INTERNATIONAL JOURNAL OF AGRICULTURE & BIOLOGY ISSN Print: 1560–8530; ISSN Online: 1814–9596 19–1756/2020/24–2–255–262 DOI: 10.17957/IJAB/15.1432 http://www.fspublishers.org



Full Length Article

### Relationship Chemical Component of Cell Wall and Mechanical Strength of Inflorescence Stem of Herbaceous Peony

Yan Sun<sup>1</sup>, Chengzhong Li<sup>1</sup>, Zongqing Jiang<sup>1</sup>, Qing Tian<sup>2</sup>, Daqiu Zhao<sup>2</sup> and Jun Tao<sup>2\*</sup>

<sup>1</sup>School of Horticulture and Landscape Architecture, Jiangsu Agri-Animal Husbandry Vocational College, Taizhou 225300, China

<sup>2</sup>College of Horticulture and Plant Protection, Yangzhou University, Yangzhou 225009, China

<sup>\*</sup>For correspondence: taojun@yzu.edu.cn; czli@jsahvc.edu.cn

Received 15 November 2019; Accepted 03 March 2020; Published 31 May 2020

### Abstract

Chemical constituents of the cell wall of stem of three herbaceous peony (*Paeonia officinalis* Pall.) varieties namely, 'Da Fugui', 'Yangfei Chuyu' and 'Hong Yinzhen', with different mechanical strengths was analyzed to investigate the relationship between the chemical component of the cell wall and the mechanical strength of the stem of the species. Results indicated that 'Da Fugui' and 'Yangfei Chuyu' with high mechanical strength of stem had of higher cellulose, lignin, and proto-pectin contents as well as with more thickness and fresh weight than the variety 'Hong Yinzhen', which had a low mechanical strength. By contrast, 'Da Fugui' and 'Yangfei Chuyu' with a high mechanical strength contained higher soluble pectin content than that in 'Hong Yinzhen' with a low mechanical strength. The mechanical strength of stem was positively correlated with lignin and proto-pectin contents but was negatively correlated with cellulose and soluble pectin contents. On 0–7 days after budding (DAB) and 14–21 DAB, the mechanical strength of the stem was positively correlated with cellulose and soluble pectin contents. On 28–35 DAB, the mechanical strength was correlated positively with cellulose content but negatively with soluble pectin content. Data suggested that increased amount of cellulose and soluble pectin during the early budding stage and enhancing amount of lignin during the late budding stage in the inflorescence stem of plants increased the thickness as well as improves the fresh weight of the stem, which proved beneficial to improve the mechanical strength of herbaceous peony. © 2020 Friends Science Publishers

Keywords: Peony; Stem; Strength; Wall component

### Introduction

Plant cell wall is a net structure composed of various substances, such as cellulose, pectin, hemicellulose, and so on (McCormick 2018; Zheng *et al.* 2018). Cell wall components support plant cells, tissues, and corpus (Barnes and Anderson 2018). The mechanical strength of plants corresponds to the physical property of their cell wall, which also helps crops adapt to different cultivation environments. The inflorescence stem of some herbaceous peony varieties exhibits a poor mechanical strength, and this negative trait is manifested as a bending stem on a few days after budding (DAB), which condition strongly affects the cut-flower production and ornamental values of herbaceous peony. Therefore, breeders of herbaceous peony aim to breed cut-flower cultivars with a starched stem (Varu and Barad 2016; Xue *et al.* 2018).

The variations and forms of the mechanical strength of a plant stem are related to the variation of cell wall components. The main chemical components of the cell wall are cellulose, pectin, and lignin, which exhibit synergic interactions in different growth stages; these components mechanically support the entire plant by affecting the strength of the cell wall of a plant stem (El Hage et al. 2018; Hatfield et al. 2018). Therefore, the composition and content of these substances could improve the mechanical strength of plants. Cellulose is the main component of the cell wall of plants, and this component provides support for plants (Kotake et al. 2011). High cellulose content yields tough plant tissues and improve their rupture strength (Liu et al. 2016). In African daisy (Gerbera jamesonii Bolus), the stem contains less crude fiber than the other plant parts; as a consequence, a curving stem is formed (Hamedan et al. 2019). Lignin is cross-linked with cell wall components via a covalent bond; thus, the mechanical strength of the cell wall is enhanced (Salmén et al. 2016). For instance, cell wall components, such as lignin, of a brittle culm mutant are significantly lower than those of wild-type brittle culm; as such, the mutant exhibits a low mechanical strength and easily breaks than the wild-type plant (Zhang et al. 2016; Hirano et al. 2017). Pectin is mainly distributed in the intercellular layer, and this component not only binds cells

To cite this paper: Sun Y, C Li, Z Jiang, Q Tian, D Zhao and J Tao (2020). Relationship chemical component of cell wall and mechanical strength of inflorescence stem of herbaceous peony. Intl J Agric Biol 24:255–262

together but also solidifies and reinforces tissues. Pectin is present in the intercellular layer in two forms, namely, water-soluble pectin and water-insoluble proto-pectin (Bethke *et al.* 2016). Fruit firmness decreases as fruit maturity increases; the concentration of proto-pectin, which is alkali-soluble pectin, decreases as the concentration of water-soluble pectin increases (Szatanik-Kloc *et al.* 2017). Therefore, the main cell wall components, such as cellulose, lignin, and pectin, are related to the mechanical strength of plant stem. However, studies have rarely described the relationship between the mechanical strength of the stem of herbaceous peony and its cell wall components.

In this study, stems of 'Da Fugui', 'Yangfei Chuyu', and 'Hong Yinzhen' varieties of herbaceous peony (Paeonia officinalis Pall.) were used as test materials in Yangzhou area. These varieties exhibit different mechanical strengths. The mechanical strength, growth index, and content of cell wall components of each stem were determined within 35 DAB, and the last determination was during blooming stage. The morphological characteristics and the vibration of the mechanical strength of the cell wall of each stem were compared. The relationship of the cell wall components with the mechanical strength of the stem was also examined from the budding stage to the blooming stage. This study aimed to discuss the morphological and physiological mechanisms of the variation in the mechanical strength of the stem of herbaceous peony during development. Our results provided a theoretical basis of breeding herbaceous peony with a high mechanical strength.

### **Materials and Methods**

#### Test materials and experimental details

The test was conducted in Herbaceous Peony Germplasm Resources Garden of the Gardening and Plant Protection College in Yangzhou University from March 2013 to May 2013. The growth status of three selected varieties, namely, 'Da Fuigui', 'Yangfei Chuyu', and 'Hong Yinzhen', was relatively uniform. Samples were collected every seven days from the budding stage to the blooming stage. Stems, which grew and developed consistently with each other, were randomly harvested. The inflorescence stems were cut and separated into three segments, 5 cm length from the upper apex or distal of the stem as the top segment, the same length from the proximal and the midst as the bottom and the middle one, respectively. Stems from 3 plants corresponding to each variety were tested for the experiment. Plant height was measured with a tape; parts of the basal stem were clipped and then brought to the lab. Flower buds and leaves were washed; afterward, 10 cm of upper stem, middle stem, and basal stem was clipped to determine the morphological index and mechanical strength. After the samples were treated with liquid nitrogen, the stems were placed in an ultra-cold storage freezer at -80°C.

## Determination of stem thickness and fresh weight and mechanical strength

The thickness of the stem was measured by using a Vernier caliper; the fresh weight was determined by using electronic scales. The mechanical strength (in Newton [N]) of the stem 5 cm underneath the flower was determined with the method of Li *et al.* (2015) using a strength tester (NK-2, Hangzhou Zhejiang). Each group was composed of three herbaceous peonies, and measurement was repeated thrice.

# Content determination of the main cell wall components of herbaceous peony stem

The cell wall components of the stem of herbaceous peony were determined in accordance with a previously described method (Rose et al. 1998). Briefly, the stems were ground into fine powder in liquid nitrogen and extracted with 95% alcohol, then washed twice with boiling alcohol and methyl alcohol: chloroform (1:1 v/v), respectively. Finally, the cell wall residues were dried overnight at 50°C and used for analysis. The experiment was performed in triplicate. Pectin was extracted in accordance with Majumder and Mazumdar (2002). Different methods were applied to determine the contents of the following cell wall components: sulfate-carbazole method for the watersoluble pectin together with the proto-pectin content (Blumenkrantz and Asboe-hansen 1973), anthronesulfuric acid method for cellulose content (Updegraff 1969) and Müsel et al. (1997) method for lignin content.

#### **Data processing**

The mechanical strength and the morphological characteristics of the stem were evaluated by using SPSS 16.0. The contents of each cell wall component in different development stages were also compared and subjected to correlation analysis in SPSS 16.0. Differences in each parameter among the three varieties were analyzed by LSD test at 5% significance level using one-way ANOVA. The graphical presentation of data was done using Microsoft Excel 2003.

### Results

# Changes in mechanical strength, stem thickness, fresh weight and plant height during development

**Mechanical strength:** The changes of the three varieties were similar (Fig. 1). In particular, it gradually increased and reached its maximum value on 35 DAB. Among the three varieties, 'Da Fugui' yielded the highest mechanical strength; by contrast, 'Hong Yinzhen' exhibited the lowest. The strength of stem with different parts was different. The top stem of 'Da Fugui' was 16.46 N, which was 1.07 times stronger than the two other varieties. At the same time,





**Fig 1:** Changes in inflorescence stem mechanical strength of three herbaceous peony cultivars (A: upper stem; B: middle stem; C: bottom stem

the middle stem of 'Da Fugui' was 73.22 *N*, which was 1.13 and 6.60 times stronger than 'Yangfei Chuyu' and 'Hong Yinzhen', respectively. While the basal stem of 'Da Fugui' was 171.78 *N*, which was 1.11 and 2.16 times stronger than 'Yangfei Chuyu' and 'Hong Yinzhen', respectively.

**Stem thickness:** The changes of the three varieties were also similar with gradually increasing trend (Fig. 2). 'Yangfei Chuyu' was higher than that of 'Da Fugui' and 'Hong Yinzhen'. The top stem of 'Yangfei Chuyu' was 0.50 cm on 35 DAB, was 1.02 and 1.67 times thicker than those of 'Da Fugui' and 'Hong Yinzhen', respectively. The middle stem of 'Yangfei Chuyu' was 0.99 cm, revealing that was 1.01 and 2.36 times thicker than those of 'Da Fugui' and 'Hong Yinzhen', respectively. The basal stem of 'Yangfei Chuyu' was 1.23 cm; showing that 1.03 and 1.43 times thicker than those of 'Da Fugui' and 'Hong Yinzhen', respectively.

**Fresh weight:** In particular, the fresh weight of the stems gradually increased, reaching its maximum at 35 DAB. The stem of 'Da Fugui' was heavier than the two other varieties.



**Fig 2:** Changes in inflorescence stem thickness of three herbaceous peony cultivars

The top stem of 'Da Fugui' was 1.80 g, which was 1.16 and 2.28 times heavier than those of 'Yangfei Chuyu' and 'Hong Yinzhen'. The middle stem of 'Da Fugui' was 3.07 g,which was 1.02 and 3.41 times heavier than those 'Yangfei Chuyu' and 'Hong Yinzhen'. The basal stem of 'Da Fugui' was 4.75 g, which was 1.08 and 2.70 times heavier than those of 'Yangfei Chuyu' and 'Hong Yinzhen' (Fig. 3).

**Plant height:** The height of these varieties gradually increased, while 'Yangfei Chuyu' was significantly taller than the two other varieties (Fig. 4). All three varieties reached their maximum height at 35 DAB. 'Yangfei Chuyu' was 78.8 cm, 'Da Fugui' and 'Hong Yinzhen' was 56.7 and 66.8 cm respectively. Likewise, the changes in the stems of the three varieties were similar.

# Dynamic change in cell wall components of stem during development

**Cellulose:** The cellulose content of the three varieties initially increased, but subsequently decreased, and reached



Fig 3: Changes in inflorescence stem fresh weight of three herbaceous peony cultivars

the lowest value on day 35 of budding (Fig. 5A). The lowest cellulose content of 154.64  $\mu g \cdot mg^{-1}$  was detected in 'Hong Yinzhen'. This value was 45.33 and 35.55% in 'Da Fugui', and 'Yangfei Chuyu', respectively. The cellulose contents of the middle stem were also different among the three varieties. The cellulose contents of 'Da Fugui' and 'Yangfei Chuyu' decreased on days 0-35 of budding, while the cellulose content of 'Hong Yinzhen' initially increased and then decreased (Fig. 5B). The lowest cellulose content of 173.10  $\mu g \cdot mg^{-1}$  was found in the middle stem of 'Hong Yinzhen' on day 35 of budding; this finding was 53.58% of the cellulose content of 'Da Fugui' and 39.84% of the cellulose content of 'Yangfei Chuyu'. The cellulose contents of the basal stem of the three varieties decreased (Fig. 5C). Among the three varieties, 'Hong Yinzhen' yielded the lowest cellulose content of 293.24  $\mu g \cdot mg^{-1}$  on day 35 of budding; this finding was 76.18% of the cellulose content of 'Da Fugui' and 67.13% of the cellulose content of 'Yangfei Chuyu'.



Fig 4: Changes in plant height of three herbaceous peony cultivars

Lignin: The changes in the lignin content of the stem of the three varieties were almost the same on 0-35 DAB (Fig. 6). In particular, the lignin content gradually increased. The lignin content of 'Da Fugui' was higher than that of the two other varieties. The lignin content of the top stem of 'Da Fugui' reached 113.59  $\mu$ g·mg<sup>-1</sup>, which was 1.19 and 1.70 times higher than those of 'Yangfei Chuyu' and 'Hong Yinzhen', respectively. The lignin content of the middle stem of 'Da Fugui' reached 117.85  $\mu$ g·mg<sup>-1</sup>, which was 1.18 and 2.40 times higher than those of 'Yangfei Chuyu' and 'Hong Yinzhen', respectively. The lignin content of the basal stem of 'Da Fugui' reached 126.21  $\mu g \cdot mg^{-1}$ , which was 1.22 and 1.55 times higher than those of 'Yangfei Chuyu' and 'Hong Yinzhen', respectively.

Pectin: The changes in the water-soluble pectin content of the three varieties were almost the same as the lignin (Fig. 7). In general, the water-soluble pectin contents decreased. The content of 'Da Fugui' was significantly lower than that of the two other varieties (P < 0.01). The content of the top stem of 'Da Fugui' on day 35 of budding was 11.07  $\mu$ g·mg<sup>-1</sup>, which was 63.69% of 'Yangfei Chuyu' and 32.13% of 'Hong Yinzhen'. The pectin content of the middle stem of 'Da Fugui' was 9.76  $\mu$ g·mg<sup>-1</sup>, which was 34.75% of 'Yangfei Chuyu' and 23.78% of 'Hong Yinzhen'. The content of the basal stem was 17.22  $\mu$ g·mg<sup>-1</sup>, which was 47.09% of 'Yangfei Chuyu' and 28.09% of 'Hong Yinzhen'. For the proto-pectin, in general, the change of contents was contrast with that of water-soluble pectin (Fig. 8). The content of 'Da Fugui' was significantly higher than that of the two other varieties on day 35 of budding (P < 0.01). The content of the top stem of 'Da Fugui' was 132.69  $\mu$ g·mg<sup>-1</sup>, which was 1.07 and 1.97 times higher than those of 'Yangfei Chuyu' and 'Hong Yinzhen', respectively. The content of the middle stem of 'Da Fugui' was 143.12  $\mu$ g·mg<sup>-1</sup>, which was 1.10 and 1.47 times higher than those of 'Yangfei Chuyu' and 'Hong Yinzhen', respectively. The content of the basal stem of 'Da Fugui' was 177.94  $\mu$ g·mg<sup>-1</sup>, which was 1.37 and 1.65 times higher than those of 'Yangfei Chuyu' and 'Hong Yinzhen', respectively.



**Fig 5:** Changes in cellulose contents in the inflorescence stems of three herbaceous peony cultivars

# Correlation analysis of the factors affecting mechanical strength of stem

Mechanical strength of the top stem of the three varieties exhibited a highly significant positive correlation with plant height, stem thickness, and stem fresh weight (Table 1). The mechanical strength of the stem showed a significant negative correlation with the cellulose and water-soluble pectin contents of the cell wall. The mechanical strength of the stems of all varieties exhibited a highly significant positive correlation with the lignin content of the cell wall.

The correlation coefficients of the mechanical strength of the stem of herbaceous peony at different developmental stages and the main physical and chemical characteristics of this species are presented in Table 2. On 0–7 DAB, the mechanical strength of the stem was positively correlated with plant height, stem thickness and fresh weight, cellulose and pectin contents. The mechanical strength of the stem was also significantly correlated with plant height, stem thickness, and fresh weight, but was not correlated with the cellulose and pectin contents. Furthermore, the mechanical



**Fig 6:** Changes in lignin contents in the inflorescence stems of three herbaceous peony cultivars (A: upper stem; B: middle stem; C: bottom stem.)

strength of the stem was negatively correlated with the lignin and proto-pectin contents. Among the parameters correlated with the mechanical strength, the stem thickness yielded the highest correlation (Table 2). On 14-21 DAB, the mechanical strength of the stem was positively correlated with plant height, stem thickness, and stem fresh weight, cellulose content, and water-soluble pectin content. The mechanical strength of stem also exhibited a highly significant correlation with stem thickness and stem fresh weight. Furthermore, the mechanical strength of the stem was significantly correlated with plant height. By contrast, the mechanical strength of the stem was not significantly correlated with the cellulose and water-soluble pectin contents. The mechanical strength was negatively correlated with the lignin and proto-pectin contents. Among the parameters correlated with the mechanical strength, stem thickness ( $R = 0.900^{**}$ ) exhibited the largest correlation coefficient. On 28-35 DAB, the mechanical strength of the stem was positively correlated with stem thickness, stem fresh weight, lignin content, and proto-pectin content. The

 
 Table 1: Correlation coefficients of mechanical strength and some physical and chemical characteristics of herbaceous peony inflorescence stems in different parts

Correlation index	Top stem		
	'Dafuigui'	'Yangfei CHuyu'	'Hong Yinzhen'
Stem thickness	0.977**	0.982**	0.981**
Stem fresh weight	0.956**	0.973**	0.987**
Plant height	0.949**	0.964**	0.975**
Cellulose contents	-0.761**	-0.822**	-0.740**
Lignin contents	0.784**	0.885**	0.814**
Soluble pectin contents	-0.726**	-0.829**	-0.821**
Proto-pectin contents	0.728**	0.808**	0.824**



**Fig 7:** Changes in soluble pectin contents in the inflorescence stems of three herbaceous peony cultivars

mechanical strength of the stem exhibited a highly significant correlation with stem thickness and stem fresh weight. The mechanical strength of the stem was significantly correlated with the lignin content, but was not significantly correlated with the proto-pectin content. Stem thickness ( $R = 0.961^{**}$ ) showed the largest correlation coefficient. Moreover, the mechanical strength of the stem was negatively correlated with plant height, cellulose



Fig 8: Changes in proto-pectin contents in the inflorescence stems of three herbaceous peony cultivars

content, and water-soluble pectin content. However, the negative correlation of the mechanical strength with the water-soluble pectin was not significant.

#### Discussion

Plant stem growth indexes, such as length, thickness, and fresh weight, are the main factors affecting tissue mechanical strength (Jeon *et al.* 2016; Wu *et al.* 2017). Our study indicated that plant height was significantly correlated with the mechanical strength of the top stem of herbaceous peony (Table 1); however, this finding is not consistent with that observed in rice (Yang *et al.* 2011), wheat (Wang *et al.* 2006). In our study, plant height was positively correlated with the mechanical strength of the stem on 0–7 DAB and 14–21 DAB; however, on 28–35 DAB, plant height was negatively correlated with the mechanical strength of the stem (Table 2). That is to say that the mechanical strength gradually increased as the stem grew after the budding stage of herbaceous peony. On 28–35 DAB, although the stem stopped growth, the stem thickness was highly and

Index	Correlation index			
	0-7 days after budding	14–21 days after budding	28–35 days after budding	
Stem diameter	0.516**	0.863**	0.944**	
Stem fresh weight	0.486**	0.900**	0.961**	
Plant height	0.446**	0.273*	-0.055	
Cellulose contents	0.063	0.269	-0.203	
Lignin contents	-0.333	-0.220	0.499*	
Soluble pectin contents	0.051	0.133	-0.554*	
Proto-pectin contents	-0.496*	-0.255	0.439	

Table 2: Correlation coefficients of mechanical strength and some physical and chemical characteristics of herbaceous peony inflorescence stems in different stages

significantly correlated with the mechanical strength of the different parts of the stem of herbaceous peony and at different developmental stages. This finding is consistent with that observed in maize (Xu *et al.* 2017).

In our experiment, the fresh weight of the stem was gradually increased to the maximum. This also implied the carbohydrate was abundant in the stem, which ensures that the stem of herbaceous peony can support flowers with sufficient mechanical strength in the full-bloom stage (Table 2). So, the fresh weight of the stem of herbaceous peony was significantly correlated with the mechanical strength of the different parts of the stem and different developmental stages.

Plant cell wall can provide mechanical strength for cells, tissues, and the entire plant, and this part is composed of several substances, including cellulose, lignin and pectin (Padayachee *et al.* 2017). It was showed that the excessive cellulose content was closely related to curvature of stems, and it was consistent with that found in hemp fibers (Liu *et al.* 2015), but inconsistent with that observed in rice (Li *et al.* 2003) and wheat (Wang *et al.* 2006). It is possibly caused by the differences in the stalk structures of herbaceous peony, rape, and members of the grass family. We believe that high cellulose content is favorable for the maintenance of erectness at early developmental stage.

The lignin content of the stem of herbaceous peony was significantly correlated with the mechanical strength of the stem (Table 1), and is consistent with that observed in wheat (Tripathi *et al.* 2003). On 0–7 DAB and 14–21 DAB, the lignin content of the stem was negatively correlated with mechanical strength, but this finding was not significant. On 28–35 DAB, the lignin content of the stem was positively correlated with mechanical strength. This revealed that low lignin content is favorable for stem growth in early development stage; in later development stages, high lignin content is necessary to enhance the mechanical strength of stems to maintain the starched form of this plant part. This phenomenon is possible because stem growth occurs as a result of cell differentiation, expansion, and extension at the early developmental stage (Geitmann and Ortega 2009).

The content of water-soluble pectin is decreased during pectin degradation in the cell wall (Cybulska *et al.* 2015; Chen *et al.* 2015). In this process, the pectin lyase disrupts the chemical bond between polyoxymethylene galacturonic acid and arabinose (Brown *et al.* 2005). The decomposition of cell wall components and an increase in hydrolase activity in the cell wall result in curving stem (Lashermes *et al.* 2016). The pectin content of herbaceous peony exhibited a significant negative correlation with the mechanical strength of the stem. By contrast, the protopectin content showed a positive correlation with the mechanical strength of the stem (Table 1). Therefore, low water-soluble pectin content and high proto-pectin content can increase the firmness of the cell wall, and this condition favors the increase in the mechanical strength of stems. This result is consistent with that observed in the fruit firmness of pear (Argenta *et al.* 1981) and peach (Wahab *et al.* 2016).

The optimum time to harvest herbaceous peony cut flowers is the firm budding stage. In this experiment, this stage was on 28–35 DAB. Correlation analysis revealed that the most relevant factors that determine the mechanical strength of the stem of herbaceous peony are stem thickness, stem fresh weight, lignin content, and water-soluble pectin content (Table 2). Therefore, the mechanical strength of the stem of herbaceous peony could be significantly enhanced by increasing stem thickness, stem fresh weight, and lignin content and by reducing water-soluble pectin content through cultivation management measures. Moreover, herbaceous peony with stems exhibiting high mechanical strength, stem fresh weight, and stem thickness could be optimum models to breed herbaceous peony cut flower.

#### Conclusion

The mechanical strength of stem was positively correlated with lignin and proto-pectin contents but was negatively correlated with cellulose and soluble pectin contents. It is suggested that enhancing the amount of lignin during the late budding stage in plants by cultivated measurements, such as increase the thickness as well as improve the fresh weight of the stem, would be beneficial to improve the mechanical strength of herbaceous peony stem.

#### Acknowledgments

This work was supported by the Natural Science Foundation of China (31772341, 31972448), the Young Talent Support Project of Jiangsu Provincial Association for Science and Technology, the Fifth Phase of "Project 333" Science Funding Program of Jiangsu Province (BRA2019084), and Jiangsu Modern Agricultural Industrial Technology System (JATS[2019]374, 448). We thank Dr. Bin Xu of Nanjing Agricultural University for his kind revision of the manuscript.

#### References

- Argenta LC, JP Mattheis, X Fan, C Amarante (1981). Managing'Bartlett' pear fruit ripening with 1-methylcyclopropene reapplication during cold storage. *Postharvest Biol Technol* 31:125–130
- Barnes WJ, CT Anderson (2018). Release, recycle, rebuild: cell-wall remodeling, autodegradation, and sugar salvage for new wall biosynthesis during plant development. *Mol Plant* 11:31–46
- Bethke G, A Thao, G Xiong, B Li, NE Soltis, H Noriyuki, AH Rachel, K Fumiaki, JK Daniel, P Markus, G Jane (2016). Pectin biosynthesis is critical for cell wall integrity and immunity in *Arabidopsis thaliana*. *Plant Cell* 28:537–556
- Blumenkrantz N, G Asboe-Hansen (1973). New method for quantitative determination of uronic acids. Anal Biochem 54:484–489
- Brown DM, LAH Zeef, J Ellis, R Goodacre, SR Turner (2005). Identification of novel genes in Arabidopsis involved in secondary cell wall formation using expression profiling and reverse genetics. *Plant Cell* 17:2281–2295
- Chen H, S Cao, X Fang, H Mu, H Yang, W. Wu (2015). Changes in fruit firmness, cell wall composition and cell wall degrading enzymes in postharvest blueberries during storage. *Sci Hortic* 188:44–48
- Cybulska J, A Zdunek, A Kozioł (2015). The self-assembled network and physiological degradation of pectins in carrot cell walls. *Food Hydrocolloid* 43:41–50
- El Hage F, D Legland, N Borrega, MP Jacquemot, Y Griveau, S Coursol, V Mechin, M Reymond (2018). Tissue lignification, cell wall pcoumaroylation and degradability of maize stems depend on water status. J Agric Food Chem 66:4800–4808
- Geitmann A, JKE Ortega (2009). Mechanics and modeling of plant cell growth. Trends Plant Sci 14:467–478
- Hamedan HJ, MM Sohani, A Aalami, NM Javad (2019). Genetic engineering of lignin biosynthesis pathway improved stem bending disorder in cut gerbera (*Gerbera jamesonii*) flowers. *Sci Hortic* 245:274–279
- Hatfield RD, H Jung, JM Marita, H Kim (2018). Cell Wall Characteristics of a maize mutant selected for decreased ferulates. *Amer J Plant Sci* 9:446–466
- Hirano K, R Masuda, W Takase, Y Morinaka, M Kawamura, Y Takeuchi, H Takagi, H Yaegashi, S Natsume, R Terauchi, T Kotake, Y Matsushita, T Sazuka (2017). Screening of rice mutants with improved saccharification efficiency results in the identification of constitutive photomorphogenic 1 and gold hull and internode 1. *Planta* 246:61–74
- Jeon HW, JS Cho, EJ Park, KH Han, YI Choi, J Ko (2016). Developing xylem-preferential expression of PdGA20ox1, a gibberellin 20-oxidase 1 from *Pinus densiflora*, improves woody biomass production in a hybrid poplar. *Plant Biotechnol J* 14:1161–1170
- Kotake T, T Aohara, K Hirano, A Sato, Y Kaneko, Y Tsumuraya, H Takatsuji, S Kawasaki (2011). Rice brittle culm 6 encodes a dominant-negative form of CesA protein that perturbs cellulose synthesis in secondary cell walls. J Exp Bot 62:2053–2062
- Lashermes G, A Gainvors-Claisse, S Recous, I Bertrand (2016). Enzymatic strategies and carbon use efficiency of a litter-decomposing fungus grown on maize leaves, stems, and roots. *Front Microbiol* 7; Article 1315
- Li C, Y Sun, D Zhao, J Tao (2015). Relationship between mechanical strength and morphological index of inflorescence stem of herbaceous peony (*Paeonia lactiflora* Pall.). Acta Agric Zhejiangensis 27:182–188
- Li Y, Q Qian, Y Zhou, M Yan, L Sun, M Zhang, ZM Fu, YH Wang, B Han, XM Pang, MS Chen, JY Li (2003). BRITTLE CULM 1, which encodes a COBRA-like protein, affects the mechanical properties of rice plants. *Plant Cell* 15:2020–2031

- Liu J, N Wu, H Wang, J Sun, B Peng, P Jiang, E Bai (2016). Nitrogen addition affects chemical compositions of plant tissues, litter and soil organic matter. *Ecology* 97:1796–1806
- Liu M, D Fernando, AS Meyer, B Madsen, G Daniel, A Thygesen (2015). Characterization and biological depectinization of hemp fibers originating from different stem sections. *Indust Crop Prod* 76:880–891
- Majumder K, BC Mazumdar (2002). Changes of pectic substances in developing fruits of cape-gooseberry (*Physalis peruviana* L.) in relation to the enzyme activity and evolution of ethylene. *Sci Hortic* 96:91–101
- McCormick S (2018). Nanoscale imaging of xyloglucan in plant cell walls. Plant J 93:209–210
- Müsel G, T Schindler, R Bergfeld, K Ruel, G Jacquet, C Lapierre, V Speth, P Schopfer (1997). Structure and distribution of lignin in primary and secondary cell walls of maize coleoptiles analyzed by chemical and immunological probes. *Planta* 201:146–159
- Padayachee A, L Day, K Howell, MJ Gidley (2017). Complexity and health functionality of plant cell wall fibers from fruits and vegetables. *Crit Rev Food Sci Nutr* 57: 59–81
- Rose JKC, KA Hadfield, JM Labavitch, AB Bennett (1998). Temporal sequence of cell wall disassembly in rapidly ripening melon fruit. *Plant Physiol* 117: 345–361
- Salmén L, JS Stevanic, AM Olsson (2016). Contribution of lignin to the strength properties in wood fibres studied by dynamic FTIR spectroscopy and dynamic mechanical analysis (DMA). *Holzforschung* 70:1155–1163
- Szatanik-Kloc A, J Szerement, J Cybulska, G Jozefaciuk (2017). Input of different kinds of soluble pectin to cation binding properties of roots cell walls. *Plant Physiol Biochem* 120:94–201
- Tripathi SC, KD Sayre, JN Kaul (2003). Growth and morphology of spring wheat (*Triticum aestivum* L.) culms and their association with lodging: Effects of genotypes, N levels and ethephon. *Field Crop Res* 8:271–290
- Updegraff DM (1969). Semimicro determination of cellulose inbiological materials. *Anal Biochem* 32:420–424
- Varu DK, AV Barad (2016). Effect of stem length and stage of harvest on vase-life of cut flowers in tuberose (*Polianthes tuberosa* L.) cv. Double. J Hortic Sci 5:42–47
- Wahab M, Z Ullah, M Sajid, M Usman, K Sohail, S Nayab, M Ullah (2016). Effect of calcium sources as foliar applications on fruit quality of peach cultivars. *Prog Hortic* 48:167–172
- Wang J, J Zhu, Q Lin, X Li, N Teng, Z Li, B Li, A Zhang, J Lin (2006). Effects of stem structure and cell wall components on bending strength in wheat. *Chinese Sci Bull* 51:815–823
- Wu L, W Zhang, Y Ding, J Zhang, ED Cambula, F Weng, Z Liu, C Ding, S Tang, L Chen, S Wang, G Li (2017). Shading contributes to the reduction of stem mechanical strength by decreasing cell wall synthesis in Japonica rice (*Oryza sativa* L.). *Front Plant Sci* 8; Article 881
- Xu C, Y Gao, B Tian, J Ren, Q Meng, P Wang (2017). Effects of edah, a novel plant growth regulator, on mechanical strength, stalk vascular bundles and grain yield of summer maize at high densities. *Field Crop Res* 200:71–79
- Xue J, Y Tang, S Wang, R Yang, Y Xue, C Wu, X Zhang (2018). Assessment of vase quality and transcriptional regulation of sucrose transporter and invertase genes in cut peony (*Paeonia lactiflora* 'Yang Fei Chu Yu') treated by exogenous sucrose. *Posthar Biol Technol* 143:92–101
- Yang Y, Z Zhu, Y Zhang, T Chen, Q Zhao, L Zhou, S Yao, Y Zhang, S Dong, C Wang (2011). Relationship between lodging resistance and stem morphological traits in different rice varieties (lines). *Jiangsu J* Agric Sci 27:231–235
- Zhang M, F Wei, K Guo, Z Hu, Y Li, G Xie, Y Wang, X Cai, L Peng, L Wang (2016). A novel FC116/BC10 mutation distinctively causes alteration in the expression of the genes for cell wall polymer synthesis in rice. *Front Plant Sci* 7; Article 1366
- Zheng Y, W Wang, Y Chen, E Wagner, DJ Cosgrove (2018). Xyloglucan in the primary cell wall: assessment by FESEM, selective enzyme digestions and nanogold affinity tags. *Plant J* 93:213–228