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COMMENTARY

Arabidopsis: two-hundredths anniversary of its name and the possibility of a hidden universal regulatory signal

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Abstract
In 1821, the Swiss botanist A. P. de Candolle (1788–1841) introduced the term "Arabidopsis" to denote a group of dicotyledonous plants (family Brassicaceae). Here, we recount the history of Arabidopsis research from 1588 to 2020, with a focus on light and plant development. We document that plant stem cell research, with commercial applications, is essentially based on Arabidopsis-thaliana. Then, we discuss scoto- and photomorphogenesis in this model plant and introduce the light-auxin-connection. Based on these insights, we argue that an as yet unknown "hidden signal" must be involved in the phenomenon of scotomorphogenesis, also known under the name etiolation. We conclude that Arabidopsis will serve in the foreseeable future as the model organism of choice with respect to the causal analysis of the actions of light and phytohormones during plant development.

Keywords Arabidopsis · Auxin · Evolution · Light · Plant development

Abbreviations

SPHN	*Socie´te´ de Physique et d'Histroire Naturelle*
IAPT	International Association for Plant Taxonomy
BR	Brassinosteroids
Pcz	Propiconazole
PAR	Photosynthetically Active Radiation
IAA	Indole-3-acetic acid

Introduction

Seventy years ago, the *Socie´te´ de Physique et d'Histroire Naturelle* (SPHN), also known as "International Association for Plant Taxonomy" (IAPT), was founded in Stockholm (Sweden). Best known for the publication of the journal *Taxon*, a leading periodical devoted to systematics, phylogeny and taxonomy of fungi, algae and plants, the SPHN regularly announces the award of the "Augustin-Pyramus de Candolle Prize" (Covan and Staflen 1982). Who was A. P. de Candolle (Fig. 1)? Born in the former Republic of Geneva (now Switzerland) on February 4, 1788, this gifted scientist became the founder of a novel system of plant classification that provided an empirical background for an evolutionary history of the vegetation of the world. Accordingly, the "A. P. de Candolle Prize" recognizes the author of the best scientific study of a taxonomic group of fungi, algae or plants. In addition to being an outstanding botanist, A. P. de Candolle was one of the first biologists to introduce the idea of "Nature's war", which inspired Charles Darwin (1809–1882) to develop his principle of descent with modification by means of natural selection (Kutschera 2003). Moreover, de Candolle discovered that the leaf movements of plants follow, in constant light, an approximately 24-h-cycle so that there may exist an internal "biological clock". The Swiss botanist died on 9. Sept. 1841 in Geneva. Two of his descendants, his son Alphonse Pyrame de Candolle (1806–1893), and his grandson Casimir de Candolle (1836–1918), continued his work on the taxonomy of plants (Morton 1981).

Two hundred years ago, A. P. de Candolle submitted a manuscript to his publisher in Paris, wherein he proposed the name "Arabidopsis" for a group of small cress species, one of which was formally described as *Pilosella siliquosa*.

Dedicated to the memory of Winslow R. Briggs (1928–2019).

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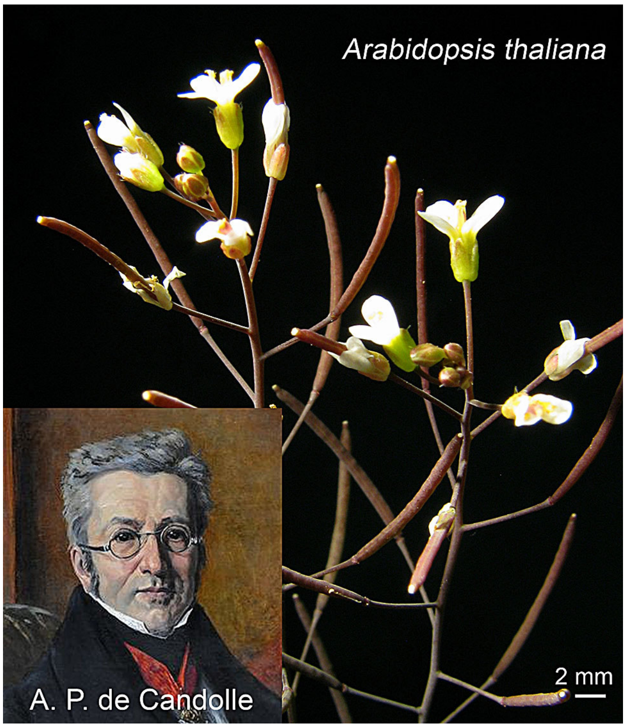

Fig. 1 The botanist Augustin Pyramus de Candolle (1788–1841) (historical painting) and original photograph of a flowering sporophyte of *Arabidopsis thaliana*. Two hundred years ago, de Candolle introduced the name "Arabidopsis" to denote a group of plants in his monograph *Regni Vegetabilis Systema Naturale*, published in 1821

Today, de Candolle's section name "Arabidopsis" dominates the modern plant sciences.

From the father of Floristics to Laibach's recommendation

In 1588, the German physician and botanist Johann Thal (1542–1583) published posthumously a book entitled *Sylva Hercynia*, which was a register of the plants that inhabited the Harz, a Mittelgebirge (low mountain range or highland area) of Central Europe. In this book, Thal (1588) described a plant under the species name *Pilosella siliquosa*, which later became known as "Thal's Kresse" (thale, or mouse-ear cress). One of the earliest depictions of *A. thaliana* is shown in Fig. 2 (Sturm 1796). It should be noted that, today, the genus *Pilosella* (family Asteraceae) represents a clade within the sunflower family (common names: aster, daisy or composite). This group of plants is a distant relative of the Brassicaceae (Crucifera), also known as the mustard family.

In 1821, A. P. de Candolle published Vol. 2 of his book *Regnis Vegetabilis Systema Naturale*. In a chapter on the Cruciferae, he introduced "Section VI. Arabidopsis". The author characterized these plants as follows: "Siliquae lineares compressae, stigmata sessili truncato subemarginato. Flores albi, Pedicelli embracteati, breves, vix calycis longitudine" (de Candolle 1821, p. 480).

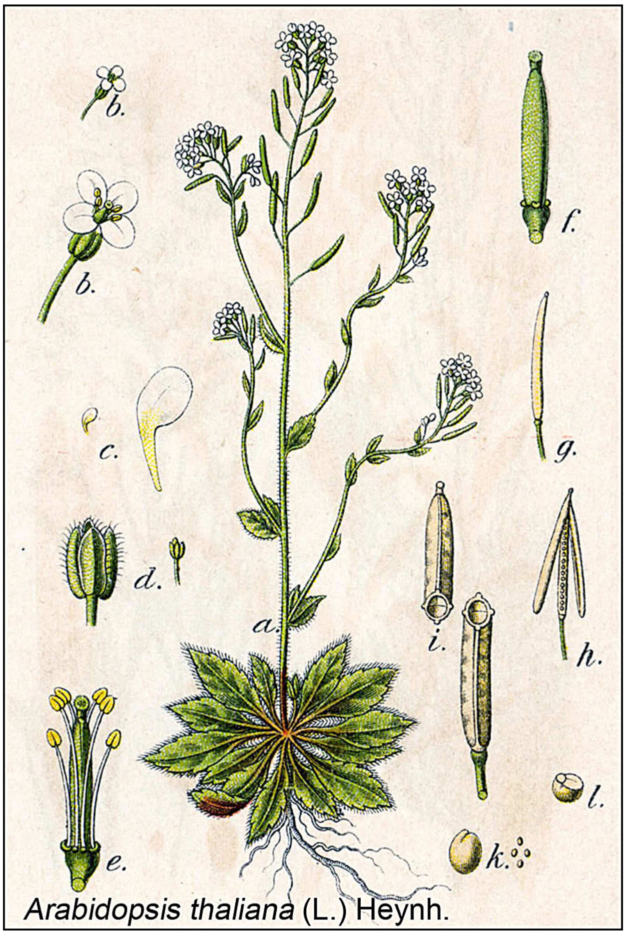

Fig. 2 Original description of the flowering plant *Pilosella siliquosa*, as described in Johann Thal's (1542–1583) monograph *Sylva Hercynia*, published in 1588 (adapted from an original drawing in Sturm 1796)

Two decades later, Holl and Heynhold (1842) established the genus *Arabidopsis* and described in their classical monograph only one species, which today is known under the name *Arabidopsis thaliana* (L.) Heynh. The letter "L." refers to Linnaeus, who first described this plant under another name in his classical books. One century later, the German botanist Friedrich Laibach (1885–1967) established the mustard plant *A. thaliana* (L.) Heynh. as a model organism for the experimental analysis of plant genetics and developmental biology of photoautotrophic organisms (Laibach 1943). Earlien Laibach (1907) had determined the haploid chromosome number in *A. thaliana* to be five. Based on this insight, the first mutagenesis-experiments on this small, self-fertilizing plant were carried out during the late 1940s.

As described by Provart et al. (2016) (see also Kutschera and Niklas 2016), *A. thaliana* has the properties of an ideal model system for basic research: small size for ease of growth in large populations (laboratory), well established classical genetics, ease of crossing, a short generation time, high fecundity (up to 10.000 small seeds per plant), small genome size, and the possibility to perform mutational screens in the laboratory. Based upon these traits and its amenability to all classical genetic processes, Arabidopsis joined the ranks of Security Council of Model Genetic Organisms "as a broad" phylogenetic representative, along with the other members, including lambda (virus), *Bacillus subtilis* (gram positive bacterium), *Escherichia coli* (gram negative bacterium), *Saccharomyces cerevisiae* (fungus), *Chlamydomonas reinhardtii* (alga), *Caenorhabditis elegans* (worm), *Drosophila melanogaster* (arthropod), *Mus musculus* (vertebrate), and humans (Fink 1998). In the next sections, we focus on plant development with reference to light and hormones.

Arabidopsis and stem cell research

Although multicellular organisms evolved independently in the Kingdoms Plantae and Animalia, the so-called "stem cell systems" developed in both branches of eukaryotic life. Here, we will focus on land plants (embryophytes), which are characterized by a process called "post-embryonic organ development". In this context, stem cell systems, localized within the meristems, are of special significance (Greb and Lohmann 2016). Figure 3 shows an adult, flowering *A. thaliana* plant (sporophyte) and the three meristems that harbor different stem cell systems.

Aggarwal et al. (2020) have documented that plant stem cells can be used commercially, notably in the cosmetics industry. The undifferentiated plant stem cells can be used to produce commercial products with antioxidant and anti-inflammatory properties (Aggarwal et al. 2020). The range of applications of plant stem cells in industry is broad and is largely untapped. Advances in Arabidopsis stem cell research have and will continue to lead the development of new products for human use.

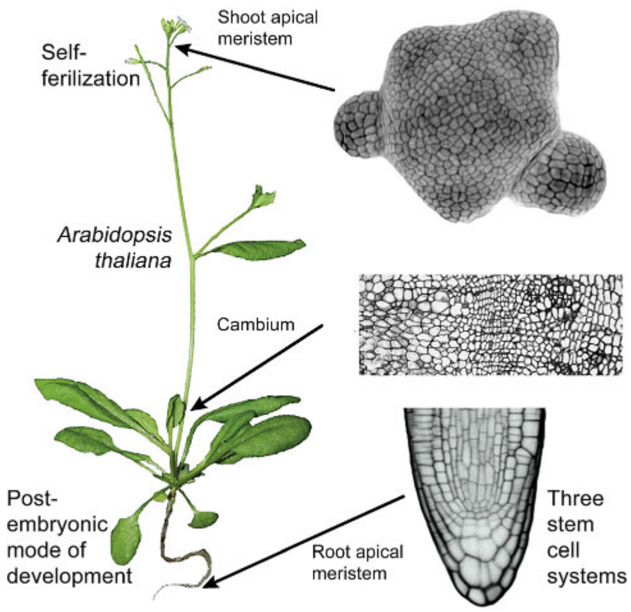

Fig. 3 Mature flowering sporophyte, with attached root, of *Arabidopsis thaliana*. Three stem cell systems are active throughout plant development. They are localized within the shoot apical meristem, the cambium, and the root apical meristem (adapted from Greb and Lohmann 2016)

Fig. 4 Photograph of mature *A. thaliana*-plants growing in soil (greenhouse, Department of Plant Biology, Carnegie Institution for Science, Stanford-CA, USA). The inset shows the upper part of two representative dark-grown seedlings raised either in the presence or absence of the brassinosteroid biosynthesis inhibitor Propiconazole (original photographs)

Plant development in darkness and light

Figure 4 shows adult, fully de-etiolated *Arabidopsis*-plants growing in garden soil that are about to reproduce via flowering and self-fertilization. However, the tiny seeds of this model plant germinate in moist soil and first establish an etiolated seedling that must grow into the light. The Inset (Fig. 4) shows an experiment documenting the role of the plant hormone brassinosteroid (BR) during seedling development in darkness. When seeds are grown in the presence of the BR-inhibitor Propiconazole (Pcz) (Hartwig et al. 2012), they develop a morphology as those grown in white light. Pcz is a specific inhibitor of BR biosynthesis (Hartwig et al. 2012). Both, BR and auxin promote cell elongation in an interdependent manner (Nemhauser et al. 2004). Growth in the absence of light is achieved by hormonal influence on cell elongation. Evidently, light-dependent morphology is repressed in darkness and some of these mechanisms can be artificially de-repressed, for example by Pcz application and other chemical treatments or known genetic defects in maintaining etiolated state. This suggests that the phenomenon of scotomorphogenesis is primed for early photomorphogenesis and that some of the light-dependent steps can be activated in darkness. An accompanying article in this issue presents a new hypothesis, for the first time invoking the need for a universal biochemical signal to promote scotomorphogensis as an actively regulated mechanism. A brief introduction to this topic is presented here.

A plausible model for auxin action at the organ level

Light triggers photomorphogenesis by suppressing auxin action. Figure 5 shows an experimental system to document this basic feature of plant life using *A. thaliana* as model organism. Under shaded conditions or daily light/-dark cycles, auxin activity increases as light intensity of Photosynthetically Active Radiation (PAR, 400–700 nm) decreases. Auxin-mediated responses can lead to prolonged periods of growth in the absence of light. For example, shoots of bamboo species Moso (*Phyllostachys edulis*) can grow more than 1 m per night (ca. 100 mm/h) by internode elongation attributed to increased IAA synthesis and response (reviewed in Kutschera and Khanna 2020). Auxin activity exhibits organ specificity and is fine-tuned to optimize growth and development. Innate mechanisms involved in regulating auxin-mediated growth responses have been well described. We postulate that these internal mechanisms are influenced by a yet unknown external signal to orchestrate the complexity of auxin activity at the organ level, similar to the influence of light in suppressing auxin activity with spatial and temporal specificity. We hypothesize that this external universal signal acts in contrast to light at all levels of plant growth and development.

Here we propose that developmental regulation mediated by auxin at the whole organ level is similar in coordination to the organ-level modifications mediated by PAR (visible spectrum). We suggest a plausible theory that a yet unknown environmental cue coordinates auxin action at the organ level, which we introduce as "Aleph", denoted by the symbol "ℵ". Aleph is the first letter of semitic "ABJD", it is one of the oldest alphabets (Proto-Canaanite alphabet, 1050 BC), which gave rise to the Greek alpha "A" (Darnell, J., *BBC News*, Nov. 15, 1999). Because of its ancient origin, we chose Aleph to represent the plausibly yet unidentified environmental signal(s). We propose that a signal (in the absence of PAR) is needed to orchestrate the observed specificity of dark-adapted growth

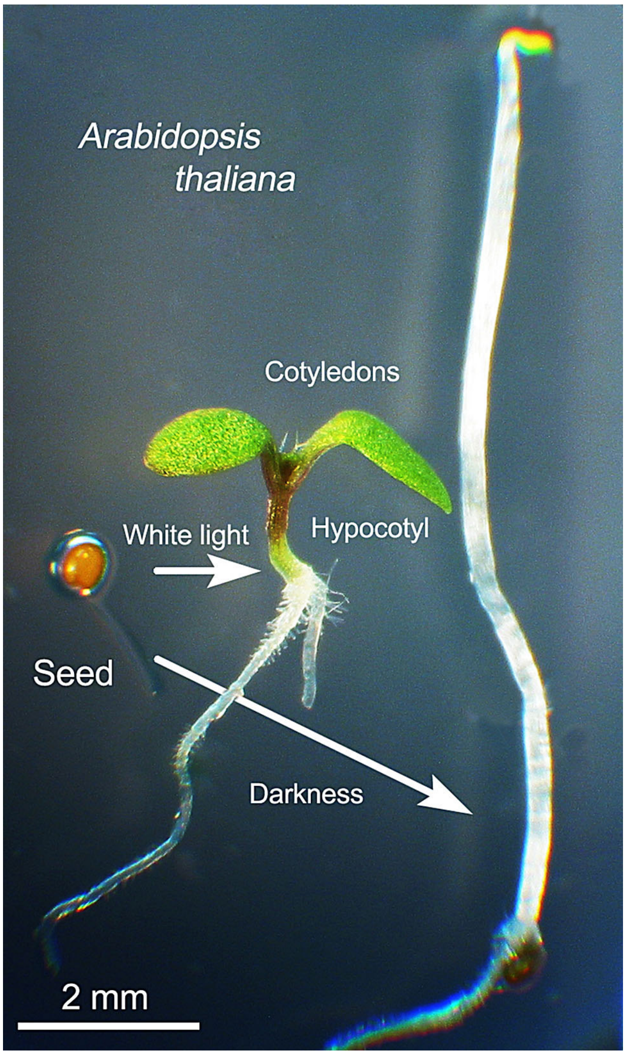

Fig. 5 Germination and seedling growth (photo- vs. scotomorphogenesis) of two representative *A. thaliana*-individuals raised on mineral salts-agar (in the absence of sucrose). The 5-day old seedlings were either grown in white-light or in darkness (original experiment)

responses, which were originally discovered and described by Sachs in 1887, using his self-recording auxanometer (Kutschera and Khanna 2020).

We propose that ℵ, like its counterpart "light photon" represented by γ, is an informational signal (of yet unknown properties) influencing growth responses in the absence of PAR, and that its effect is suppressed in the presence of PAR. We are currently investigating a likely downstream signal transduction pathway involved in the perception and transmission of this signal. In this hypothesis, ℵ mediates dark-adapted growth through the regulation of specific molecular, cellular and developmental changes, including the auxin-mediated secretion of glycoproteins into the outer epidermal wall (Kutschera and Khanna 2020). This hypothesis is supportive of stem elongation mechanisms described by Sachs in 1887, and elaborated by generations of plant scientists. Arabidopsis is well poised as a model plant, and it will continue to provide invaluable insights into plant growth and development, including the possibility that scotomorphogenesis is an externally regulated growth mechanism like photomorphogenesis (Kutschera and Wang 2019).

Conclusions

The "Augustin-Pyramus de Candolle Prize", announced on May 28, 2019 for the year 2020, by the SPHN (see Introduction) will be awarded to a plant scientist who has contributed significantly to the systematics of photoautotrophic organisms (or fungi) with reference to their evolutionary history. The founder of the name "Arabidopsis" (de Candolle 1821) was also an evolutionist who proposed the concept of the "war in nature" long before Charles Darwin picked up and elaborated on this idea (Kutschera 2003). Here we have shown that this model plant continues to be used to study the survival strategy of seedlings raised in darkness or irradiated with light (scoto- vs. photomorphogenesis). Arabidopsis-research has elucidated how environmental cues such as light and temperature influence hormonal responses and regulate gene expression to cause specific morphogenic changes. We hypothesize that another, yet unknown universal signal, dubbed Aleph (ℵ), influences growth and development in the absence of light. We conclude that the 200-year old name, Arabidopsis, represents a small plant with a remarkable history and future opportunities (Deng et al. 2014).

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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