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-Mini Review-

Pioneering work of Anton Karsch (1822-1892) suggesting the role for intercellular space in plant tissue as the path for cell-cell communication during plant-pathogen interaction

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Abstract

Recently, we have described in two independent articles that a pioneering work of Anton Karsch (1822-1892) who is known as a medical doctor (internist), an ecologist, a plant collector, a microbiologist, an early cell biologist, and an philosopher. Anton Karsch, published in 1855, a work suggesting the role for intercellular space in plant tissue as the paths for spread of pathogenic microorganisms and also for cell-cell communication required for combatting the invading pathogenic microorganisms. It is also noteworthy that the entrance of air-borne spores of pathogenic fungus into the leafy tissue through the opening stomata which is recently studied by plant cell biologists, has been already described by Karsch. This short article briefly introduces the key works of Karsch from the view point by plant biologists of today.

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Keywords: Anton Karsch, intercellular space, microscope, *Phytophthora infestans*, plant cell, plant immunity, stomata, thing-in-itself (ding an sick)

1. Introduction—Pieces of Westphalia

All truly wise thoughts have been thought already;
we must think them over again honestly

Johann Wolfgang von Goethe

In our life, we often face the situation that a newly invented idea has been already proposed and tested by someone else in the past, in a similar or different form. In this short article, we describe such story we experienced in our plant biological research finding and shocked by a similarity between the recently proposed plant pathological model and a classical proposal.

Anton Karsch (formally, Anton Ferdinand Franz Karsch, but authored most of articles and books as Dr. Karsch; June, 19th, 1822—March, 15th, 1892) is known as (i) a medical doctor (internist), (ii) an ecologist, (iii) a plant collector, (iv) a microbiologist, (v) an early cell biologist, and (vi) an philosopher born and lived in Germany. His life was dedicated to collect the natural pieces of the region of Westphalia (Westfalen). The works of Karsch as a locally acted ecologist based in the region of Westphalia is well recognized among the scholars and his book focusing on the biota (especially flora) in Westphalia is still revived and available today (Fig. 1).

Recently, in two independent articles both in Japanese (Kawano, 2013) and in English (Kawano and Bouteau, 2013), we have introduced a series of works of Karsch documented in 1855. The works of Karsch appeared as seven different articles in the first issue of the first volume of a German journal of science and philosophy, “Natur und Offenbarung” (Nature and Revelation), widely covering various area including biology and philosophy. In fact, Karsch was one of four founding editors of “Natur und Offenbarung” which continued for 36 years since February 1855. Note that the launch of this interdisciplinary science journal in Germany covering astronomy, geology, electronic communication, botany, medicine and philosophy, actually precede those of “Nature” in United Kingdom (1869) and Science in United States (1880).

As we have obtained the first volume of “Natur und Offenbarung” in the city of Bonn in December, 2006, original copies of “Natur und Offenbarung” are preserved and circulated in the market today. More conveniently, digitalized versions became partly available online (URL:

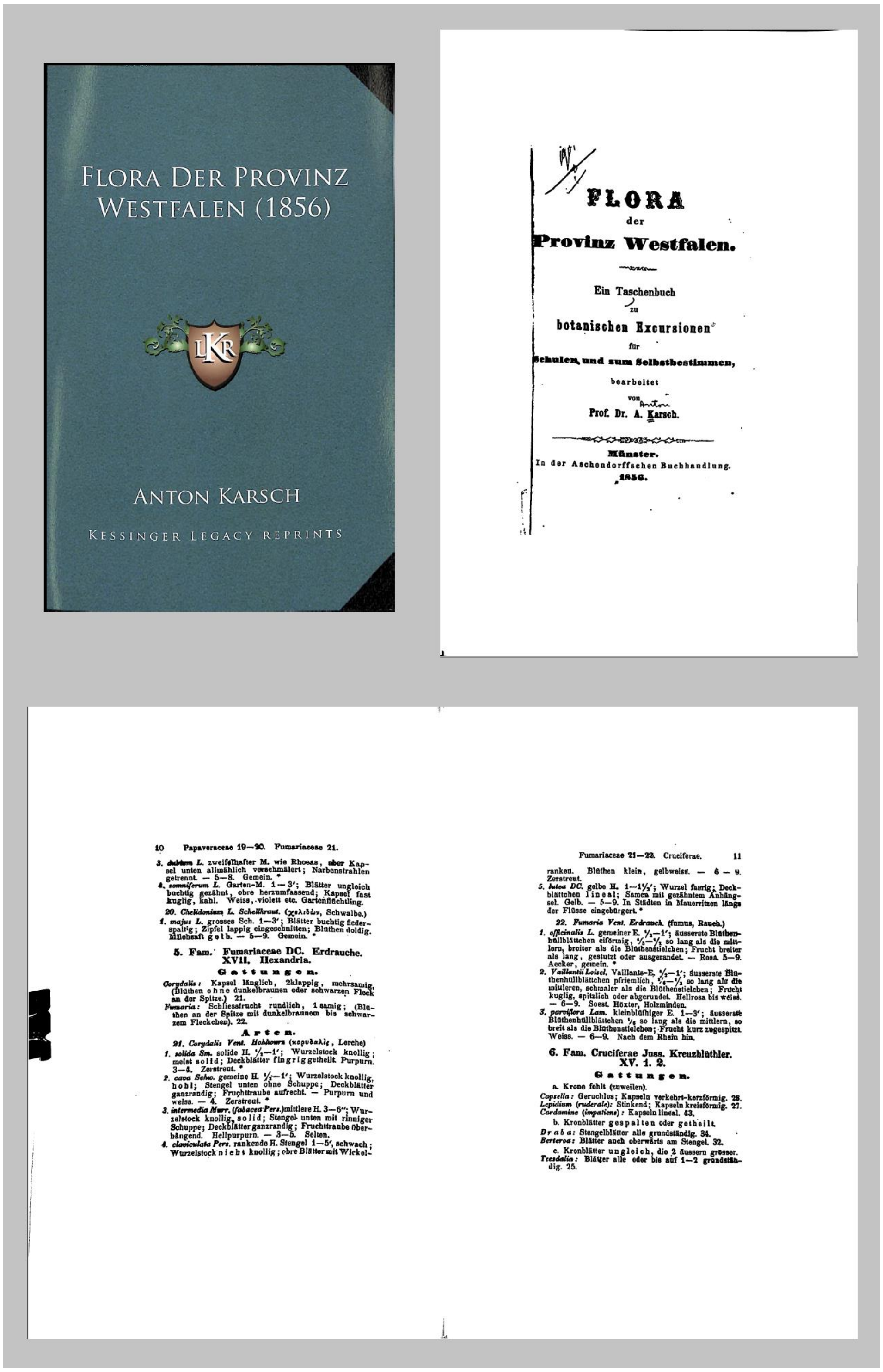


Fig. 1. A book authored by Karsch (Flora der Provinz Westfalen) originally authored in 1856, but recently reprinted simply by binding the photocopied images (Kessinger Publishing, LLC; www.kessinger.net). (Top) Newly designed cover and original cover image. (Bottom) Snapshot of the text, describing the family of Cruciferae now classified as Brassicaceae.

(http://books.google.co.jp/books?id=4_0GAAAAcAAJ&printsec=frontcover&hl=ja&source=gbs_ge_summary_r&cad=0#v=onepage&q&f=false).

A part of philosophical works (Karsch, 1855a-c) dealt with the idea of "thing-in-itself" (ding an sick) proposed by Arthur Schopenhauer (1788-1860), a German philosopher. Karsch was also interested by the use of microscopes which was surely considered as "new technology" at that time and thus authored the articles entitled "microscopic form of life 1 and 2" (Mikroskopische Lebensformen; Karsch, 1855d, e), "From the life of a gnat" (Aus dem Leben einer Mücke; Karsch, 1855f), presenting the drawings of microscopic structures of bacteria, protozoa, blood cells and insects.

His interests also covered the behaviors of higher plants surrounded by pathogenic microorganisms (Karsch, 1855g). In our recent articles a piece of Karsch's works were compared with the recently proposed plant pathological model and suggested that both the classical and recent works are indicative of the role for intercellular space in plant tissue as the paths for spread of pathogenic microorganisms and also for cell-cell communication required for combatting the invading pathogenic microorganisms.

2. Outbreak of plant diseases and plant responses

Historically, humans have long been suffered by the loss of crops due to the outbreak of plant diseases. One of the symbolic incidents, known as Irish potato famine occurred in 19th century and we can find out the remaining impact of the aforementioned incident even today. In 1997, Tony Blair, British Prime Minister (terms, 1997-2007) has issued a statement on Irish potato famine apologizing on behalf of the British authority for the first time in 1.5 centuries after the incidents (The Independent, Monday 02, June, 1997).

It is known that the Irish potato famine was caused by a single clonal genotype of *Phytophthora infestans*, an oomycete that causes the serious potato disease known as late blight or potato blight (Goodwin et al., 1994). Today, survey by Goodwin et al. (1994) revealed that a single clonal lineage of Irish potato famine fungus dominated most populations worldwide. Therefore, *P. infestans* is used as model plant pathogenic organism in the fields of phytopathology, and more generally, in physiology, cell biology, biochemistry and molecular biology of plant-microbe interactions.

In 1983, Doke (Nagoya Univ., Japan) reported that the infection by *P. infestans* (late blight pathogen of potato) into potato tubers causes the generation of a member of reactive oxygen species (ROS), superoxide anion radicals ($O_2^{\bullet -}$) at the host cells' plasma membrane, in the incompatible interactions (Doke, 1983a). This was the first report on the generation o ROS in plant-microbe interaction which is specifically responsive to the attacks by pathogenic microorganisms. As his work demonstrated that the members of ROS possibly function as the chemical signals required for induction of hypersensitive responses as typified by host cell death and they are most likely generated and released in the intercellular space, plant biologists and pathologists now consider the space called apoplast (outside the cells) surrounded by multiple cells in plant tissue as one of the key paths, or media of a series of reactions and/or events determining the behaviors and/or fate of the plant cells challenged by pathogens.

Following the first observation, Doke (1983b) further predicted that the recognition of plant pathogens by plant cell surface leading to "oxidative burst" takes place on the interface (extracellular matrix) of both the plant cells and pathogenic cells, based on the observation that treatments of potato tuber protoplasts with the cell wall preparation from *P. infestans* readily induce the ROS production. This suggested that chemical components derived from pathogenic microorganisms (cell wall-derived elicitors) trigger the burst of ROS production in the apoplast in order to stimulate the plant defense mechanisms.

3. Medal of Honor with Purple Ribbon.

In November, 2006, from the hands of his majesty Emperor Akihito (the 125th Emperor of Japan, a renowned marine biologist), the Medal of Honor with Purple Ribbon was handed to Prof. Noriyuki Doke of Nagoya University for honoring his pioneering works (carried out since early 1980's) leading to the discovery that members of ROS (especially superoxide anion, O_2^-) could be produced from the plant tissues challenged by the pathogenic microorganisms (Yoshioka et al., 2008).

We understood that the honor was also given to the area of plant biology emphasizing the role of extracellular (intercellular) communications by plant and microbial cells, which has markedly developed in the last two decades.

4. Intercellular-space as the site of species-species contacts and recognition followed by early signaling events.

To date, multiple roles of ROS have been proposed in direct microbicidal actions, strengthening of cell wall through oxidative cross-linking of glycoproteins, induction of intracellular signaling pathway such as the synthesis and release of salicylic acid (SA), a stress-related and plant defense-related phytohormone, and activation of mitogen-activated protein kinase (MAPK) cascade, or activation of systemic acquired resistance associated with systemic propagation of the oxidative burst (Kawano et al., 1998, 2004). We have recently outlined the relationship between the roles of ROS and behaviors of plant defense-related signaling molecules chiefly, of SA through the crosstalk between intracellular and extracellular signaling events leading to long-distance spread of defense signals (Yoshioka et al., 2008; Kawano and Bouteau, 2013). The production of ROS, mostly $O_2^{\bullet-}$, hydrogen peroxide (H_2O_2), and hydroxyl radicals ($HO^{\bullet}$), at the cell surface is one of the earliest events detectable during the incompatible interactions between plants and pathogens (Yoshioka et al., 2001) and also plant cellular recognition of exogenously applied SA (Kawano et al., 1998; Kawano and Muto, 2000).

5. A work by Karsch in 1855 emphasizing the possible role of intercellular space and stomata as the path of pathogen entrance and the path of intercellular communication

In the middle of 19th century, *P. infestans* was also described under the name of *Botrytis infestans* (Cline, 2006). A classical study describing the interaction between *B. infestans* and potato leaves (Karsch, 1855g), has suggested that apoplastic space, as such in the leafy tissues, is the key path to the cell-to-cell communication within plants, thus the events of pathogenic invasion and resultant plant responses through this path are of great importance. Note that the terms related to "intercellular space" and "communication" were used in this early study (underlined words in Fig. 2a). The authors were impressed by frequent uses of such modern scientific terms in the journal published in 19th century.

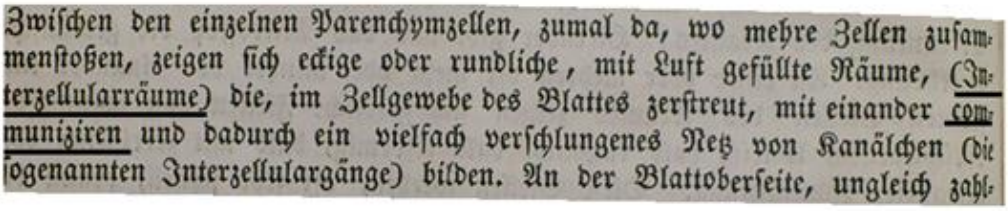
Followings are original German text (A) and its translation to English (B), stating that the importance of intercellular space during the early phase of pathogen attacks and also at the phase of pathogenic propagation and disperse:

(A) *Zwischen den einzelnen Parenchymzellen, zumal da, wo mehre Zellen zusammenstoßen, zeigen sich eckige oder rundliche, mit Luft gefüllte Räume, (Interzellularräume) die, im Zellgewebe des Blattes zerstreut, mit einander communizieren und dadurch ein vielfach verschlungenes Nets von Kanälchen (die sogenannten Interzellulargänge) bilden.*

(B) Between the parenchymal cells, especially where several cells meet, square or round air-filled spaces (intercellular spaces) can be found, being scattered in the tissues of the leaf, communicate with each other and thus forming the tangled nets of small channels (called Interzellulargänge).

Today, stomata in the epidermis of terrestrial plants are known to be pivotal for (i) CO_2 absorption, (ii) transpirational water loss, and (iii) entry of pathogens (Zhang et al., 2008). The work by Karsch clearly pointed out the importance of stomata for potential points of entry for pathogenic microorganisms into plants.

(a)


Zwischen den einzelnen Parenchymzellen, zumal da, wo mehre Zellen zusam-
menstoßen, zeigen sich eckige oder rundliche, mit Luft gefüllte Räume, (In-
terzellularräume) die, im Zellgewebe des Blattes zerstreut, mit einander com-
muniziren und dadurch ein vielfach verschlungenes Netz von Kanälchen (die
sogenannten Interzellulargänge) bilden. An der Blattoberseite, ungleich zahl-

(b)

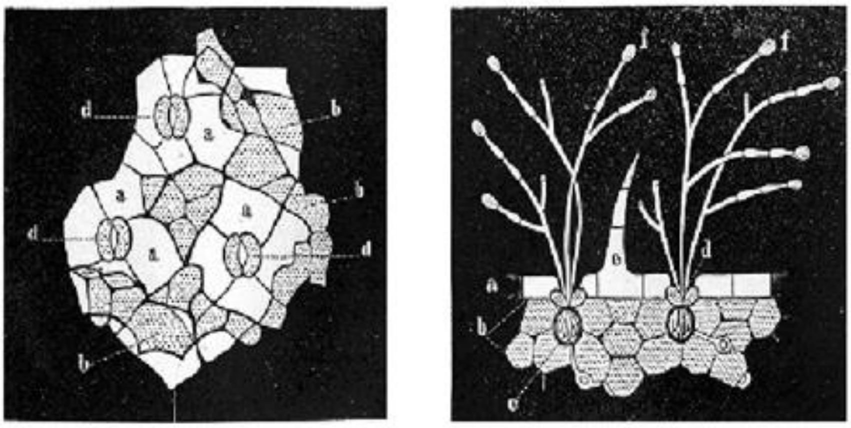


Fig. 2. Snapshots of text and illustrations by A. Karsch (1855g, pp. 65-66). (a) Importance of intercellular space and communication between the plant cells during plant-microbe interaction was pointed. Two key words, interzellularräume (intercellular space) and communiziren (to communicate) are underlined. (b) Leaf anatomy highlighting the stomatal aperture and intercellular network as the path of late potato blight infection and outbreak.

6. Controls in stomatal aperture as the point of plant defense and pathogenic counter defense

Since the stomata on the leaves connect the internal environment in the plants and the aerial environment surrounding plants through gas exchange, it is natural to relate the air-borne entry of fungal spores and the gating behavior of stomata. As suggested by Karsch (see Fig. 2b), stomata have long been considered as the gates for entry and further spread of pathogenic microbes. To our knowledge today, roles of stomata in plant defense mechanism so called plant innate immunity against foliar diseases is now documented (Melotto et al., 2006, 2008).

Upon attacks by pathogens or treatments with elicitors — pathogen-derived molecules which trigger a series of defense-related reactions in plants — such as chitosan, stomatal closure is rapidly induced as examined in tomato (*Solanum lycopersicum* L.) and Asiatic dayflower (*Commelina communis*) (Lee et al., 1999). By doing this, plants might limit the chance of further fungal invasion through stomata (Mori et al., 2001).

Note that Asiatic dayflower is one of the best materials for microscopic observation of stomatal behaviors. Fig. 3 shows a typical image of highly populated stomata on epidermis peeled out of the leaf of Asiatic dayflower for demonstration in our laboratory.

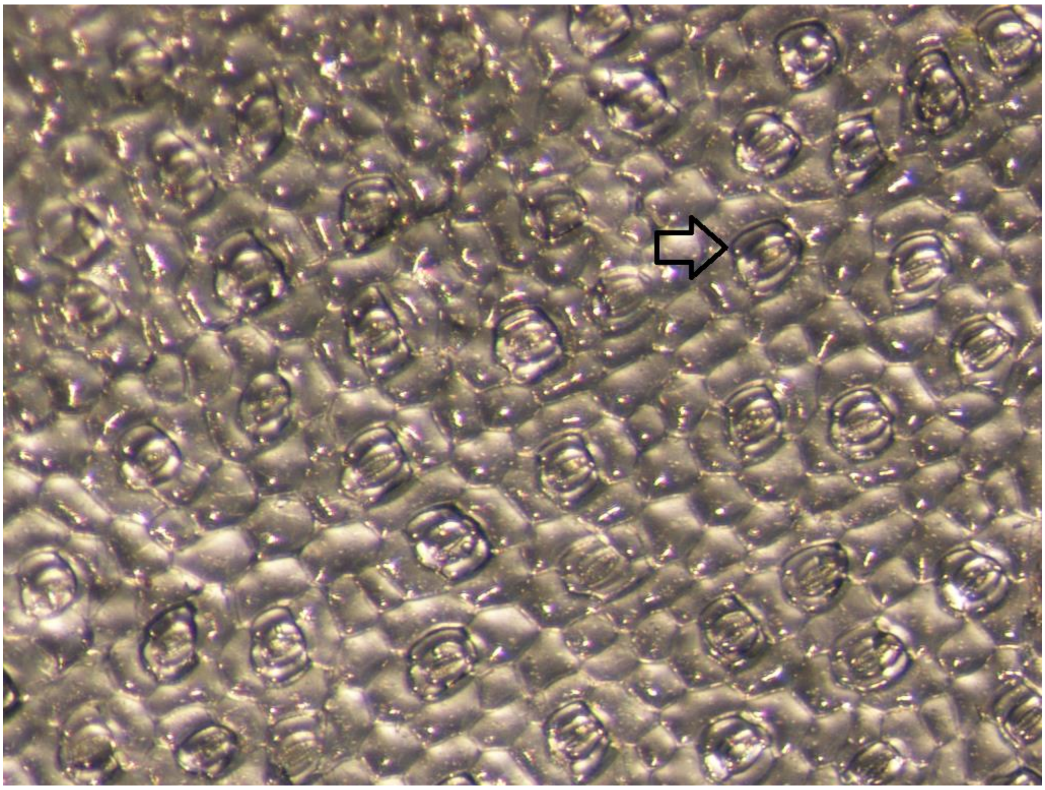


Fig. 3. Stomata on the epidermis of Asiatic dayflower observations under a stereomicroscope (SMZ645; Nikon, Tokyo, Japan). Arrow, typical stoma.

According to the model reported by Lee et al. (1999), additions of elicitors are resulted in generation of ROS and in turn, stomatal closure is stimulated by ROS. There are two distinct enzyme models for apoplastic generation of $O_2^{\bullet -}$ upon treatment of model plant cells (tobacco BY-2 cells) with chitosan oligomers and chitin oligomers involving extracellular peroxidase and NADPH oxidase, respectively (Kawano et al., 2000). In addition to elicitors, perception of multiple pathogen-associated molecular patterns (designated as PAMPs) of bacterial origins, including flagellin, lipopolysaccharide and elongation factor Tu, reportedly induce closure of stomata in epidermal peels of *Arabidopsis* leaves (Melotto et al., 2006). Since perception of PAMPs is the sign that plants are dangered by the risk of infection, members of PAMPs such as flg22 derived from bacterial flagellin, emergently interferes with naturally occurring light-induced stomatal opening, by inhibiting the inward K^+ channels of guard cells that mediate K^+ uptake during stomatal opening (Zhang et al., 2008). The PAMP-triggered stomatal response involving K^+ channel regulation is dependent on signaling via cognate PAMP receptors and a heterotrimeric G-protein (Zhang et al., 2008).

Interestingly, for the purpose of enhanced penetration into the leaves by pathogenic microbes, some plant pathogens such as *Pseudomonas syringae* pv. tomato DC3000 (Zeng et al., 2011) and the causal agent of grapevine downy mildew, *Plasmopara viticola* (Allègre et al., 2007), are known to produce some host-specific toxins which eventually open the stomatal cells. Such pathogen-derived toxins include fusicoccin which irreversibly stimulates plant H^+ ATPases (Eun and Lee, 2000) and coronatine produced by several pathogenic strains of *Pseudomonas syringae*, which antagonizes PAMPs-mediated plant immunity (Lee et al., 2013). For an instance, coronatine suppresses the inhibitory actions of flg22 on both inward K^+ currents and stomatal opening. This indicates the interplay between plant and pathogen in the regulation of plant ion channels.

As above, pathogen-derived molecules are involved in plant defense and counter defense. In addition, plants possess the mechanisms for minimizing the chance of pathogenic penetration through stomata via production of phytohormones, chiefly the action of SA is comparable with that of elicitors. It has been reported that stomatal closure is induced after application of SA, a defense-related plant hormone, to epidermal peels of *Commelina communis* L. (Lee, 1998), *Vicia faba* L. (Manthe et al., 1992; Mori et al., 2001) and *Arabidopsis thaliana* (Khokon et al., 2011). The mechanism responding to pathogen-derived elicitors may be involved in the resistance at the site of infection, while the mechanism responding to SA may be important for minimizing the chance of further spread of pathogens (Mori et al., 2001).

Importantly, Mori et al. (2001) has shown the evidence in support of the involvement of peroxidase-mediated $O_2^{\bullet -}$ generation and secondarily induced calcium signaling in the early signaling phase of SA-induced stomatal closure in *Vicia faba*. Moreover, the SA-induced stomatal closure in *Vicia faba* and *Arabidopsis thaliana* was reportedly inhibited by pre-treatment with scavengers of ROS such as catalase and superoxide dismutase (SOD), and an pharmacological inhibitor of peroxidase, suggesting the involvement of peroxidase-mediated production of extracellular ROS during the action of SA leading to stomatal closure (Mori et al., 2001, Khokon et al., 2011). Contrarily, pharmacological inhibition of NADPH oxidase (respiratory burst oxidase homologs, *RBOHs*) nor mutation of *atrboh*D and *atrboh*F showed no inhibition on the SA-induced stomatal closures (Khokon et al., 2011). This suggests that, unlike the action of abscisic acid (Marinosend et al., 2011; Suzuki et al., 2011) and chitin oligomers (Kawano et al., 2000) stimulating the oxidative burst via activation of NADPH oxidase, the peroxidase-dependent mechanism is solely responsible for the rapid stomatal regulation by SA. As expected, SA-induced stomatal closure-mediated defense could be counteracted by aforementioned pathogen-derived toxins such as coronatine produced by *Pseudomonas syringae* pv. tomato DC3000 (Tsai et al., 2011).

As discussed above, the view proposed by Karsch is still hotly studied by plant biologist of today.

7. Conclusion

In this short article, we described a story we experienced in our plant biological research finding and shocked by a similarity between the recently proposed plant pathological model and a classical proposal. A pioneering work of Anton Karsch published in 1855 firstly suggested the role for intercellular space in plant tissue as the paths for spread of pathogenic microorganisms and also for cell-cell communication required for combatting the invading pathogenic microorganisms.

References

Allègre, M., Daire, X., Héloir, M.C., Trouvelot, S., Mercier, L., Adrian, M., and Pugin, A. (2007) Stomatal deregulation in Plasmopara viticola-infected grapevine leaves. New Phytol. 173: 832-840.

Cline, E. (2006) Phytophtora infestans. Systematic Mycology and Microbiology Laboratory, ARS, USDA (retrieved Nov. 20, 2012, from /sbmlweb/OnlineResources/FungiOnline.cfm)

Doke, N. (1983a) Involvement of superoxide anion generation in the hypersensitive response of potato tuber tissues to infection with an incompatible race of *Phytophthora infestans* and to the hyphal wall components. Physiol. Plant Pathol. 23:345-357.

Doke, N. (1983b) Generation of superoxide anion by potato tuber protoplasts during the hypersensitive response to hyphal wall components of *Phytophthora infestans* and specific inhibition of the reaction by suppressors of hypersensitivity. Physiol. Plant Pathol. 23: 359-367.

Eun, S. O. and Lee, Y. (2000) Stomatal opening by fusicoccin is accompanied by depolymerization of actin filaments in guard cells. Planta 210: 1014-1017.

Goodwin, S. B., Cohen, B. A., and Fry, W. E. (1994) Panglobal distribution of a single clonal lineage of Irish potato famine fungus. Proc. Natl. Acad. Sci. USA 91: 11591-11595.

Karsch (1855a) Arthur Schopenhauer und das Ding an sich. Erster Artikel. Die Welt als Vorstellung. Natur und Offenbarung 1: 90-98.

Karsch (1855b) Arthur Schopenhauer und das Ding an sich. Zweiter Artikel. Die Welt als Wille. Natur und Offenbarung 1: 182-195.

Karsch (1855c) Arthur Schopenhauer und das Ding an sich. Dritter Artikel. Kritische Prüfung. Natur und Offenbarung 1: 227-243.

Karsch (1855d) Mikroskopische Lebensformen. Erster Artikel. Die Monaden. Natur und Offenbarung 1: 20-33.

Karsch (1855e) Mikroskopische Lebensformen. Zweiter Artikel. Die Vibrionen. Natur und Offenbarung 1: 127-135.

Karsch (1855f) Aus dem Leben einer Mücke. Natur und Offenbarung 1: 266-278.

Karsch (1855g) Die Kartoffelkrankheit. Natur und Offenbarung 1: 60-71.

Kawano, T. (2013) Anton Karsch (1822-1892), a plant collector who widely studied from the philosophy of Schopenhauer and to the microscopic elucidation of cellular structure. CIEE J. Univ. Kitakyushu 11: 99-111.

Kawano, T. and Bouteau, F. (2013) Crosstalk between intracellular and extracellular salicylic acid signaling events leading to long-distance spread of signals. Plant Cell Reports 32: 1125-1138.

Kawano, T. and Muto, S. (2000) Mechanism of peroxidase actions for salicylic acid-induced generation of active oxygen species and an increase in cytosolic calcium in tobacco suspension culture. J. Exper. Bot. 51: 685-693.

Kawano, T., Furuichi, T., and Muto, S. (2004) Controlled free salicylic acid levels and corresponding signaling mechanisms in plants. Plant Biotechnol. 21: 319-335.

Kawano, T., Sahashi, N., Takahashi, K., Uozumi, N., and Muto, S. (1998) Salicylic acid induces extracellular superoxide generation followed by an increase in cytosolic calcium ion in tobacco suspension culture: The earliest events in salicylic acid signal transduction. Plant Cell Physiol. 39: 721-730.

Kawano, T., Sahashi, N., Uozumi, N., and Muto, S. (2000) Involvement of apoplastic peroxidases in the chitosaccharide-induced immediate oxidative burst and cytosolic Ca^{2+} increase in tobacco suspension culture. Plant Peroxid. Newslett. 14: 117-124.

Khokon, M. A. R., Okuma, E., Hossain, M.A., Munemasa, S., Uraji, M., Nakamura, Y., Mori, I. C., and Murata, Y. (2011) Involvement of extracellular oxidative burst in salicylic acid-induced stomatal closure in *Arabidopsis*. Plant Cell Environ 34: 434-443.

Lee, J. S. (1998) The mechanism of stomatal closing by salicylic acid in *Commelina communis* L. J. Plant Biol. 41: 97-102.

Lee, L., Ishiga, Y., Clermont, K., and Mysore, K. S. (2013) Coronatine inhibits stomatal closure and delays hypersensitive response cell death induced by nonhost bacterial pathogens. Peerj 1: e34.

Lee, S., Choi, H., Suh, S., Doo, I. S., Oh, K. Y., Choi, E. J., Taylor, A. T. S., Low, P. S., and Lee, Y. (1999) Oligogalacturonic acid and chitosan reduce stomatal aperture by inducing the evolution or reactive oxygen species from guard cells of tomato and *Commelina communis*. Plant Physiol. 121: 147-152.

Manthe, B., Schulz, M., and Schnable, H. (1992) Effects of salicylic acid on growth and stomatal movement on *Vicia faba* L.: evidence for salicylic acid metabolism. J. Chem. Ecol. 18: 1525-1539.

Marinosend, D., Dunand, C., Puppo, A., Pauly, N. (2011) A burst of plant NADPH oxidases. Trends Plant Sci. 17: 9-15.

Melotto, M., Underwood, W., Koczan, J., Nomura, K., He, S. Y. (2006) Plant stomata function in innate immunity against bacterial invasion. Cell 126: 969-980.

Melotto, M., Underwood, W., and He, S. Y. (2008) Role of stomata in plant innate immunity and foliar bacterial diseases. Annu. Rev. Phytopathol. 46: 101-122.

Mori, I. C., Pinontoan, R., Kawano, T., and Muto, S. (2001) Involvement of superoxide generation in salicylic acid-induced stomatal closure in *Vicia faba*. Plant Cell Physiol. 42: 1383-1388.

Suzuki, N., Miller, G., Morales, J., Shulaev, V., Torres, M. A., Mittler, R. (2011) Respiratory burst oxidases: the engines of ROS signaling. Curr. Opin. Plant Biol. 14: 691-699.

Tsai, C. H., Singh, P., Chen, C. W., Thomas, J., Weber, J., Mauch-Mani, B., and Zimmerli, L. (2011) Priming for enhanced defence responses by specific inhibition of the Arabidopsis response to coronatine. Plant J. 65: 469-479.

Yoshioka, H., Bouteau, F. and Kawano, T. (2008) Discovery of oxidative burst in the field of plant immunity: Looking back at the early pioneering works and towards the future development. Plant Signal. Behav. 3: 153-155.

Yoshioka, H., Sugie, K., Park, H. J., Maeda, H., Tsuda, N., Kawakita, K., and Doke, N. (2001) Induction of plant gp91phox homolog by fungal cell wall, arachidonic acid, and salicylic acid in potato. Mol. Plant Microbe Interact. 14: 725-736.

Zeng, W., Brutus, A., Kremer, J. M., Withers, J. C., Gao, X., Jones, A. D., and He, S. Y. (2011) A genetic screen reveals Arabidopsis stomatal and/or apoplastic defenses against Pseudomonas syringae pv. tomato DC3000. PLoS Pathog. 2011 7:e1002291.

Zhang, W., He, S. Y., and Assmann, S. M. (2008) The plant innate immunity response in stomatal guard cells invokes G-protein-dependent ion channel regulation. Plant J. 56: 984-996.

植物-病原間相互作用における細胞間コミュニケーションのための経路としての植物組織中の細胞間隙の役割を示唆する Anton Karsch (1822-1892) の先駆的研究

要約

19 世紀のドイツで活躍した Anton Karsch (1822-1892) は、医師(内科医)、生態学者、植物収集家、微生物学者、初期の細胞生物学者として知られ、さらに哲学分野においても著述を残している。最近、我々は、Karsch による植物分野での先駆的研究に関する2つの独立した論文を執筆した。Karsch は、1855 年に、植物に感染する病原微生物の侵入やその後の拡散に対して植物が採り得る防御反応における細胞間コミュニケーションのための経路として、植物組織中の「細胞間隙」が果たす重要な役割について示唆する研究を発表している。近年の植物細胞生物学者が研究対象としている、気孔の開閉制御を介した、病原性カビの浮遊胞子の葉組織への侵入防止機構が、19 世紀の Karsch によって描写されていることは注目に値する。本論文では、今日の植物生物学者からの視点から見て重要な研究の源流としての Karsch の仕事を簡潔に紹介する。