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From Facts and False Routes: How Plant Hormone Research Developed

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Abstract Our understanding of how plant hormones work has tremendously increased over the last decades. However, such progress was not possible without those who laid the foundation of the work which was sometimes much more tedious in early days than today. Therefore, we thought it timely to follow-up on historical aspects of plant hormone research. The development in the field of auxins, cytokinins, gibberellins, abscisic acid, jasmonates, brassinosteroids, and ethylene are accompanied with personal recollections. Plant hormones cannot go without plant growth regulators which have been developed for commercial reasons, but are also used in many cases nowadays as tools to investigate a specific role of a hormone *in planta*. This issue is also hopefully a useful collection for those scientists who want to get an overview of how their "favorite hormone" started.

Keywords Plant hormone · History · Editorial

A Special Issue on the History of Plant Hormone Research

"What a timely and great idea!" Such, and similar, words were found by colleagues when Hartwig Lüthen and myself told them that we would like to edit a special issue on the history of hormone research (Fig. 1). The idea for such a special issue on the history of plant hormones or in a broader sense plant growth regulators occurred during a recent meeting on auxins and cytokinins in Prague (Vaňková and others 2014). As detailed in the article by Lüthen (2015), with which this issue starts, our intention was initially to overcome some gaps in the awareness of the historical roots of hormone research. While the current trend in plant hormone research has developed into using a plethora of novel and high-tech techniques to investigate the role of specific proteins, compounds and genes on a tissue specific or even cellular level, there was also remembrance that one can do "classical" physiological experiments with better equipment available now and the use of the tools available from *Arabidopsis* and other model plants. Stimulating was also the introduction by Miroslav Kaminek on the history of these meetings, which started out originally as cytokinin conferences (Vaňková and others 2014). Initially, we came up with the idea "to write up all the old stuff…", so that young scientists can maybe better understand where their specific topic comes from and how that was originally developed. As pointed out by Hedden and Sponsel (2015) in this issue it is necessary to look "… particularly on the earlier work, which tends to become lost in the mists of time."

There have been many false routes, that is, during the identification of indole-3-acetic acid (IAA) that has been compiled by Wildman (1997) in a historical overview dealing with the identification of the "heteroauxin" IAA from the many efforts to identify the "Wuchsstoff" from human urine and compounds termed "auxin" at that time which were later shown to be nonexistent (also mentioned in Lüthen 2015).

On the other hand, the development that seemed slow in terms of progress, for example, in the identification of receptors for various hormones, is now at "racing speed".

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Fig. 1 The editors of this special issue. Jutta Ludwig-Müller, Institut für Botanik, Technische Universität Dresden, Germany (*left*) and Hartwig Lüthen, Institut für Botanik, Universität Hamburg, Germany (*right*), who is also author of the article on the history of auxin physiology

As mentioned above, novel techniques to identify plant hormones, to identify proteins at the cellular level and to use the plethora of publicly available databases and plant resources have dramatically changed plant hormone research. Some aspects will be covered in this special issue.

When asking colleagues in different hormone fields if they would like to contribute, we received very positive comments. Some of the contributors in the journal issue have already had this idea themselves, but found it more intriguing to prepare such an overview for a special issue. The idea was to cover most of the currently known compounds classified as plant hormones. We have selected not only the "classic five" auxin, cytokinin, gibberellin, abscisic acid, and ethylene, which were the textbook plant hormones during our own studies. We have decided to cover also some of the "newcomers" such as jasmonic acid and brassinosteroids, but did not include the relatively "young" salicylic acid and strigolactones, but these will be mentioned if they are relevant to cross-talk in signaling pathways, for example, in the review by Wasternack (2015) (Fig. 2). Finally, we have covered some selected aspects of plant growth regulators and their application (Rademacher 2015) (Fig. 3). In this overview the cross-talk of different hormones and growth regulators is also discussed.

Several of the articles presented show two common themes: first, the interaction and good collaboration between groups when it was essential for supporting and advancing a new finding, and second, the interesting personalities of the researchers involved. The latter can be deducted from many personal recollections of the respective authors.

The issue starts with two articles on the history of auxin research, because IAA was the first soluble plant hormone (see ethylene below) to be identified as heteroauxin in the 1930s (Wildman 1997), but indirectly its history dates back to Darwin (1880) (see also Lüthen 2015). However, as pointed out by Dörffling in this issue (Fig. 4), the discovery of abscisic acid cannot be really separated from IAA, because a typical growth assay was used to isolate a growth inhibitory compound from the "inhibitor complex ß" (Dörffling 2015). Moreover, some aspects on auxin determination are presented by Tivendale and Cohen (2015) (Fig. 5). They note that the history of auxin determination

Fig. 2 Claus Wasternack, Institute for Plant Biochemistry, Halle, Germany, has strongly impacted from the beginning the field of jasmonate research. He works in an institution which is associated with the recognition that jasmonates are plant hormones. His contribution on the history of jasmonates (Wasternack 2015)

Fig. 3 Wilhelm Rademacher, Limburgerhof, Germany. Dr. Rademacher's contributions in the area of plant growth regulators, especially those related to the gibberellin pathway are well acknowledged in the plant hormone community. His overview on some aspects in the history of plant growth regulators (Rademacher 2015)

Fig. 4 Karl Dörffling, Institut für Botanik, Universität Hamburg, Germany, worked on various aspects of abscisic acid physiology throughout his long career. In Germany he also contributed with a textbook on plant hormones in the 1980s. His story on some aspects in the history of plant growth regulators (Dörffling 2015)

is intertwined with the history of analytical (bio)chemistry. Further, some techniques, even though they date back to the beginning of auxin research, are still in use, but powerful instrumentation-based techniques are nowadays adequate to measure not only auxin but also other plant hormones (covered partially in the articles for other hormones). While covering the methods leading to modern auxin analysis, they also detail how artifacts could be produced.

Cytokinin history is presented by Kaminek (2015) (Fig. 6). Here, we not only learn how cytokinin biology got on the track, but also many personal recollections, mainly about Folke Skoog, the "father" of cytokinin research. Like for the other hormones, especially auxin, the period of the discovery was a way back and forth until finally an active cytokinin could be isolated and identified. The rhyme cited in the introduction of Kaminek's contribution could be the preface for other hormones as well.

Gibberellins are covered by Hedden and Sponsel (2015) (Fig. 7). They describe the origin of gibberellin research to begin in the 19th century in Japan as the discovery of a plant disease—the foolish rice seedlings ("bakanae"). This plant hormone had its origin in plant pathology. However, after evidence for a certain substance that caused growth in rice, other discoveries followed quickly. That gibberellins are present in plants had been demonstrated in the late 1950s—this discovery established gibberellins as a new class of plant hormones. In this overview, some evolutionary aspects of gibberellins are also covered. This links actually back to the fungi producing gibberellins because here the evolution seems to have occurred independently of vascular plants.

The discovery of abscisic acid (ABA) is described by Dörffling (2015) with a very personal introduction. The search for a growth inhibitor from several plant species began this story. Tightly connected are many bioassays that had to be carried out to find the compound(s) responsible for growth inhibition. Looking into the dormancy phenomenon of plants as well as abscission of different organs was another strategy that played a role in the historical way to ABA.

A contribution also involving very much the people that have initiated or were/are of importance to the field are presented in the review of Wasternack (2015) on jasmonates. Thus, many photos of eminent researchers in the field have been included, because advances in a research area depend so much on the researcher personalities involved. Moreover, this article contains many personal remarks of the authors, for example, novel discoveries presented during the respective conferences.

How ethylene research thrived over the years, actually with the first plant hormone receptor identified for this gaseous hormone, is described by Bakshi and others (2015). As nicely pointed out, the history of ethylene as a plant growth-affecting compound goes way back to the 1800s, where scientists started to investigate the effect of illuminating gas on plants and in 1901 ethylene was identified as the active compound (Neljubow 1901). So ethylene can be possibly regarded together with auxin as the "oldest" known plant hormone substance, and it was among the first plant hormones for which a receptor could be clearly identified 90 years later. The authors also nicely point out that ethylene, because of its gaseous nature, was long neither believed to be a plant hormone nor a pheromone, and only the ability to detect it via gas

Fig. 5 Nathan Tivendale (*left*) and Jerry D. Cohen (*right*), Department of Horticultural Science and Microbial and Plant Genomics Institute, University of Minnesota, USA. Jerry Cohen has been involved in the development of the technology to use heavy-labeled isotopes coupled with gas chromatography–mass spectrometry for auxin determination from plants. Their contribution on the history of auxin analytics (Tivendale and Cohen 2015)

Fig. 6 Miroslak Kaminek from the Institute of Institute of Experimental Botany, Prague, Czech Republic, is a pioneer in cytokinin research. Starting with physiology, his work has extended to analytical methods and biochemistry later. His story on the history of cytokinins (Kaminek 2015)

chromatography increased the interest in this compound as a plant hormone (Bakshi and others 2015).

Last but not least, we include brassinosteroids that constitute a very unique steroidal plant hormone class and an overview is presented by Clouse (2015) (Fig. 8). Although the description of the "brassins" in the literature by Mitchell and others can be found in the year 1970, although the history of brassinosteroid research indirectly goes back much longer. As outlined by Clouse (2015) the group of Mitchell conducted bioassays with an extract of pollen tubes from varying plant sources already in the 1940s, even though they could not elucidate the growth promoting principle for a long time. Despite these early discoveries, the identity of brassinosteroids was not yet unequivocally proven due to the mixture of compounds present in these extracts. The first indirect report on brassinosteroids is thus much older than the description of the chemical nature of one compound, namely brassinolide, that was reported by a large group of researchers in 1979 (Grove and others 1979), a fact that was observed also for other plant hormones covered in this issue.

We also invited an article on applied aspects, because plant hormone research could not have been as successful without growth regulators or inhibitors of certain biosynthetic pathways, transport molecules or receptors as outlined by Rademacher (2015) (Fig. 3). Certainly, the commercial aspect has helped in many cases the research community, even though in many instances the two developments were separated from each other. Nowadays some of the growth regulators are routinely used in pharmacological approaches to understand plant hormone function in vivo. The conclusion is promising for all research fields, namely that "plant growth regulators do not only have a history, but also a future".

The articles are a result of the authors' discussion with colleagues and friends and their own perception and contribution to the field. This aspect makes the articles presented here so special. By purpose, we did not give too much advice on what the article should look like, because we also wanted to recruit personal ideas, experiences and stories. We have therefore received luckily very different reviews reflecting the different personalities of the authors. We realize that the issue is biased, but that was also partially intentional. For these articles, we would like to thank all our contributors for their time and input, but also those colleagues who helped during discussions, proofreading,

Fig. 7 Valerie Sponsel (*left*), Department of Biology, The University of Texas at San Antonio, USA and Peter Hedden (*right*), Rothamsted Research, Harpenden, Hertfordshire AL5 2JQ, United Kingdom, have both contributed on various important aspects during their career on gibberellin physiology, biochemistry and signal transduction. Their contribution on 100 years of gibberellin research (Hedden and Sponsel 2015)

Fig. 8 Steven Clouse, Department of Horticultural Science, North Carolina State University, USA is one of the leading scientists in the brassinosteroid field. The contributions together with other imminent researchers in the field are groundbreaking for our understanding how brassinosteroid signaling works. A summary is given in his article on the history of brassinosteroids (Clouse 2015)

and so on to complete the individual reviews. Certainly, there are much more aspects in the history of plant hormones that could have been covered, but we do hope that our readers will appreciate as much as we do the interesting and dedicated contributions in this special issue.

References

Bakshi A, Shemansky JM, Chang C, Binder B (2015) History of research on the plant hormone ethylene. J Plant Growth Regul 34. doi:10.1007/s00344-015-9522-9

Clouse S (2015) A history of brassinosteroid research from 1970 - 2005: Thirty-five years of phytochemistry, physiology, genes and mutants. J Plant Growth Regul 34. doi:10.1007/s00344-015-9540-7

Dörffling K (2015) The discovery of abscisic acid—a retrospect. J Plant Growth Regul 34. doi:10.1007/s00344-015-9525-6

Grove MD, Spencer GF, Rohwedder WK, Mandava NB, Worley JF, Warthen JD, Steffens GL, Flippen-Anderson JL, Cook JC (1979) Brassinolide, a plant growth-promoting steroid isolated from *Brassica napus* pollen. Nature 281:216–217

Hedden P, Sponsel V (2015) A century of gibberellin research. J Plant Growth Regul 34. doi:10.1007/s00344-015-9546-1

Kaminek M (2015) Tracking the story of cytokinin research. J Plant Growth Regul 34. doi:10.1007/s00344-015-9543-4

Lüthen H (2015) What we can learn from old auxinology. J Plant Growth Regul 34. doi:10.1007/s00344-015-9527-4

Mitchell JW, Mandava NB, Worley JF, Plimmer JR, Smith MV (1970) Brassins: a new family of plant hormones from rape pollen. Nature 225:1065–1066

Neljubow D (1901) Über die horizontale Nutation der Stengel von *Pisum sativum* und einiger anderer Pflanzen. Ber Bot Zentralbl 10:128–139

Rademacher W (2015) Plant growth regulators – backgrounds and uses in plant production. J Plant Growth Regul 34. doi:10.1007/s00344-015-9541-6

Tivendale ND, Cohen JD (2015) Analytical history of auxin. J Plant Growth Regul 34. doi:10.1007/s00344-015-9519-4

Vaňková R, Petrášek J, Zažímalová E, Kamínek M, Motyka V, Ludwig-Müller J (2014) Auxins and Cytokinins in Plant Development … and Interactions with Other Phytohormones 2014. J Plant Growth Regul 33:709–714

Wasternack C (2015) How jasmonates earned their laurels - past and present. J Plant Growth Regul 34. doi:10.1007/s00344-015-9526-5

Wildman S (1997) The auxin-A, B enigma: scientific fraud or scientific ineptitude? Plant Growth Regul 22:37–68