

1 **Meeting Report: Plant Vascular Biology 2013:**
2 **Vascular trafficking**

3
4 **Robertas Ursache^{1,*}, Jung-ok Heo^{1,*} and Ykä Helariutta^{1,#}**

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6 ¹ Institute of Biotechnology/Department of Bio and Environmental Sciences, University
7 of Helsinki, FIN-00014, Finland

8 * These authors contributed equally to this work.

9 #To whom correspondence should be addressed. E-mail: yrjo.helariutta@helsinki.fi

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12 **Abstract**

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14 About 200 researchers from around the world attended the Third International
15 Conference on Plant Vascular Biology (PVB 2013) held in July 2013 at the Rantapuisto
16 Conference Center, in Helsinki, Finland (<http://www.pvb2013.org>). The plant vascular
17 system, which connects every organ in the mature plant, continues to attract the
18 interest of researchers representing a wide range of disciplines, including development,
19 physiology, systems biology and computational biology. At the meeting, participants
20 discussed the latest research advances in vascular development, long and short
21 distance vascular transport and long-distance signaling in plant defense, in addition to
22 providing a context for how these studies intersect with each other. The meeting
23 provided an opportunity for researchers working across a broad range of fields to share
24 ideas and to discuss future directions in the expanding field of vascular biology. In our
25 report, we summarize the latest advances in understanding the mechanism of vascular
26 trafficking presented at the meeting.

27

28 **Key words:** Plant Vascular Biology 2013, vascular development, vascular trafficking,
29 phloem transport, plasmodesmata.

30

31 **Introduction**

32

33 The plant vascular system serves as the main route for long- and short distance
34 transport of various compounds throughout the plant body as well as a means of long-
35 distance communication (Fig. 1). It consists of two major tissues types – xylem, which

36 conducts water and nutrients, and phloem, which transports mainly organic
37 compounds. Over the last decade, significant progress has been made in
38 understanding how the vascular system forms and functions, and important new
39 findings in this regard were presented at the PVB 2013 meeting. Despite remarkable
40 progress in understanding the formation of vascular tissues, one of the central
41 questions discussed during the conference was how various signals are transported via
42 the vascular tissues to orchestrate various biological processes throughout the plant
43 with such precision. In this brief report, we highlight some of the answers provided
44 during the PVB 2013 meeting.

45

46 **Long Distance Communication – Signaling Dynamics**

47

48 In this session, molecular mechanisms which enable long-distance trafficking of
49 macromolecules were presented, with a focus on the non-cell-autonomous function of
50 those molecules.

51 Phloem is a major intermediary tissue through which many molecules move, including
52 signaling molecules (De Lucas and Brady, 2013) (Fig. 1). Its structural property as a
53 conduit was emphasized by Noll Gundula (University of Münster, Germany). He
54 highlighted the functional differences between phloem proteins (p-proteins) and
55 forisomes. Both are encoded by the same sieve occlusion gene family (SEO) which
56 plays an important role in rapid wound sealing. (Ernst *et al.*, 2012; Ernst *et al.*, 2011;
57 Froelich *et al.*, 2011; Jekat *et al.*, 2013). William Lucas and his colleague Ham Byung-
58 kook (University of California, Davis, USA) shed light on the mechanism of phloem-
59 mobile RNA translocation in cucurbits. Exploiting the histological advantages of phloem
60 sap extraction, they demonstrated that the ribonucleoprotein (RNP) complex, an
61 assembly between phloem-specific mobile RNAs and RNA-binding proteins (RBPs),
62 mediates the cell-to-cell trafficking of RNA species (Li *et al.*, 2011). They have
63 previously shown that the *Cucurbita maxima* RNA-binding protein 50 (CmRBP50)
64 requires phosphorylation of its C-terminal serine residue for the establishment of a
65 stable RNP complex (Li *et al.*, 2011). As an extension of this discovery, they presented
66 an advanced regulatory mechanism of long-distance trafficking of phloem small-RNAs,
67 additionally highlighting the biological meaning of this communication in terms of gene
68 silencing. With regard to gene silencing, a presentation by Chiou Tzyy-Jen (Academia
69 Sinica, Taiwan) gave us a new insight into how mobile microRNA is involved in the

70 maintenance of phosphate (Pi) homeostasis. Previous work has shown that miR399
71 plays an important role in the maintenance of Pi homeostasis by negatively regulating
72 the expression of PHO2, a ubiquitin-conjugating E2 enzyme 24 (UBC24) (Aung *et al.*,
73 2006; Chiou *et al.*, 2006). In her talk, Tzyy-Jen proposed that initial upregulation of
74 miRNA399 occurs in the shoot under Pi deficient conditions. Rootward movement of
75 miR399 via phloem then results in the cleavage of PHO2 transcripts in the root,
76 stimulating both Pi uptake from the roots and shootward translocation of Pi (Lin *et al.*,
77 2008; Pant *et al.*, 2008). Their recent studies identified PHO1 and several
78 PHOSPHATE TRANSPORTER1 (PHT1) proteins as the downstream targets of PHO2
79 in this regulatory pathway (Huang *et al.*, 2013; Liu *et al.*, 2012).

80 The importance of auxin transport as a major morphogenetic signal in plants was
81 revisited by Ottoline Leyser (Sainsbury Laboratory University of Cambridge, UK).
82 Continuous growth in plants is primarily dependent on the activity of meristems located
83 at the tip of the root and shoot. Long distance source-to-sink transport of auxin has
84 been proposed to play a critical role in coordinating the activity of meristems and
85 systemic growth in general. This coordination process is exemplified by the formation of
86 a vascular connection between axillary buds and the main stem (Domagalska and
87 Leyser, 2011). In her keynote address, Leyser provided a comprehensive overview of
88 bud activation, focusing especially on the role of the spatiotemporal regulation of auxin
89 transport dynamics.

90 The research presented in this meeting reflected the increasing use of micrografting as
91 a technique to dissect and understand long distance transport of signals between the
92 shoot and root. An example of the successful application of this technique was provided
93 during Leslie Sieburth's (University of Utah, USA) talk, where she presented a
94 mechanism for the coordination of shoot growth and development by a signal derived
95 from the root. It has been previously reported that the *Arabidopsis bypass 1 (bps1)*
96 mutant root produces a mobile *bps1* signal (Adhikari *et al.*, 2013; Van Norman *et al.*,
97 2011) that functions in the shoot to arrest its growth. As an extension of this discovery,
98 Sieburth provided evidence that the mobile *bps1* signal is also involved in maintenance
99 of the shoot apical meristem (SAM).

100

101 **Mechanisms and dynamics of vascular trafficking**

102

103 Drought obviously has a major impact on water uptake by plants and the conductive
104 properties of their vascular system. Despite significant progress in understanding how

105 plants tolerate drought, the mechanisms by which trees react to the drought remain
106 elusive. Drought leads to impaired water transport from the soil to the leaves via the
107 xylem and thus results in plant mortality via hydraulic failure (McDowell *et al.*, 2008;
108 Sperry *et al.*, 1998). However, there have been very few reports about what happens in
109 the phloem in response to drought. Sanna Sevanto (Los Alamos National Laboratory,
110 USA) and colleagues showed that a loss of both conductivity and carbohydrate
111 reserves can coincide in trees during drought. Furthermore, the loss of turgor in
112 phloem restricts access to carbohydrate reserves while hydraulic control of respiration
113 prolongs survival. These studies indicate that phloem plays a key role in drought-
114 related mortality, although the exact cascade of events at the cellular level is a question
115 which remains to be addressed.

116 Sucrose is the major transport form of carbohydrates in plants; it is transported from the
117 sites of production in the leaves to sink tissues via the tube-like phloem network (Van
118 Bel, 2003). This network is interconnected via plasmodesmata. As demonstrated
119 previously, the flux and direction of sucrose is controlled by SUC/SUT type sucrose
120 transporters (Aoki *et al.*, 2003; Riesmeier *et al.*, 1993; Sauer, 2007; Sauer and Stolz,
121 1994; Slewinski *et al.*, 2009), proton-driven sucrose transporters that play an essential
122 role in cell-to-cell and long-distance distribution of sucrose within the plant body.
123 Conformational changes in these transporters accompanying the transport of sucrose
124 were previously observed (Carpaneto *et al.*, 2010). Furthermore, Dietmar Geiger
125 (University Würzburg, Germany) and coworkers are investigating the mechanisms of
126 reaction cycle of sucrose transporters – the binding of protons to the carrier and its
127 effect on the protein trafficking.

128 Continuing on the theme of sucrose transport, David Braun (University of Missouri,
129 USA) discussed how important it is to understand the molecular mechanisms of carbon
130 partitioning, the process by which photoassimilates are transported from their site of
131 synthesis in the leaves to the rest of the plant body. Although several studies have
132 demonstrated that the control of carbon partitioning is essential for plant growth and
133 development, an understanding of the genetic control of carbon partitioning remains
134 elusive. The aforementioned sucrose transporters (SUTs) are the best known genes
135 that directly load sucrose into the phloem (Lalonde *et al.*, 2004; Sauer, 2007).
136 Characterization of all SUT family members will open up new directions of investigation
137 into the control of carbon partitioning in plants. Furthermore, it will allow the
138 development of new tools for biotechnological approaches to enhance crop yield and
139 biofuel production (Slewinski *et al.*, 2009).

140 The osmotically active transport of sugars via phloem is a key process in phloem
141 function (Ayre, 2011) because it leads to the creation of the hydrostatic pressure
142 gradient between source and sink, the mechanism postulated by (Münch, 1930) to
143 drive the mass flow of phloem sap. Phloem transport is already known to be controlled
144 by an active loading step between bundle sheath cells (BSCs) and the sieve element
145 companion cell complex (SECCC). The abundance of cell connections between the
146 BSC and SECCC determines whether phloem loading will be symplasmic or
147 apoplasmic (Liesche and Schulz, 2012). Alexander Schulz (University of Copenhagen,
148 Denmark) and colleagues are investigating the conversion of diffusional pre-phloem
149 transport into bulk flow via symplastic loaders. Their findings suggest an important role
150 for cell-specific water accessibility along the pre-phloem pathway that needs further
151 investigation.

152 Nitrogen is one the most important nutrients for plants and serves as a major precursor
153 of such critical compounds as chlorophyll, nucleic acids and amino acids. Lack of
154 nitrogen severely affects plant metabolism and growth. Following uptake, nitrogen is
155 immediately used in metabolism, transiently stored, or transported via the vasculature
156 to sink tissues by a large number of well-described nitrogen transporters (Rentsch *et*
157 *al.*, 2007). Several studies suggest that these transporters play an important role in
158 organic nitrogen uptake, source-to-sink transport, and sink loading for growth and
159 development. Mechthild Tegeder (Washington State University, USA) discussed the
160 identification and characterization of transport processes controlling the partitioning of
161 organic nitrogen between source and sink. She demonstrated that cellular import
162 systems are essential for the partitioning of nitrogen at the scale of the whole plant
163 body. In addition, she provided data demonstrating the importance of nitrogen
164 transporters as key regulators of plant metabolism, growth and development (Tegeder,
165 2012; Tegeder and Rentsch, 2010).

166 Michael Knoblauch (Washington State University, USA) highlighted the importance of
167 sieve tube structure and its impact on long distance transport. Sieve tube structure has
168 a major impact on transport and unloading; however, questions concerning the basic
169 structure and function of sieve tubes remain unanswered due to their inaccessibility and
170 sensitivity to injury. The detailed structure of sieve plates has been previously
171 investigated by using scanning electron microscopy (Mullendore *et al.*, 2010). These
172 studies provided vital insight into the geometry of pores, plates and sieve elements.
173 New methods to investigate sieve tubes based on *in vivo* high resolution microscopy

174 were discussed, together with the role of phloem proteins encoded by the sieve
175 element occlusion gene family.

176 An earlier study performed by Carel Windt and colleagues (Forschungszentrum Jülich,
177 Germany) in tomato truss demonstrated that most water transport occurs via the xylem
178 (Windt *et al.*, 2009). This was determined with the help of Magnetic Resonance Imaging
179 (MRI) flowmetry, which provides information not only about the volume of the flow but
180 also flow conducting area and average linear velocity (Windt *et al.*, 2006). Carel Windt
181 is using this technique in various plant species to investigate what fraction of the xylem
182 cross-sectional area conducts water flow.

183 A novel technique to analyze the three-dimensional xylem network of *Arabidopsis* was
184 presented by Ildoo Hwang (Pohang University of Science and Technology, Korea).
185 Based on this technique, a flexible framework of the xylem network for water
186 management with multiple layers of regulation was proposed. Such a framework may
187 explain how hydraulic regulation is accomplished at the whole-plant level.

188

189 **The role of plasmodesmata in vascular trafficking**

190

191 Neighboring plant cells communicate with each other via symplastic transport through
192 the plasmodesmata (PDs) or via the extracellular apoplastic space. PDs are
193 microscopic plasma membrane-lined channels which traverse the cell wall of adjacent
194 cells allowing the movement of various molecules through the symplastic space (Burch-
195 Smith *et al.*, 2011; Cilia and Jackson, 2004; Lucas *et al.*, 2009; Maule, 2008; Oparka
196 and Roberts, 2001; Sevilem *et al.*, 2013). Despite their role in plant development,
197 physiology and defense, the mechanism and regulation of trafficking through
198 plasmodesmata remains poorly understood. A new perspective on the role of PD in the
199 transport of sugars and amino acids was presented by Sylvie Dinant (INRA, France)
200 during the PVB 2013 meeting. Sylvie Dinant and her colleagues described the role of
201 NHL26, a phloem protein targeted to the PD, in regulating PD permeability, which
202 affects sugar signaling at the interface between companion cells and sieve elements.
203 Overexpression of *NHL26* leads to slow growth, accumulation of carbohydrates in
204 leaves, higher shoot biomass and defects in sugar export. These data suggest that
205 *NHL26* plays an important role in the regulation of plasmodesmata permeability and
206 sugar signaling in companion cells (Vilaine *et al.*, 2013).

207 Cell-to-cell signaling has been shown to play a critical role in the response to various
208 environmental changes, including plant defense. Before an immune signal spreads

209 throughout the plant body, local cell-cell signaling is required to confine the infection.
210 During this process, PD undergo various structural modifications. Several studies have
211 demonstrated that the permeability, dilation, or structure of PD can be altered in
212 response to infection by microbial pathogens (Benitez-Alfonso *et al.*, 2010; Carpaneto
213 *et al.*, 2010; Schoelz *et al.*, 2011; Ueki and Citovsky, 2011). Jung-Youn Lee (University
214 of Delaware, USA) presented evidence for the role of salicylic acid (SA) signaling
215 components in regulating cell-to-cell connectivity. Application of SA leads to increased
216 callose deposition at the PD and subsequent closure, a response which requires the
217 presence of plasmodesmata-located protein, PDLP5. Mutations in SA signal
218 transduction cause PD closure upon infection by bacterial pathogens. These data
219 suggest that the crosstalk between PDLP5 and the SA signaling pathway plays a
220 critical role in regulating PD permeability upon bacterial pathogen attack (Lee *et al.*,
221 2011; Wang *et al.*, 2013).

222 Kay Schneitz (Technische Universität München, Germany) presented an interesting
223 talk about the role of the kinase STRUBBELIG in regulating inter-cell-layer
224 communication and tissue morphogenesis. In *Arabidopsis*, the atypical transmembrane
225 leucine-rich repeat receptor-like (LRR-RLK) *STRUBBELIG* (*SUB*) has been shown to
226 be critical for a number of developmental processes (Chevalier *et al.*, 2005; Fulton *et*
227 *al.*, 2009; Kwak *et al.*, 2005; Vaddepalli *et al.*, 2011; Yadav *et al.*, 2008). *SUB* functions
228 in a non-cell-autonomous manner to mediate inter-cell-layer signaling across cell layers
229 in the ovule, the floral meristem (Yadav *et al.*, 2008), and the root (Kwak and
230 Schiefelbein, 2008). The three *STRUBBELIG*-LIKE MUTANT (*SLM*) genes
231 *ANGUSTIFOLIA* (*AN*), *QUIRKY* (*QKY*) and *ZERZAUST* (*ZET*) are considered central
232 players in *SUB*-mediated signal transduction pathways, as the phenotype of these
233 mutants is similar to *sub* mutants in certain respects.

234 Short range cell-to-cell communication in plants involves the selective trafficking of
235 various transcription factors through PD. For example the *KNOTTED1* (*KN1*)
236 homeobox (*KNOX*) family transcription factors and are essential for stem cell
237 establishment and maintenance and use the PD pathway (Bolduc *et al.*, 2008; Kim *et*
238 *al.*, 2002b; Lucas *et al.*, 1995; Xu *et al.*, 2011). David Jackson and coworkers showed
239 that *KN1* trafficking requires the chaperonins, a group of cytosolic chaperones which
240 are necessary to fold specific substrate proteins. Chaperonins are known to be
241 essential for the cell-to-cell trafficking of a subset of mobile transcription factors, and a
242 critical role for chaperonin-dependent protein trafficking has also been demonstrated in
243 plant stem cell function (Xu *et al.*, 2011). Currently, David Jackson and colleagues are

244 investigating the mechanisms by which chaperonins mediate plasmodesmal transport.
245 These studies may lead to the discovery of new genes controlling trafficking through
246 the PD.

247 The symplastic movement of various signaling molecules through the PD has been
248 shown to play an important role in some developmental programs, including embryonic
249 cell fate and postembryonic organ development (Chevalier *et al.*, 2005; Kim *et al.*,
250 2002a; Nakajima *et al.*, 2001; Xu and Jackson, 2010; Xu *et al.*, 2011). Beyond the well-
251 studied role of hormones, the mechanisms that define lateral root architecture remain
252 poorly understood. Yoselin Benitez-Alfonso (University of Leeds, United Kingdom) and
253 colleagues demonstrated that symplastic connectivity plays a critical role in initiating
254 lateral root meristems and determining their position. This connectivity is regulated by
255 PD-localized glucanases, which control callose accumulation and molecular trafficking
256 through PD. This discovery represents a great step forward in our understanding of
257 lateral root formation (Benitez-Alfonso *et al.*, 2013).

258 Another process where cell-to-cell communication through plasmodesmata plays a
259 critical role is dormancy in trees. Earlier studies in trees showed that PD undergo
260 structural modifications in response to a short photoperiod, resulting in a lower size
261 exclusion limit of PD in the SAM (Rinne *et al.*, 2001; Ruonala *et al.*, 2008).
262 Consequently, after the buds are formed, the SAM shifts into a dormant state by closing
263 the PD in all its cells via callose deposition (Rinne *et al.*, 2001; Rinne and van der
264 Schoot, 1998; Ruonala *et al.*, 2008). When the early winter chill comes, it results in the
265 SAM shifting from its disconnected dormant state to a reconnected quiescent state, at
266 the same time as it increases its freezing-tolerance. Christiaan van der Schoot and
267 colleagues (Norwegian University of Life Sciences, Norway) identified a group of genes
268 that are critical for the transition between the two phases. These genes are members of
269 the GH17 family of carbohydrate-active 1,3-beta-glucanases, which are enzymes that
270 degrade PD-callose. Their expression is controlled by several factors, such as day
271 length, temperature and genes involved in gibberellic acid biosynthesis and signaling
272 (Rinne *et al.*, 2011).

273 Jae-Yean Kim (Gyeongsang National University, Korea) showed that callose deposition
274 plays an important role in establishing PIN-driven auxin gradients.

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276 **Gene regulatory networks in vascular development**

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278 The establishment of proper tissue layers is a prerequisite for intercellular trafficking.
279 With regard to this issue, an entire session was allocated to vascular development.
280 Siobhan Brady (UC Davis, USA) presented a global-scale view of genetic regulatory
281 networks in root vascular development, focusing especially on cell type specification
282 (De Lucas and Brady, 2013). Ji-Young Lee (Seoul National University, Korea) proposed
283 a genetic regulatory mechanism by which xylem cells are distinguished from the
284 procambium domain. She presented two mobile transcription factors from an AT-hook
285 family transcription factor, *AHL3* (*AT-HOOK MOTIF NUCLEAR LOCALIZED PROTEIN*
286 *3*) and *AHL4*. According to the proposed model, the movement of *AHL4* from the
287 procambium to the xylem plays a key role in establishing tissue boundaries in the root
288 meristem. In particular, the protein complex of *AHL4* and *AHL3* was shown to propel
289 *AHL4* movement (Zhou *et al.*, 2013), implying an intriguing regulatory mechanism
290 between transcription factors.

291 Plant hormones and their signaling pathways have been considered as a major
292 controller of vascular cell division and specification (De Lucas and Brady, 2013), an
293 issue that was addressed by several talks in the session. For example, Hiroo Fukuda
294 (University of Tokyo, Japan) proposed a model integrating brassinosteroid (BR)
295 signaling into vascular stem cell fate determination. It has been previously shown that
296 the TDIF-TDR (Tracheary Element Differentiation Inhibitory Factor-TDIF Receptor)
297 pathway plays a role in vascular stem cell maintenance. *WOX4*, in particular, is known
298 to be a key gene involved in promoting cell proliferation in the procambium and
299 cambium as a positive regulator of the TDIF-TDR pathway (Hirakawa *et al.*, 2010).
300 Fukuda showed that BR signaling functions in conjunction with the TDIF-TDR-*WOX4*
301 signal in determining vascular stem cell fates, with the two pathways sharing a common
302 target.

303

304 **Biotic plant interactions**

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306 The importance of plants' response to biotic stimuli was evinced by several talks in this
307 session. Speakers presented the result of research into the process of infection by root-
308 knot nematodes and plant responses to this invasion. Upon invasion by root-knot
309 nematodes, giant cells are formed in the stele of host roots. Since these cells later
310 serve as feeding sites, it has been proposed that the formation of vascular tissues
311 around them and sustained vascular continuity are critical for the survival of the
312 nematodes (Absmanner *et al.*, 2013). Ulrich Hammes (Regensburg University,

313 Germany) provided evidence that the vascular tissues encircling the giant cells are
314 actively dividing protophloem. In combination with his results, Derek Goto (Hokkaido
315 University, Japan) showed various mutants that repress the nematode infection and
316 proposed a genetic regulatory mechanism involved in nematode infection, focusing on
317 the initial events in particular.

318 Long-distance signal trafficking serves as a pivotal mechanism for the communication
319 between plant and bacteria. For instance, legume species that host rhizobacteria adopt
320 an auto-regulatory mechanism controlling nodulation as a part of stable symbiotic
321 relationship (Reid *et al.*, 2013). In this meeting, Peter Gresshoff (University of
322 Queensland, Australia) introduced the CLAVATA1-like receptor kinase in soybean,
323 which is responsible for the systemic regulation of nodulation. Dubbed GmNARK
324 (Nodulation Auto-regulation Receptor Kinase), this kinase was previously found to
325 interact with the CLE peptides (CLV3-related peptides) (Lim *et al.*, 2011; Reid *et al.*,
326 2011). Of the three CLE peptides in soybean – GmRIC1, GmRIC2, and GmNIC1 –
327 GmRIC1 and GmRIC2 were shown to interact with GmNARK in the shoot, inducing the
328 shoot-derived inhibitor (SDI) signal which subsequently regulates nodulation in the root.
329 It was also proposed that the CLE domain has nodulation suppression residues that are
330 crucial for long-distance signal transmission (Reid *et al.*, 2013). However, the
331 underlying mechanism behind this is still unclear.

332 Pradeep Kachroo (University of Kentucky, USA) shared his research on unraveling the
333 signaling pathways that control defense responses in plants. He highlighted the role of
334 several components of the systemic acquired resistance (SAR) pathway, including the
335 nine carbon dicarboxylic acid azelaic acid (AA), the phosphorylated sugar glycerol-3-
336 phosphate (G3P), and two lipid transfer proteins DIR1 (Defective in Induced
337 Resistance) and AZI1 (AA insensitive). SAR has been observed in a variety of flowering
338 plants and can be induced by a broad spectrum of pathogens. Experimental evidence
339 was presented demonstrating that a feedback regulatory loop involving G3P, DIR1, and
340 AZI1 regulates the precise induction of the SAR (Glover and Kachroo, 2013; Kachroo
341 and Robin, 2013; Yu *et al.*, 2013). Cyril Zipfel (The Sainsbury Laboratory, UK)
342 presented evidence of an antagonistic interaction between BR signaling and the innate
343 immune response in plants. Plant immunity is primarily triggered via the recognition of a
344 pathogen-associated molecular pattern (PAMP) by surface-localized pattern-
345 recognition receptors (PRRs). The interplay between BR signaling and the immune
346 response was demonstrated on the grounds that BR signaling can inhibit PRRs-
347 mediated immune signaling (Albrecht *et al.*, 2012).

348 Aart van Bel (University of Giessen, Germany) highlighted the effect of early biotic and
349 abiotic stimuli on the gating of Ca²⁺-permeable channels. As described earlier by Aart
350 van Bel and colleagues, infection of plants by phytoplasma, bacteria that are obligate
351 parasites of phloem, results in Ca²⁺ influx into phloem sieve tubes, leading to callose
352 deposition and sieve plate occlusion. In addition, phytoplasma infection may cause
353 gating of sieve-element Ca²⁺ channels, leading to sieve-tube occlusion with consequent
354 dramatic effects on both the spread of the infection and photoassimilate distribution
355 (Musetti *et al.*, 2013). Moreover, various injuries initiate longitudinal electrical waves
356 which also enhance Ca²⁺ concentration in sieve elements by altering the gating of Ca²⁺
357 channels in the plasma membranes. The passage of an electrical wave associated with
358 calcium influx leads to a temporary reorganization of the phloem symplasm. Lateral
359 waves of calcium influx and the symplasmic reorganization may trigger the production
360 of an arsenal of long-distance messages ranging from phytohormones to
361 macromolecules in vascular cells along the sieve tubes (van Bel *et al.*, 2011a; van Bel
362 *et al.*, 2011b).

363

364 **Concluding remarks**

365

366 Significant progress has been made in the past several years in the area of plant
367 vascular biology. A number of recent insights into the molecular mechanisms
368 controlling vascular patterning, trafficking and biotic interactions were presented during
369 the meeting. At the same time, it illustrated our need to understand the integration of
370 these processes to control plant growth and development. We noticed a growing
371 interest in understanding long and short distance communication and its impact on
372 vascular tissue formation. These studies will greatly contribute to biotechnologies that
373 can improve agricultural performance. Overall, it was a truly productive meeting, and
374 we look forward to the next Plant Vascular Biology meeting which will be held in China
375 in 2016.

376

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390 **Fig. 1.** Representative image of vascular trafficking. The whole plant image in the
391 middle demonstrates long-distance signal trafficking. Arrowheads indicate source-to-
392 sink translocation of signaling molecules either through phloem (blue arrows) or xylem
393 (pink arrows). Symplastic communication between sieve elements and companion cells
394 is marked with green arrows in the magnified phloem image.

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