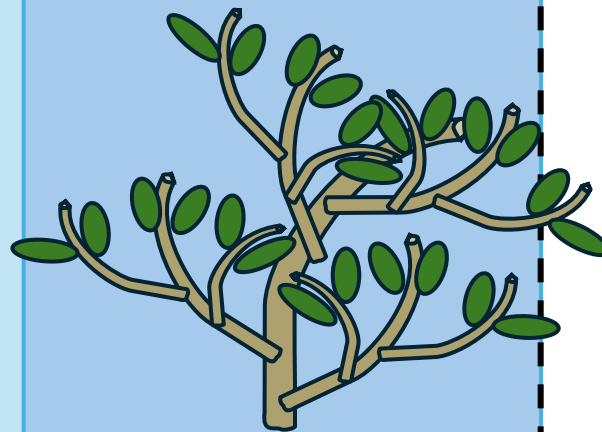
考察 ～木本植物の水流ストレス環境適応～

河川

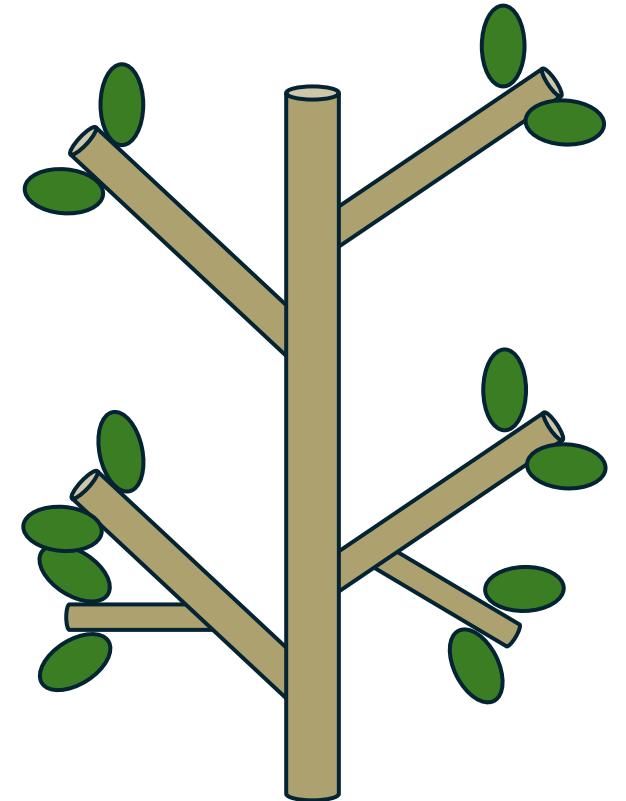
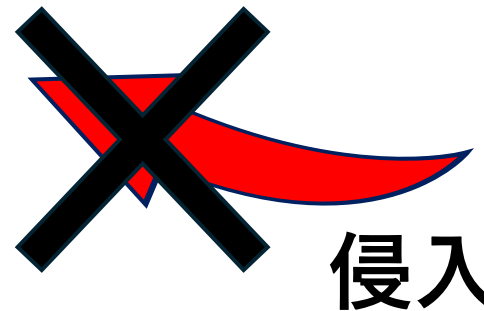
柔軟性獲得



特殊環境に適応



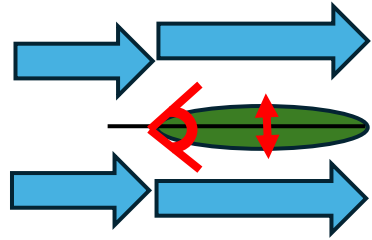
キシツツジ



モチツツジ

まとめ ～溪流沿い植物の水流ストレス環境適応～

草本植物

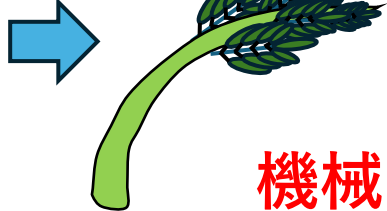


狭葉化

(Imaichi and Kato, 1992)

+

水流



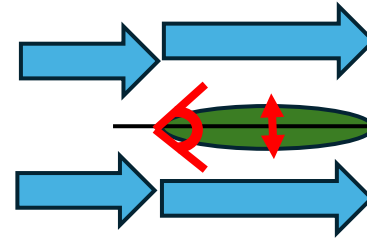
支持器官の柔軟化



機械的組織の細胞長の短小化

(Shiba and Fukuda, 2024; 2025)

木本植物

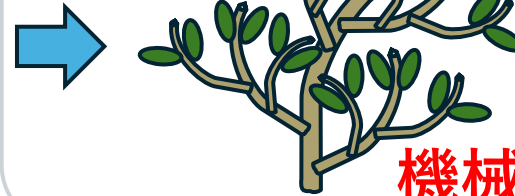


狭葉化

(Ueda et al., 2012)

+

水流



支持器官の柔軟化



機械的組織の細胞長の短小化

類似した形質を獲得することでストレスを低減させ適応

本研究の成果

JSPS25
Kumamoto
PE07

溪流沿い植物キシツツジの枝における 力学的・解剖学的分類形質



○柴政幸, 黒滝 魁斗, 福田達哉 (都市大・院・自然) e-mail: msykshiba48@gmail.com

1. 序論

目的
木本性溪流沿い植物キシツツジの支持器官は水流ストレスに対する適応形質を有するのか？

背景
☆ 溪流沿い環境は水流による機械的ストレスを受ける
☆ 草本性溪流沿い植物ヤシャゼンマイの葉柄は柔軟性を有して、水流ストレスを低減 (Shiba et al., 2024, 2025)
☆ 木本植物の支持器官も同様の変化なのか？

2. 研究対象と方法

研究対象
キシツツジ (*Rhododendron ripense*)
☆ ツツジ科ツツジ属；低木；山間部の溪流沿いに生育
☆ 近縁陸上種 **モチツツジ** (*R. macrosepalum*) との **交雑** や **葉形態比較** に関する研究が行われている (Ueda et al., 2012; Yokoyama et al., 2013)

計測・解析方法
2025年10月頃、採集
キシツツジ 枝 109本, 徳島県三好市山城町 吉野川沿い
モチツツジ 枝 80本, 静岡県浜松市天竜区 観音山林道沿い



キシツツジの花, 雄しべ10本



モチツツジの花, 雄しべ5本

1. 枝の力学的特性①の比較

曲げ弾性率 E
→ 材料の変形しにくさ
 $y = ax + b$
 $E = a \times 100$

応 σ 曲げ強度

まとめ

結論
キシツツジの枝は折れにくく、曲がりやすい構造を有して柔軟性を獲得していた

根拠
↑ なぜなら
☆ キシツツジの枝は、力が加わった際によく曲がりやすい①
☆ 外層の皮層組織を肥厚させ、力が枝の内部に分散しやすく、折れにくくなっている②, 考察1
☆ 薄い細胞壁と短い細胞長により、“細胞自体の変形しやすさ”と“細胞間のずれ”の累積が大きな変位につながる③, 考察2
→ ヤシャゼンマイの葉柄と同様の変化

3. 結果

1. 枝の力学的特性①の比較

応力 (MPa) vs ひずみ (%)

曲げ弾性率 (MPa) vs キシモチ

破断ひずみ (%) vs キシモチ

キシツツジは弱い力で変形して、よく曲がる
モチツツジは強い力で変形するが、すぐ折れる

2. 枝の組織構造②の比較

組織	キシツツジ (%)	モチツツジ (%)
皮層組織	24%	14%
形成層	68%	64%
髓組織	7%	22%

キシツツジモチツツジ 枝の組織構造の模式図

3. 維管束形成層の細胞構造③の比較

日本植物分類学会にて報告

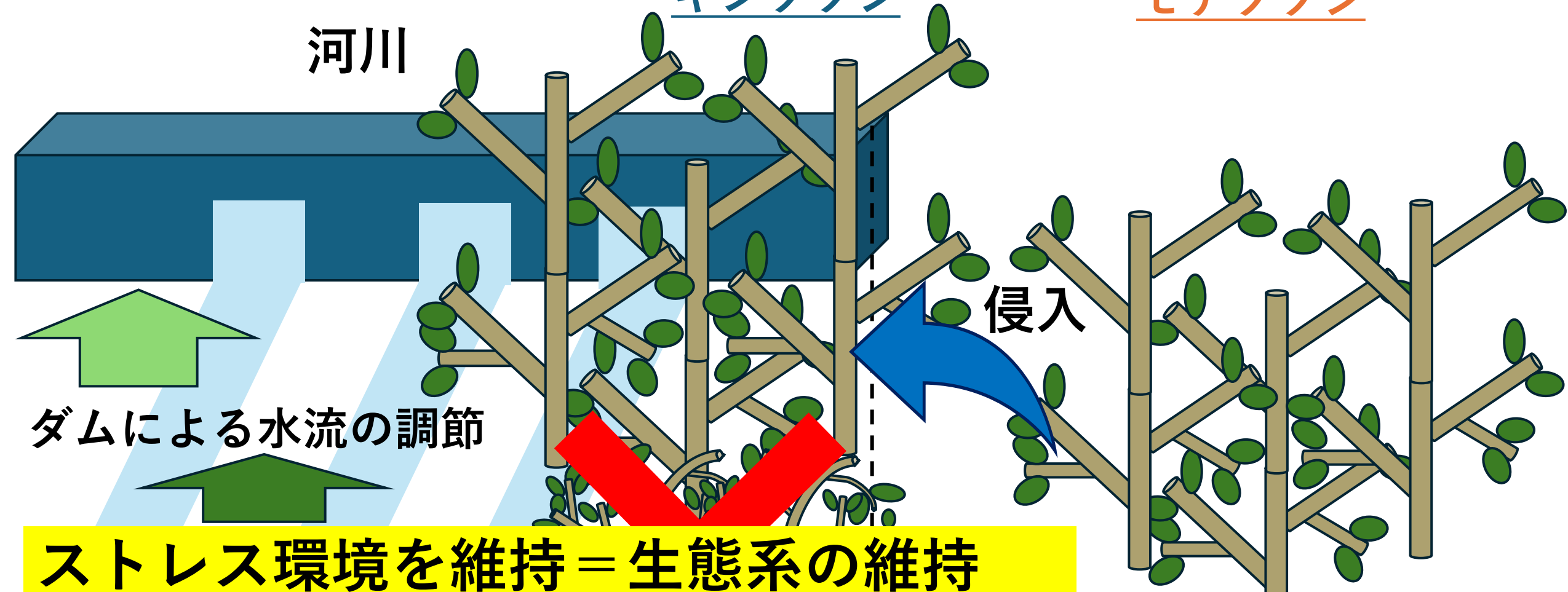
2026年3月5日ー3月8日 於：熊本大学

考察 ～木本植物の水流ストレス環境適応～

キシツツジ

モチツツジ

河川



ダムによる水流の調節

侵入

ストレス環境を維持＝生態系の維持

高さを伸ばせないキシツツジは
モチツツジとの競争に負けてしまう



ご清聴ありがとうございました



引用文献

- Bonetti S, Breitenstein D, Fatichi S, Domec JC, Or D (2020) Persistent decay of fresh xylem hydraulic conductivity varies with pressure gradient and marks plant responses to injury. *Plant, Cell & Environment* 44: 371-386.
- Brodribb TJ, Holbrook NM, Zwieniecki MA, Palma B (2004) Leaf hydraulic capacity in ferns, conifers and angiosperms: impacts on photosynthetic maxima. *New Phytologist* 165: 839–846.
- Franceschini T, Martin-Ducup O, Schneider R (2016) Allometric exponents as a tool to study the influence of climate on the trade-off between primary and secondary growth in major north eastern American tree species. *Annals of Botany* 117: 551–563.
- Gärtner H, Schweingruber FH (2013) Preparation Techniques for Plant Stem Analysis. *Verlag Dr. Kessel*, Remagen, Germany.
- Gibson LJ, Ashby MF (1997) Cellular Solids: Structure and Properties. *Cambridge University Press*, Cambridge, United Kingdom.
- 古野 毅, 澤辺 攻 (2011) 木材科学講座 2 組織と材質, 海青社, 大津.
- Imaichi R, Kato M (1992) Comparative leaf development of *Osmunda lancea* and *O. japonica* (Osmundaceae): Heterochronic origin of rheophytic stenophylly. *Journal of Plant Research* 105: 199–213.
- Jacobsen AL, Ewers FW, Pratt RB, Paddock III WA, Davis SD (2005) Do Xylem Fibers Affect Vessel Cavitation Resistance?. *Plant Physiology* 139: 546–556.
- Jensen JK, Wilkerson CG (2017) *Brachy podium* as an experimental system for the study of stem parenchyma biology in grasses. *PLoS One* 12(3):e0173095.
- Kasuga J, Arakawa K, Fujikawa S (2007) High accumulation of soluble sugars in deep supercooling Japanese white birch xylem parenchyma cells. *New phytologist* Volume 174(3): 569-579.
- Kato M (2007) Distribution of Osmundaceae. *Bull. Natl. Mus. Nat. Sci. Ser. B Bot.* 33, 81–90.

引用文献

- Meng TT, Wang H(2015) Responses of leaf traits to climatic gradients: adaptive variation versus compositional shifts. *Biogeosciences* 12 : 5339–5352.
- Malasri S, Siow W, Harvey M, Aung PT, Jordan R , Shiue P, Brown R(2013) Estimating Tote Drop Height & Impact Acceleration from a Transportation Recorder. *IoPP Journal of Packaging* : 1-10.
- Malasri S(2013) Plastic Tote Distribution. *International Journal of Advanced Packaging Technology* 1(1): 40-52.
- Niklas KJ (1992) Plant Biomechanics. *University of Chicago Press*, Chicago and London.
- Nobel P(2006) Parenchyma–Chlorenchyma Water Movement during Drought for the Hemiepiphytic Cactus *Hylocereus undatus*. *Annals of Botany* 97: 469–474.
- Ohga K, Muroi M, Hayakawa H, Ito K, Yokoyama J, Tebayashi S, Arakawa R, Fukuda T (2012) Comparative morphology and anatomy of non-rheophytic and rheophytic types of *Adenophora triphylla* var. *japonica* (Campanulaceae). *American Journal of Plant Sciences* 3: 805–809.
- Shiba M, Tate T, Fukuda T (2021) Rheophytic Adaptation of *Eurya japonica* Thunb. (Ternstroemiaceae) . *International Journal of Biology* 13(2):65.
- Setoguchi H, Kajimaru G(2004) Leaf Morphology of the Rheophyte, *Rhododendron* f. *otakumi* (Ericaceae). *Acta Phytotax, Geobot* 55 (1):45-54.
- Shiba M, Mizuno T, Fukuda T(2023) Effect of strong wind on laminae and petioles of *Farfugium japonicum* (L.) Kitam. var. *japonicum* (Asteraceae). *Plant Sci.* 14:1182266.
- Shiba M, Fukuda T(2024) Rheophytic *Osmunda lancea* (Osmundaceae) exhibits large flexibility in the petiole *Sci Rep* 14, 2866.
- Shiba M, Fukuda T(2025) Mechanical flexibility of fertile frond stipes in the rheophytic fern *Osmunda lancea*. *Sci Rep* 15: 29664.

引用文献

- Sperry JS, Sullivan JEM(1992)Xylem Embolism in Response to Freeze-Thaw Cycles and Water Stress in Ring-Porous, Diffuse-Porous, and Conifer Species. *Plant Physiol* 100: 605-613.
- Su Q, Chen L, Dai C, Fei B, Chen X, Luo X, Fang C, Ma X, Zhang X, Liu H (2023) Structure and mechanisms of foam-like bamboo parenchyma tissue. *Journal of Materials Research and Technology* 27: 617-629.
- Tanaka Y, Sugano SS, Shimada T, Hara-Nishimura I(2012)Enhancement of leaf photosynthetic capacity through increased stomatal density in Arabidopsis. *NewPhytologist* 198: 757–764.
- Ueda R, Minamiya Y, Hirata A, Hayakawa H, Muramatsu Y, Saito M, Fukuda T (2012)Morphological and anatomical analyses of rheophytic *Rhododendron ripense* Makino(Ericaceae) *Plant Species Biology*, 233-240.
- Voelker SL, Lachenbruch B, Meinzer FC, Strauss SH(2011)Reduced wood stiffness and strength, and altered stem form, in young antisense 4CL transgenic poplars with reduced lignin contents. *New Phytologist* 189: 1096-1109.
- Vorbeck SW, Speck O, Speck T, Dondl PW,(2021)Influence of structural reinforcements on the twist-to-bend ratio of plant axes: a case study on *Carex pendula*. *Scientific Reports* 11: 21232.
- Wu T, (2016) Morphological Response of Eight *Quercus* Species to Simulated Wind Load. *PLoS One* 11(9):e0163613.
- Yatabe Y, Nishida H, Murakami N (1999)Phylogeny of Osmundaceae inferred from *rbcL* nucleotide sequences and comparison to the fossil evidences. *J. Plant Res.* 112, 397–404.
- Yokoyama N, Hayakawa H, Matsuyama K, Muroi M, Ohga K, Ito K, Fukuda T (2012)Morphological and Molecular Analyses of Rheophytic *Rhododendron ripense* and Its Allied Dryland Species *R. macrosepalum* (Ericaceae). *Environmental Control in Biology* 50 (3) : 305-312
- Zhang B, Gao Y, Zhang L, Zhou Y(2020)The plant cell wall: Biosynthesis, construction, and functions FA. *Journal of Integrative Plant Biology* 63: 251-272.