Review Article

Morphological and Genetic Studies on Weeping Tree Architecture in Ornamental Plants

Yichi Zhang[1–6†], Tangchun Zheng[1–5†], Xiaokang Zhuo[1–6] and Qixiang Zhang[1–6*]
[1]*Beijing Key Laboratory of Ornamental Plants Germplasm Innovation & Molecular Breeding, Beijing Forestry University, Beijing, China*
[2]*National Engineering Research Center for Floriculture, Beijing Forestry University, Beijing, China*
[3]*Beijing Laboratory of Urban and Rural Ecological Environment, Beijing Forestry University, Beijing, China*
[4]*Engineering Research Center of Landscape Environment of Ministry of Education, Beijing Forestry University, Beijing, China*
[5]*Key Laboratory of Genetics and Breeding in Forest Trees and Ornamental Plants of Ministry of Education, Beijing Forestry University, Beijing, China*
[6]*Beijing Advanced Innovation Center for Tree Breeding by Molecular Design, Beijing Forestry University, Beijing, China*
[*]For correspondence: zqxbjfu@126.com
[†]These authors contributed equally to this work

Abstract

Tree architecture is considered as an important ornamental trait. Through molecular genetics, a more rapid breeding process of selecting upright or weeping tree form can benefit the development of ornamental horticulture. This review introduced these two major atypical tree architectures, associated with the discovery in both genetic and hormonal potential link at molecular level in previous studies, with the aim of providing theoretical basis for tree architecture improvement in ornamental. © 2019 Friends Science Publishers

Keywords: Tree architecture; Weeping; Gravitropic set-point angle; Molecular marker

Introduction

Tree architecture is considered as an important trait when it comes to horticultural studies. The weeping tree architecture is described as branches growing downward instead of upward, compared to the upright counterpart. Previous studies have mainly focused on physiological-level, for example, the analysis regarding to hormone regulation mechanisms in different plants, as well as morphological level.

With regard to characterize tree architecture, growth parameters are firstly introduced in this review. Furthermore, hormone-related studies regarding weeping tree architecture were summarized to provide physiological evidence. A systematic list of reported weeping woody plants, along with the conjecture behind, was further attached to outline the candidate genus for future weeping tree architecture studies.

Upright and Weeping Tree Architecture

Tree architecture is influenced by multiple factors, such as branch angles and orientation, branch size, overall height, pattern and periodicity of branching, changes in growth rate and hormone transportation (Srivastava, 2002; Hollender and Dardick, 2015; Wang *et al.*, 2018). In addition, and environmental factors such as light, temperature, nutrition (Wang and Li, 2008) may act as abiotic stresses which damage the process of growth. Hence, the formation of tree architecture is believed to be a complex process, and its main control factor still remains a mystery.

To categorize tree forms, Hallé *et al.* (1978) first described 23 universal architectural models for the predetermined growth potential of trees under no biotic or abiotic stress, which could be used to deduct the growing process of certain species. Apart from these models, several non-standard tree architectures were also described, such as pillar peach and weeping architecture. The former appears to be a pillar or column, while the latter performs distinct horizontally growing or pendulous branches with or without a pillar appearance (Hallé *et al.*, 1978; Tworkoski and Scorza, 2001). These two kinds of tree architecture with apparent branching characteristics will be described in this review in detail.

Branch Angles and Orientation

The absorption of light for photosynthesis may be blocked

---

in the competition with adjacent trees, which is directly affected by the branch angles (Hollender and Dardick, 2015). There are three branch angles: the initial crotch angle, the equilibrium angle (Wilson, 2000) and the geotropic angle (Hollender and Dardick, 2015). The initial crotch angle is defined as the angle of the shoot at the point of connection to the branch, which signifies the beginning of the shoot branching (Hollender and Dardick, 2015). The equilibrium angle is formed as the branch grows, between the main stem and the branch. It is also called the angle of inclination or the gravitational set-point angle (GSA) (Brown, 1971; Digby and Firn, 1995). Digby and Firn (1995) first developed the model of GSA (Fig. 1) to describe the process of alternation of angle in plant organ, taking *Tradescantia fluminensis* (a perennial plant in South America) and *Oplismenus hirtellus* (a perennial grass for ground cover) as materials, in response to explain the phenomenon of changing angles because of the altered light in the growing environment. They suggested that when taking human reference plant (vertical axis) for description and when the GSA was 180°, the traditional terms, positive and negative orthogravitropism, presented exactly the opposite descriptions. Hence, the GSA was defined as the angle in response to gravity where a plant organ grows without the impact of gravity to rectify the growing orientation (Digby and Firn, 1995). We may introduce this model to describe the branches of weeping trees or archer trees because the pendulous growth habit happens at a certain phase in response to gravity and is believed not to be gravity-induced.

The geotropic angle is more upward, formed at the tip of lateral branch (Brown, 1971). Apparently, trees in form of upright habit have narrower branch angles. Different from *Arabidopsis*, where the branch angle response principally to gravity, trees have more extensive secondary growth (Hollender and Dardick, 2015). Moreover, because the initial crotch angle and the equilibrium angle are genetically determined, they rely on hormone gradients or communications between the main and lateral branch instead of gravitropic sensing (Tomlinson, 1983; Hollender and Dardick, 2015).

Pillar Peach

The pillar peach performs as shorter lateral shoots, small stem diameter, decreased sylleptic branching and narrow crotch angles (Tworkoski *et al*., 2006). This tree architecture is desirable for orchard thanks to its high-density production systems comparing with the standard trees, which grows more upward (Sajer *et al.*, 2012).

Weeping Architecture

Weeping architecture has previously been reported in woody plants such as *Betula pendula* (Salojärvi *et al.*, 2017), *Prunus mume* (Lv and Chen, 2003; Zhang *et al.*,

2015), *P. persica* (Werner and Chaparro, 2005) and *Morus alba* (Yamanouchi *et al.*, 2009), etc. (Fig. 2). Trees with a weeping architecture have distinct pendulous downward-growing branches. The shoots grow upwards in the beginning. However, in the process of growth, their tips turn downwards, and then the growth carries in this orientation. This change in shoot direction releases other subordinate lateral buds from precedent apical dominance, which promises newer shoot branching on the main branch. Interestingly, the new shoots continue to bend in the following growth process (Hollender and Dardick, 2015). This growth habit is well appreciated in the ornamental horticulture (Hill and Hollender, 2019), and the reasons for the bending habit remain to be explored. Studies have found that the changes in gibberellin (GA) content, timing of reaction wood formation and altered gravitropism could be the reasons for explaining the weeping habit, yet the relation of causes and consequences is still unclear for the moment (Hollender and Dardick, 2015).

Besides, Werner and Chaparro (2005) designated archer tree architecture (AR) in the weeping category, which is a semi-weeping appearance, as well as a distinguished curvature in the developing shoots, discovered in hybridization of peaches. Sometimes, the fruit weight may lead to branch bending downwards only the very ends of branch (Lespinasse, 1980). It is worth noting that this kind of tree form does not belong to the category of weeping architecture.

Physiology of Upright or Pendulous Growth–role of Hormones

Former studies showed that in *P. persica,* auxin levels increased in pillar trees were much more than those in the standard trees, and the altered hormone may have caused this upright growth habit. The mechanism of hormone regulation in trees is complex because multiple hormones transaction ways have been found in different species. Various reasons for hormone alternation also add to the mystery.

Apical dominance and apical control both affect the shoot branching. Apical dominance is the phenomenon where the main shoot grows predominantly and suppresses the lateral vegetative buds in the meantime (Cline, 1991). Apical control is described as the suppression of lateral branch growth by those in the higher place after a dormancy period (Wilson, 2000). If the distal shoot is removed, its corresponding lateral branches may grow faster in an upward direction.

Apical dominance can be suppressed by the decapitation of branch or high light density. When the lateral shoots are released from apical dominance, the buds closest to the shoot apex grow firstly, while other dormant buds far from the apex show no change (Cline, 1991). Apical dominance leads to a smaller absorption of light due to the suppression of lateral branches. Therefore, when an

increase in light occurs, the lateral shoots may amplify the light absorption by shoot branching (Hollender and Dardick, 2015). However, apical control is considered to be relative to several hormones, yet the connection is unclear.

Main signal for regulating apical dominance remains uncertain. Many experiments showed that auxin might be the main hormone that causes apical dominance. Former studies have shown that when auxin is synthesized at the shoot apex, they inhibit the lateral buds on the same stem. Decapitation of shoot apex or a decrease of auxin lead to the release of apical dominance for lateral shoots (Wickson, 1958; Srivastava, 2002). After the decapitation in pea plants, an increase of cytokinin (CK) levels was measured in the stem and lateral buds. It is suggested that CK is synthesized in the stem and then transported to lateral buds for further growth (Sae *et al*., 2009). Furthermore, Mason *et al.* (2014) suggested that auxin is not reason for explaining apical dominance in peas. An increase of sucrose in lateral buds after decapitating and exogenous sucrose could release the dormancy of lateral buds. Nakamura *et al*. (1994) have found that GA can recover the upright growing trend in pendulous peach and pendulous Japanese cherry (*Prunus spachiana*), yet indoacetic acid (IAA) showed no influence on inhibiting the weeping tendency in both peach and Japanese cherry branches. Therefore, the mechanism for apical dominance related to hormones remains to be further proved.

Molecular Basis for Upright or Pendulous Growth

Genetic studies for upright and weeping form: Scientists have discovered part of the mechanism of tree architecture at the molecular level, including the orthologous genes related to upright tiller growth habit in rice and maize, and branch angle control gene in *Arabidopsis* (Dardick *et al.*, 2013; Yoshihara *et al*., 2013). Previous reports on weeping character in woody plants covered *Betula*, *Castanea*, *Malus, Morus* and *Prunus* genus (Table 1).

Interaction of genes: The pillar (PI) growth is reported to be controlled by a single recessive gene, called *broomy (br)* (Yamazaki *et al.*, 1987), and it is of incomplete dominance (Werner and Chaparro, 2005). However, Sajer *et al.* (2012) suggested that the *br* gene showed a codominant inheritance. Nevertheless, the heterozygotes and two kinds of homozygous can be distinguished whether the *br* gene is incomplete dominant or codominant.

The weeping growth habit is also controlled by a single recessive gene, called *pleurer (pl)* (Monet *et al*., 1987; Yamazaki *et al.,* 1987). This gene was proposed to be incompletely dominant because the heterozygous of weeping habit could also be detected from the homozygous (Bassi and Rizzo, 2000). Also, the *pl* gene may be connected with GA signaling and/ or regulating wood composition, because weeping trees have longer branch internodes than the standard ones (Fideghelli *et al*., 2003). Hypothesis focuses on the lignification of secondary xylem and the changing of mechanical rigidity in branches
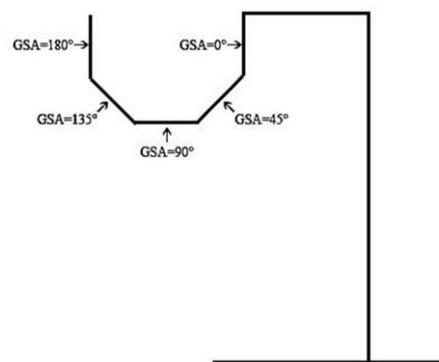

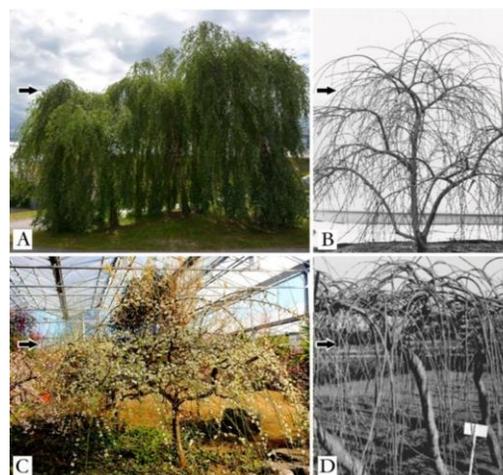**Fig. 1:** Model of gravitational set-point angle

Fig. 2: Reported woody plants with weeping architecture
A. *Betula pendula* 'Youngii' (Salojärvi *et al*., 2017); B. *Prunus pérsica* (Werner and Chaparro, 2005); C. *Prunus mume* (Chen, 2010); D. *Morus alba* 'Shidareguwa' (Yamanouchi *et al*., 2009). The arrow indicates the weeping position

(Nakamura *et al.*, 1994). To verify these hypotheses, scientists have conducted a series of experiments by comparing the untreated weeping trees with GA-treated weeping ones in Japanese weeping cherry and the weeping peach. The weeping branches formed tension wood under higher tensile stress with a larger branch diameter, and appeared to grow upright when GA was applied before the early secondary growth development (Baba *et al*., 1995; Nakamura *et al.*, 1995; Yoshida *et al*., 1999). Moreover, in *P. spachiana*, the GA_3 oxidase level is higher in the elongation parts of weeping branches, which help synthesize bioactive GA (Sugano *et al*., 2004). Some GA biosynthesis mutants in rice cultivars have also proved that plant architecture can be modified through GA pathway at the molecular level (Sasaki *et al*., 2002). Hence, the downward growth habit may occur if GA levels are not sufficient at an early stage (Hollender and Dardick, 2015). Zhang *et al.* (2015) also suggested that the weeping trait in *P. mume* may be controlled by a major gene and several minor genes according to the statistical analysis of crossing experiment between pillar and weeping group. Based on

Table 1: Research summary list: weeping architecture in woody plants reported

Variants	Conjecture	Reference
Betula pendula 'Youngii'	Possible stop codon	Salojärvi *et al.* (2017)
Castanea mollissima var. *pendula*	Single recessive gene	Tu and Qiu (2007)
Malus	Four genomic regions, including a major locus Weeping (*W*) on chromosome13 and three others on chromosomes 10 (*W2*), 16 (*W3*), and 5 (*W4*).	Dougherty *et al.* (2017)
Morus alba 'Shidareguwa'	Single recessive gene	Yamanouchi *et al.* (2009)
Prunus mume	A locus within 1.14 cM on linkage group 7 strongly responsible	Zhang *et al.* (2015)
P. mume	Single recessive gene	Lv and Chen (2003)
P. persica	Single recessive gene *pl*	Monet *et al.* (1987)
P. persica	*brbr* epistatic to the expression of *plpl*	Werner and Chaparro (2005)
P. persica	Loss of *WEEP*, a highly evolutionarily conserved SAM domain protein, is a key factor in regulating branch orientation, which appears to act autonomously and/or downstream of gravitropic hrmone signaling pathways	Hollender *et al.* (2018)
P. persica	A deletion in gene *WEEP*	Hill and Hollender (2019)
P. spachiana	Failure of a hormonal-control system related to gibberellin	Nakamura *et al.* (1994)
Salix matsudana	Genes linked to auxin (*AUX1*, *ARF9* and *PIN3*) and GA (*GID1B* and *GAI*), and TFs (*SCL3* and *KNOX1*) associated with GA probably responsible	Liu *et al.* (2017)

a series of hybridization and backcrossing, Werner and Chaparro (2005) suggested that *brbr* was epistatic to the expression of *plpl*. In other words, the weeping phenotype is not only determined by *pl* gene, but the *br* gene may also prevent the *pl* gene being expressed even if it is homozygous. This adds more complexity to the weeping phenotype. Another allele, the *weep* (*we*) gene was discovered by Kitazawa *et al.* (2005, 2008) in a Japanese morning glory gravitropic mutant (*Ipomea nil*), which found that *WE1* and *WE2*, orthologs of *Arabidopsis SCR* and *SHR* are associated with the normal gravitropic responses for *Arabidopsis* (Kitazawa *et al.*, 2005, 2008).

Considering the partial weeping branch appearance on a upright branch, the archer trees may indicate that the *TILLER ANGLE CONTROL 1* (*TAC1*) gene works for the weeping in peach (Hollender and Dardick, 2015). *TAC1* gene is associated with upright tiller growth habit in rice genome (Yu *et al.*, 2007), and is from the IGT family, to which another *LAZY1* gene in rice belongs. *LAZY1* gene is a branch angle control gene related to shoot gravitropism (Yoshihara and Moritosh, 2007). When it was silenced in *Arabidopsis* by RNAi, a weak agravitropic response occurred (Fitzelle and Kiss, 2001). Besides, Joshi *et al.* (2011) detected suppressed expression of cellulose synthase genes in *Populus*. Cellulose is necessary for the formation of secondary cell wall, so the lack of cellulose results in altered wood composition. This would further explain the consequence of weeping habit (Hollender and Dardick, 2015).

Molecular markers developed for breeding program: Molecular markers are certain pieces of DNA sequence polymorphisms which associated with a particular gene or trait. They could be utilized to identify or to select this trait on conducting simple experimental tests on a small piece of plant tissue instead of the trait itself in molecular biology and biotechnology.

In *Prunus*, some molecular markers were proposed to indicate the weeping architecture in order to increase the product of orchard peach or accelerate the process of breeding for ornamental horticulture. Li (2006) suggested that the *BPPCT020* and the *CPPCT029* as SSR markers linked to the *pl* gene in *P. persica* var. *Pendula*. With the attempt to distinguish the pillar or broomy peach (*P. persica*) from the standard trees with an efficient breeding program, Sajer *et al.* (2012) developed an AFLP marker ETGM61_291T mapped with 4.8 cM to the *broomy* (*br*) gene on one side, which was mapped on linkage group 2 (LG2), and three other AFLP markers on the other side; among them, two STS markers were obtained by converting ETGM61_291R and ETAM48_279A. Besides, Zhang *et al.* (2015) developed ten SLAF markers on a 10.54–11.68 Mb region on the seventh chromosome of Mei (*P. mume*); nine of them may affect the formation of lignin, cellulose and cell walls, and they could be used to elucidate the weeping growth trait in Mei (Zhang *et al.*, 2015). Findings in other genus also implied the use of molecular markers for breeding weeping or archer trees. Liu (2011) has proposed two SRAP markers: me4Me1-160, me4Me1-120 to quickly elucidate the dwarf weeping phenotype in *Castanea mollissima* in order to cultivate them in a high density. These two markers correspond to the phenotype of group of backcross experiment and the weeping growth habit is controlled by an independent recessive gene.

Conclusion and Future Prospects

Weeping or archer tree architecture in certain genus such as *Betula*, *Castanea*, *Malus*, *Morus*, *Prunus* and *Salix* could be limited importance for ornamental species application compared with crop use. Trees with weeping architecture have been chosen and cultivated following a certain series of procedures for an ornamental purpose in history. The phenotype of weeping tree architecture is complicated, and it is determined by both genetic and environmental factors. Although the mechanism for weeping growth habit remains unclear, various hypothesises may partially explain this phenomenon, including genetic factors on molecular level along with physiological evidences. On molecular level, the

weeping architecture is relevant with a single recessive gene *pl* in *Castanea*, *Morus* and *Prunus*. Furthermore, these genes selected to be relevant to the weeping trait have been previously predicted to affect auxin or gibberellin pathways when forming stems in woody plants.

Along with morphological and genetic mechanism of weeping architecture, trees with potential weeping branches can be introduced to gardens with an ornamental use. Further research should focus on: (1) Analyzing and proving the functions of *WEEP* gene in different typical plant species with weeping trait such as *P. persica* and *P. mume*, using genetic engineering tools to foster transgenic plants; (2) Combining physiological parameters like hormone (auxin and gibberellin) level with molecular-level test results; (3) Exploring a series of branching parameters such as branch angle and orientation as well as gravitational set-point angle, to quantify the weeping trait for better describing morphological characteristics in woody plants.

Acknowledgements

References

Baba, K.I., K. Adachi, T. Take, T. Yokoyama, T. Itoh and T. Nakamura, 1995. Introduction of tension wood in GA$_3$-treated branches of the weeping type of Japanese cherry, *Prunus spachiana*. *Plant Cell Physiol.*, 36: 983–988

Bassi, D. and M. Rizzo, 2000. Peach breeding for growth habit. *Acta Hortic.*, 538: 411–414

Brown, C.L., 1971. *Trees: Structure and Function*, pp: 125–167. Springer-Verlag, New York, USA

Chen, J.Y., 2010. *Chinese Prunus Mume Cultivars*. China Forestry Publishing House, China. (in Chinese)

Cline, M.G., 1991. Apical dominance. *Bot. Rev.*, 57: 318–358

Dardick, C., A. Callahan, R. Horn, K.B. Ruiz, T. Zhebentyayeva, C. Hollender, M. Whitaker, A. Abbott and R. Scorza, 2013. *PpeTAC1* promotes the horizontal growth of branches in peach trees and is a member of a functionally conserved gene family found in diverse plant species. *Plant J.*, 75: 618–630

Digby, J. and R.D. Firn, 1995. The gravitropic set-point angle (GSA): the identification of an important developmentally controlled variable governing plant architecture. *Plant Cell Environ.*, 18: 1434–1440

Dougherty, L., R. Singh, S. Brown, C. Dardick and K.N. Xu, 2017. Exploring DNA variant segregation types in pooled genome sequencing enables effective mapping of weeping trait in *Malus*. *J. Exp. Bot.*, 69: 1499–1516

Fideghelli, C., A. Sartori and F. Grassi, 2003. Fruit tree size and architecture. *Acta Hort.*, 622: 279–293

Fitzelle, K.J. and Z. Kiss, 2001. Restoration of gravitropic sensitivity in starch-deficient mutants of *Arabidopsis* by hypergravity. *J. Exp. Bot.*, 52: 265–275

Hallé, F., R.A.A. Oldeman and P.B. Tomlinson, 1978. *Tropical Trees and Forests: an Architectural Analysis*. Springer-Verlag, New York, USA

Hill Jr., J.L. and C.A. Hollender, 2019. Branching out: new insights into the genetic regulation of shoot architecture in trees. *Curr. Opin. Plant Biol.*, 47: 73–80

Hollender, C.A. and C. Dardick, 2015. Molecular basis of angiosperm tree architecture. *New Phytol.*, 206: 541–556

Hollender, C.A., T. Pascal, A. Tabb, T. Hadiarto, C. Srinivasan, W.P. Wang, Z.C. Liu, R. Scorza and C. Dardick, 2018. Loss of a highly conserved sterile alpha motif domain gene (*WEEP*) results in pendulous branch growth in peach trees. *Proc. Natl. Acad. Sci. USA,* 115: E4690–E4699

Joshi, C.P., S. Thammannagowda, T. Fujino, J-Q. Gou, U. Avci, C.H. Haigler, L.M. McDonnell, S.D. Mansfield, B. Mengesha and N.C. Carpita, 2011. Perturbation of wood cellulose synthesis causes pleiotropic effects in transgenic aspen. *Mol. Plant*, 4: 331–345

Kitazawa, D., Y. Hatakeda, M. Kamada, N. Fujii, Y. Miyazawa, A. Hoshino, S. Iida, H. Fukaki, M.T. Morita and M. Tasaka, 2005. Shoot circumnutating and winging movements require gravisensing cells. *Proc. Natl. Acad. Sci. USA*, 102: 18742–18747

Kitazawa, D., Y. Miyazawa, N. Fujii, A. Hoshino, S. Iida, E. Nitasaka and H. Takahashi, 2008. The gravity-regulated growth of axillary buds is mediated by a mechanism different from decapitation-induced release. *Plant Cell Physiol.*, 49: 891–900

Lespinasse, J.M., 1980. *La Conduite du Pommier II: Publication du Centre Technique Interprofessionnel des Fruits et Légumes*. Paris, France

Li, Y.M., 2006. *Physiological Characteristics of Weeping Phenomenon and its Simple Sequence Repeats Analysis in Weeping Peach (Prunus persica var. Pendula),* pp: 54. College of Horticulture Science and Engineering, Shandong Agricultural University, Taian, China

Liu, J.J., Y.F. Zeng, P.C. Yan, C.Y. He and J.G. Zhang, 2017. Transcriptional and hormonal regulation of weeping trait in *Salix matsudana*. *Genes*, 8: E359

Liu, T., 2011. *Identification of Molecular Marker Linked to the Weeping Branch Trait of Castanea Mollissima and Molecular Assisted Breeding.* [D]. Beijing Forestry University, Beijing, China

Lv, Y.M. and J.Y. Chen, 2003. Preliminary report on the genetics of pendulous characteristics of *Prunus mume*. *J. Beijing For. Univ.*, 25: 43–46

Mason, M.G., J.J. Ross, B.A. Babst, B.N. Wienclaw and C.A. Beveridge, 2014. Sugar demand, not auxin, is the initial regulator of apical dominance. *Proc. Natl. Acad. Sci. USA,* 11: 6092–6097

Monet, R., Y. Bastard and B. Gibault, 1987. Étude génétique du caractère "port pleureur" chez pecher. *Agronomie*, 8: 127–132

Nakamura, T., M. Saotome, Y. Ishiguro, R. Itoch, S. Higurashi, M. Hosono and Y. Ishii, 1994. The effects of GA$_3$ on weeping of growing shoots of the Japanese cherry, *Prunus spachiana*. *Plant Cell Physiol.*, 35: 523–527

Nakamura, T., M. Saotome and H. Tanaka, 1995. Weeping habit and gibberellin in *Prunus*. *Acta. Hort.*, 394: 273–280

Sae, S.S., T. Mina and M. Hitoshi, 2009. Auxin-cytokinin interactions in the control of shoot branching. *Plant Mol. Biol.*, 69: 429–435

Sajer, O., R. Scorza, C. Dardick, T. Zhebentyayeva, A.G. Abbott and R. Horn, 2012. Development of sequence-tagged site markers linked to the pillar growth type in peach (*Prunus persica*). *Plant Breed.*, 131: 186–192

Salojärvi, J., O.P. Smolander, K. Nieminen, S. Rajaraman, O. Safronov, P. Safdari, A. Lamminmäki, J. Immanen, T.Y. Lan, J. Tanskanen, P. Rastas, A. Amiryousefi, B. Jayaprakash, J. Kammonen, R. Hagqvist, G. Eswaran, V.H. Ahonen, J.A. Serra, F.O. Asiegbu, J.D. Barajas-Lopez, D. Blande, O. Blokhina, T. Blomster, S. Broholm, M. Brosché, F.Q. Cui, C. Dardick, S. Ehonen, P. Elomaa, S. Escamez, K.V. Fagerstedt, H. Fujii, A. Gauthier, P.J. Gollan, P. Halimaa, P. Heino, K. Himanen, C. Hollender, S. Kangasjärvi, L. Kauppinen, C.T. Kelleher, S. Kontunen-Soppela, J.P. Koskinen, A. Kovalchuk, S. Kärenlampi, A. Kärkönen, K.J. Lim, J. Leppälä, L. Macpherson, J. Mikola, K. Mouhu, A.-P. Mähönen, Ü. Niinemets, T. Oksanen, K. Overmyer, E.T. Palva, L. Pazouki, V. Pennanen, T. Puhakainen, P. Poczai, B.J.H.M. Possen, M. Punkkinen, M. Rahikainen, M. Rousi, R. Ruonala, C. van der Schoot, A. Shapiguzov, M. Sierla, T.P. Sipilä, S. Sutela, T.H. Teeri, A.I. Tervahauta, A. Vaattovaara, J. Vahala, L. Vetchinnikova, A. Welling, M. Wrzaczek, E.J. Xu, L. Paulin, A.H. Schulman, M. Lascoux, V.A. Albert, P. Auvinen, Y. Helariutta and J. Kangasjärvi, 2017. Genome sequencing and population genomic analyses provide insights into the adaptive landscape of silver birch [J]. *Nat. Genet.*, 49: 904–912

Sasaki, A., M. Ashikari, M. Ueguchi-Tanaka, H. Itoh, A. Nishimura, D. Swapan, K. Ishiyama, T. Saito, M. Kobayashi, G.S. Khush, H. Kitano and M. Matsuoka, 2002. Green revolution: a mutant gibberellin-synthesis gene in rice. *Nature*, 416: 701–702

Srivastava, L.M., 2002. *Plant Growth and Development: Hormones and Environment*. Elsevier Sci. USA

Sugano, M., Y. Nakagawa, H. Nyunoya and T. Nakamura, 2004. Expression of gibberellin *3-beta-hydroxylase* gene in a gravi-response mutant, weeping Japanese flowering cherry. *Biol. Sci. Space*, 18: 261–266

Tomlinson, P.B., 1983. Tree architecture: New approaches help to define the elusive biological property of tree form. *Amer. Sci.*, 71: 141–149

Tu, S.P. and F.X. Qiu, 2007. The character display of *Castanea mollissima* var. *pendula* sexual progenies. *Acta Hort. Sin.*, 34: 760–762

Tworkoski, T. and R. Scorza, 2001. Root and shoot characteristics of peach trees with different growth habits. *J. Amer. Soc. Hort. Sci.*, 126: 785–790

Wang, B., S.M. Smith and J.Y. Li, 2018. Genetic regulation of shoot architecture. *Annu. Rev. Plant Biol.*, 69: 25.1–25.32

Wang, Y.H. and J.Y. Li, 2008. Molecular basis of plant architecture. *Annu. Rev. Plant Biol.*, 59: 253–279

Werner, J.D. and J.X. Chaparro, 2005. Genetic interactions of pillar and weeping peach genotypes. *Hort. Sci.*, 40: 18–20

Wickson, M. and K.V. Thimann, 1958. The antagonism of auxin and kinetin in apical dominance. *Physiol. Plantarum*, 11: 62–74

Wilson, B.F., 2000. Apical control of branch growth and angle in woody plants. *Amer. J. Bot.*, 87: 601–607

Yamanouchi, H., A. Koyama, H. Machii, T. Takyu and N. Muramatsu, 2009. Inheritance of a weeping character and the low frequency of rooting from cuttings of the mulberry variety 'Shidareguwa'. *Plant Breed.*, 128: 321–323

Yamazaki, K., M. Okabe and E. Takahashi, 1987. Inheritance of some characteristics and breeding of new hybrids in flowering peaches. *Kanazawa Enshi Kempo*, 34: 46–53

Yoshida, M., H. Yamamoto, T. Okuyama and T. Nakamura, 1999. Negative gravitropism and growth stress in GA$_3$-treated branches of *Prunus spachiana* Kitamura f. *spachiana* cv. Plenarosea. *J. Wood Sci.*, 45: 368–372

Yoshihara, T. and I. Moritoshi, 2007. Identification of the gravitropism-related rice gene *LAZY1* and elucidation of *LAZY1*-dependent and -independent gravity signaling pathways. *Plant Cell Physiol.*, 48: 678–688

Yoshihara, T., E.P. Spalding and M. Ilino, 2013. *AtLAZY1* is a signaling component required for gravitropism of the *Arabidopsis thaliana* inflorescence. *Plant J.*, 74: 267–279

Yu, B., Z. Lin, H. Li, J. Li, Y. Wang, X. Zhang, Z. Zhu, W. Zhai and X. Wang, 2007. *TAC1*, a major quantitative trait locus controlling tiller angle in rice. *Plant J.*, 52: 891–898

Zhang, J., Q.X. Zhang, T.R. Cheng, W.R. Yang, H.T. Pan, J.J. Zhong, L. Huang and E.Z. Liu, 2015. High-density genetic map construction and identification of a locus controlling weeping trait in an ornamental woody plant (*Prunus mume* Sieb. et Zucc). *DNA Res.*, 22: 183–191