75 Years ago *Arabidopsis* was first suggested as a Model Plant – But how did *Arabidopsis* Col-0 become the standard Natural Accession? Here's...

A Short History of *Arabidopsis thaliana* (L.) Heynh. Columbia-0

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The Origin of *Arabidopsis thaliana* Research (1905 – 1943)

Modern work with *Arabidopsis thaliana* goes back to the German botanist Friedrich Laibach who, while working as a Ph.D. student in the laboratory of Eduard Strasburger in Bonn, analyzed the number of chromosomes in different plants that he had collected around Bonn and his hometown Limburg[1,2]. The first *Arabidopsis* plants to be experimented on were collected by Laibach in **1905**, and belonged to the natural accession Limburg (Laibach introduced a system of naming the natural accessions after the places he collected them from)[2]. Laibach found that they carried 5 pairs of chromosomes, one of the smallest numbers known at the time (he published his results in **1907**, even though *Arabidopsis* was only included in the written thesis, but not specifically mentioned in the paper)[1–3]. Unfortunately, the natural habitat of the Limburg population was destroyed shortly after to make way for the new "Autobahn" (highway), connecting the cities of Frankfurt and Köln[2]. At the time, *Arabidopsis* was '*only known to florists and taxonomists, who had nothing better to do than constantly change its name and systematic positioning*', as Laibach put it in 1965[2]. However, he became interested in the little weed, and between **1930** and 1950 collected seeds from over 150 different natural accessions (or races, as he called them) of *Arabidopsis* from anywhere he or his colleagues travelled to[2,4]. Laibach kept all of these individual seed lines meticulously organized and maintained in his Department at Frankfurt University, and his collection eventually formed the foundation of the *Arabidopsis* Information Service (AIS) seed bank in the 1960s, which itself served as the basis for the modern Columbus (ABRC), Nottingham (NASC) and Tsukuba (RIKEN) stock centres decades later[2,5,6].

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Arabidopsis thaliana First Proposed as a Plant Model (1943 – 1957)

Laibachs' interest and preliminary studies of *Arabidopsis* eventually resulted in a now famous **1943** publication titled '*Arabidopsis Thaliana* (L.) Heynh. als Objekt für genetische und entwicklungsphysiologische Untersuchungen' ('*Arabidopsis Thaliana* (L.) Heynh. as an object for genetic, developmental and physiological analyses'), in which Laibach points out the benefits of working with *Arabidopsis* (easy to grow, small genome, short lifecycle, high seed yield, can be crossed and mutated…)[3]. Based on these observations he proposed to adopt *Arabidopsis* as a model organism for plant science, pointing out how comparable it is in its suitability to the 'prime example' of other models, *Drosophila melanogaster*[3]. This proposal however, was largely ignored by the scientific community at the time, who needed almost another 40 years to finally see the light and adopt *Arabidopsis* as a plant model system[7]. One academic who shared Laibach's enthusiasm for *Arabidopsis* was György P. Rédei from Hungary, who in **1955** had just finished his Ph.D. thesis, working on tomato and wheat[8]. After reading Laibach's article, Rédei recognized the potential of *Arabidopsis* for genetic studies, and with the help of his supervisor, Prof. Györffy, he asked Laibach for some *Arabidopsis* seeds to start his own work on this new model[8]. The seeds he obtained were the four natural accessions Graz, Limburg, Estland and Landsberg[9]. Rédei took these four lines with him, when he left Europe to start his own laboratory at the University of Missouri in Columbia, Mo[9]. For the next 20 years Rédei remained the only researcher working on *Arabidopsis* in the United States; or, as his former colleague Prof. Doug Randall put it, "*George was 20 to 30 years ahead of his time*"[10]. This situation, however, made it incredibly hard for Rédei to receive funding[9]. In fact, one of his funding applications to the National Science Foundation was now famously rejected on the basis that '*the genetics panel does not believe that it is worthwhile to develop Arabidopsis as a new model organism for genetic studies because only prokaryotes can contribute significantly to new knowledge*'[9]. But Rédei refused to give up on *Arabidopsis* and from the four seed lines he had received from Laibach, chose Landsberg as his model for future work. This choice was due to that Estland phenotypically did not match its description and Graz was late flowering, while Landsberg matched the description and seemed vigorous and healthy (it is not clear on which grounds Limburg was dropped)[9].

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The Columbia and Landsberg *erecta* lines Emerge (1957 – 1965)

In **1957** Rédei used his Landsberg seeds in a mutagenesis experiment, where he irradiated the seeds with X-rays and then screened for mutants with interesting phenotypes (meanwhile, in Australia, John Langridge was doing the same for Estland seeds he had received from Laibach)[9,11–13]. Gene mutagenesis by X-ray irradiation had been described in the 1920s for *Antirrhinum* and *Drosophila*, and one of Laibach's students, Erna Reinholz, went on to establish this technique for *Arabidopsis* seeds[4,14–16]. One of the first mutants Rédei recovered was the *erecta* mutant, which, with its stunted growth, appeared to be quite sturdy, and he thought it might come in handy for further experimentation[9,17]. He published the Landsberg *erecta* mutant in a paper dealing with heterosis, despite not being sure if the importance of his observation warranted a full publication[17]. His paper therefore opens with the paragraph '*The author feels somewhat hesitant to add to the large volume of the literature on the subject but its practical importance and theoretical interest prompt the decision in favor of this brief account*'[17]. However, in his mutagenesis screen Rédei also realized that the original Landsberg population was actually not a homogenous line, but appeared to be a mix of different lines[9,11]. Therefore, he chose a single plant from the batch that he had not irradiated, to establish a new, clean line for all further studies[9,11]. Following Laibach's example of naming the different natural accessions after the location where he found them, he named his new line Columbia[9,11]. So interestingly, Columbia is an American plant by name, but a central European plant by genetic heritage – something that can be demonstrated experimentally, when analysing its genetic polymorphisms[18]. In **1959**, another plant biologist, Willem Feenstra from the University of Groningen in the Netherlands, visited Rédei in Columbia and took the Landsberg *erecta* line with him for his own research, establishing this line as a standard in Europe, while Rédei concentrated his work on his own Columbia line[9,11,19].

Arabidopsis thaliana gets its Breakthrough (1965 – 1996)

In the following two decades, interest in *Arabidopsis* research slowly increased. By the mid-**1960s**, the AIS (https://www.arabidopsis.org/ais/newaisvols.jsp) was established as a yearly newsletter to connect the small *Arabidopsis* research community, and in **1965** the first International Arabidopsis Symposium in Göttingen, Germany, already attracted a full 25 participants[20,21]. The AIS would eventually evolve into the now invaluable The Arabidopsis

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Information Resource (TAIR) database[22]. As a result of this increased interest, György Rédei decided to take up Laibach's suggestion from 1943, and published the second article calling for the acceptance of *Arabidopsis* as a plant model in **1975**, simply titled '*Arabidopsis* as a genetic tool' (where he pointed out the same benefits Laibach had already pointed out 30 years earlier)[23]. Following this publication and a couple of highly influential papers from people like Maarten Koornneef (who worked with Will Feenstra), or Chris R. Somerville and Elliott M. Meyerowitz (converts from the model organisms *Escherichia coli* and *Drosophila melanogaster*, respectively), *Arabidopsis* finally got its break in the early **1980s**[7,24–26]. With *Arabidopsis* now finally established, the third article discussing its role as a model (published in **1985** and pointing out the same benefits that Rédei and Laibach had pointed out 10 and 40 years earlier) was now published in the prestigious *Science* journal[7]. This was followed quickly by the identification of the cauliflower mosaic virus 35S promoter and the engineering of the first transgenic *Arabidopsis* plant in **1986**, a Col-0 plant, giving plant molecular biology another massive boost and adding 'can be stably transformed' to the list of characteristics that make *Arabidopsis* a good model (see also 'A Short History of the CaMV 35S Promoter'[27] & 'A Short History of Plant Transformation'[28])[29].

Col-0 takes over as the Standard Accession (1996 – today)

During the next decade, *Arabidopsis* research was mostly done using the Landsberg *erecta* accession, even though Columbia also regularly appeared, especially in US laboratories or from groups that had obtained seeds directly from Rédei. However, this was about to change when, in **1996**, Columbia was chosen as the natural accession for the sequencing and annotation of the complete *Arabidopsis* genome[30]. Despite Landsberg *erecta* being more commonly used at the time, this choice was the obvious one in this case, because the Landsberg *erecta* line had previously been subjected to X-ray irradiation, and therefore carried several unnatural mutations, while Columbia had been maintained as a clean homozygous line[11,30]. Shortly after the genome was eventually published in the year **2000**, Columbia was also chosen as the natural accession for a genome-wide mutagenesis project at the SALK institute in San Diego, resulting in the SALK collection of T-DNA insertion lines – still the biggest resource of ready-to-order *Arabidopsis* mutants[31]. Following these two massive projects, it was clear that Columbia was firmly established as the number one natural accession for *Arabidopsis* research, while the use of

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Landsberg *erecta* has been declining ever since. And this all just because the Landsberg batch that György Rédei received from Friedrich Laibach in 1955 was not a homogenous line.

Addendum> What about the '(L.)' and the 'Heynh.' behind *Arabidopsis thaliana*, and the '-0' behind Col?

The '(L.)' and 'Heynh.', which are often found after *Arabidopsis thaliana*, are so-called 'authorities' - the official author abbreviation of the person who gave the plant its name[32]. Though *Arabidopsis thaliana* was first described by Johannes Thal, who gave it the name *Pilosella siliquosa minor*, it was Carl Linnaeus who named it *Arabis thaliana* (*thaliana* in honour of Johannes Thal)[33,34]. Therefore, the '(L.)' behind genus and species is the author abbreviation for Carl Linnaeus[33,34]. Botanist Gustav Heynhold then merged similar plants into one new genus, *Arabidopsis*, signifying *Arabis-like*, and added his own author abbreviation, 'Heynh.', behind the one from Linnaeus (Heynholds book '*Flora von Sachsen*' is generally cited here, though I could only find *Arabidopsis* in his book '*Nomenclator botanicus hortensis*')[33,35,36]. The '0' behind the Col name, on the other hand, signifies the source of an individual seed line[37]. Over the years, different laboratories that received Col seeds from György Rédei have propagated and maintained their own inbred lines of the original batch. When all these lines were later donated to the seed centres, a numbering system was developed to be able to distinguish these individual lines[37]. In this system, George Rédeis' Columbia line in the ABRC stock centre would be named Col-1/CS3176, or Col-1 in short[37]. The name is made up of [wild type]-[originator]/[maintainer stock-#], with the wild type being 'Col', the originator George Rédei, who was designated the number 1, and the maintainer, the ABRC stock centre, carrying it under the stock number 3176[37]. The line donated by Shauna Somerville to the ABRC, a direct descendent of Rédeis' Col-1, is Col-2/CS907, or in short, Col-2[37]. Confusingly, the Col-0 line (Col-0/CS1092) is actually a descendent of Rédeis' Col-1 line[37]. It received the lower originator number 0 because it was already maintained and propagated in the original AIS-seed bank by Albert Kranz, and is therefore an 'older' stock[5].

Further Reading:

- Friedrich Laibach - 60 Jahre *Arabidopsis*-Forschung, 1905-1965[2]
- György P. Rédei - *Arabidopsis thaliana* (L.) Heynh. A review of the genetics and biology[33]

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- Elliot M. Meyerowitz – *Arabidopsis thaliana*[38]
- Chris R. Somerville – *Arabidopsis* blooms[39]
- György P. Rédei - A heuristic glance at the past of *Arabidopsis* genetics[9]
- Elizabeth Pennisi - *Arabidopsis* Comes of Age[40]
- Elliot M. Meyerowitz – Prehistory and history of *Arabidopsis* research[41]
- Chris R. Somerville, Maarten Koornneef - A fortunate choice[20]
- Sabina Leonelli - *Arabidopsis*, the botanical *Drosophila*[42]
- Sabina Leonelli - Growing Weed, Producing Knowledge An Epistemic History of *Arabidopsis thaliana*[43]
- Maarten Koornneef, David Meinke - The development of *Arabidopsis* as a model plant[44]
- Ute Krämer - Planting molecular functions in an ecological context with *Arabidopsis thaliana*[45]
- Nicholas J. Provart et al. - 50 years of Arabidopsis research[46]

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References

1. **Laibach F**. Zur Frage nach der Individualität der Chromosomen im Pflanzenreich. **Beih Bot Zentralbl**. **1907;**22: 191–210. Available: https://www.biodiversitylibrary.org/item/27073#page/233/mode/1up
2. **Laibach F**. 60 Jahre Arabidopsis-Forschung, 1905-1965. **Arab Inf Serv**. **1965;**1: 16. Available: http://www.arabidopsis.org/ais/1965/laiba-1965-aagle.html
3. **Laibach F**. Arabidopsis Thaliana (L.) Heynh. als Objekt für genetische und entwicklungsphysiologische Untersuchungen. **Bot Arch**. **1943;**44: 439–455. Available: http://131.130.57.230/clarotest190/claroline/backends/download.php?url=L0xhaWJhY2gtMTk0My5wZGY=&cidReset=true&cidReq=300415WS14
4. **Reinholz E**. Röntgenmutationen bei Arabidopsis thaliana (L) Heynh. **Naturwissenschaften**. **1947;**1: 26–28. Available: https://link.springer.com/article/10.1007/BF00633319

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5. **Kranz AR**. Demonstration of new and additional population samples and mutant lines of the AIS-seed bank. **Arab Inf Serv**. **1978;**15: 2–4. Available: https://www.arabidopsis.org/ais/1978/kranz-1978-aabgw.html
6. **Röbbelen G**. The LAIBACH Standard Collection of Natural Races. **Arab Inf Serv**. **1965;**2. Available: http://www.arabidopsis.org/ais/1965/roebb-1965-xxxxx.html
7. **Meyerowitz EM, Pruitt RE**. Arabidopsis thaliana and Plant Molecular Genetics. **Science**. **1985;**229: 1214–8. Available at doi:10.1126/science.229.4719.1214
8. **Koncz C**. Dedication: George P. Rédei Arabidopsis Geneticist and Polymath. Plant Breeding Reviews. Oxford, UK: **John Wiley & Sons, Inc.**; **2010.** pp. 1–33. Available at doi:10.1002/9780470650325.ch1
9. **Rédei GP**. A heuristic glance at the past of Arabidopsis genetics. Methods in Arabidopsis Research. **1992.** pp. 1–15. Available at doi:10.1142/9789814439701_0001
10. **Potter E**. From Apathy to Apogee - Hardly anyone believed George Rédei's research mattered — until it changed everything. **Mizzou**. **2014;** Available: https://mizzoumag.missouri.edu/2014/08/from-apathy-to-apogee/
11. **Rédei GP**. Supervital Mutants of Arabidopsis. **Genetics**. **1962;**47: 443–60. Available: http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=PMC1210343
12. **Langridge J**. Biochemical Mutations in the Crucifer Arabidopsis thaliana (L.) Heynh. **Nature**. **1955;**176: 260–261. Available at doi:10.1038/176260b0
13. **Langridge J**. Arabidopsis thaliana, a plant Drosophila. **BioEssays**. **1994;**16: 775–778. Available at doi:10.1002/bies.950161014
14. **Muller HJ**. Artificial transmutation of the gene. **Science**. **1927;**66: 84–87. Available at doi:10.1126/science.66.1699.84
15. **Reinholz E**. Auslösung von Röntgen-Mutationen bei Arabidopsis thaliana (L.) Heynh. und ihre Bedeutung für die Pflanzenzüchtung und Evolutionstheorie. FIAT Report No. 1006. **1945.** Available: https://www.tib.eu/de/suchen/id/TIBKAT:778643786/X-ray-mutations-in-Arabidopsis-Thaliana-L-Heynh/
16. **Stein E**. Über den Einfluß von Radiumbestrahlung auf Antirrhinum. **Z Indukt Abstamm Vererbungsl**. **1922;**29: 1–15. Available at doi:10.1007/BF01958447
17. **Rédei GP**. Single locus heterosis. **Z Vererbungsl**. **1962;**93: 164–170. Available: https://link.springer.com/article/10.1007/BF00897025
18. **Nordborg M, Hu TT, Ishino Y, Jhaveri J, Toomajian C, Zheng H, et al.** The pattern of

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polymorphism in Arabidopsis thaliana. **PLOS Biol**. **2005;**3: 1289–1299. Available at doi:10.1371/journal.pbio.0030196

19. **Feenstra WJ**. Isolation of nutritional mutants in Arabidopsis thaliana. **Genetica**. **1964;**35: 259–269. Available at doi:10.1007/BF01804894

20. **Somerville CR, Koornneef M**. A fortunate choice: the history of Arabidopsis as a model plant. **Nat Rev Genet**. **2002;**3: 883–9. Available at doi:10.1038/nrg927

21. **Röbbelen G**. Preface. **Arab Inf Serv**. **1964;**1: 1. Available: https://www.arabidopsis.org/ais/1964/preface.html

22. **Huala E, Dickerman AW, Garcia-Hernandez M, Weems D, Reiser L, LaFond F, et al.** The Arabidopsis Information Resource (TAIR): a comprehensive database and web-based information retrieval, analysis, and visualization system for a model plant. **Nucleic Acids Res**. **2001;**29: 102–5. Available at doi:10.1093/nar/29.1.102

23. **Rédei GP**. Arabidopsis as a Genetic Tool. **Annu Rev Genet**. **1975;**9: 111–127. Available at doi:10.1146/annurev.ge.09.120175.000551

24. **Koornneef M, van Eden J, Hanhart CJ, Stam P, Braaksma FJ, Feenstra WJ**. Linkage map of Arabidopsis thaliana. **J Hered**. **1983;**74: 265–272. Available at doi:10.1093/oxfordjournals.jhered.a109781

25. **Leutwiler LS, Hough-Evans BR, Meyerowitz EM**. The DNA of Arabidopsis thaliana. **Mol Gen Genet**. **1984;**194: 15–23. Available at doi:10.1007/BF00383491

26. **Somerville CR, Ogren WL**. Inhibition of photosynthesis in Arabidopsis mutants lacking leaf glutamate synthase activity. **Nature**. **1980;**286: 257–259. Available at doi:10.1038/286257a0

27. **Somssich M**. A short history of the CaMV 35S promoter. **PeerJ Prepr**. **2018;**6:e27096v2: 1–16. Available at doi:10.7287/peerj.preprints.27096v2

28. **Somssich M**. A Short History of Plant Transformation. **PeerJ Prepr**. **2019;**: 1–28. Available at doi:10.7287/peerj.preprints.27556v1

29. **Lloyd AM, Barnason AR, Rogers SG, Byrne MC, Fraley RT, Horsch RB**. Transformation of Arabidopsis thaliana with Agrobacterium tumefaciens. **Science**. **1986;**234: 464–6. Available at doi:10.1126/science.234.4775.464

30. **Arabidopsis Genome Initiative**. Analysis of the genome sequence of the flowering plant Arabidopsis thaliana. **Nature**. **2000;**408: 796–815. Available at doi:10.1038/35048692

31. **Alonso JM, Stepanova AN, Leisse TJ, Kim CJ, Chen H, Shinn P, et al.** Genome-wide

insertional mutagenesis of Arabidopsis thaliana. **Science**. **2003;**301: 653–7. Available at doi:10.1126/science.1086391

32. **McNeill J, Barrie FR, Buck WR, Demoulin V, Greuter W, Hawksworth DL, et al.** International Code of Nomenclature for algae, fungi, and plants (Melbourne Code). **Koeltz Sci Books**. **2012;**: 1–140. Available at doi:10.1111/j.1365-2699.2010.02341.x

33. **Rédei GP**. Arabidopsis thaliana (L.) Heynh. A review of the genetics and biology. **Bibliogr Genet**. **1969;**20: 1–151.

34. **Linnaeus C**. Species Plantarum. Impensis G. C. Nauk. Holmiae; **1753.** Available: https://www.biodiversitylibrary.org/item/13830#page/1/mode/1up

35. **Heynhold G**. Nomenclator botanicus hortensis. Arnoldische Buchhandlung. Dresden und Leipzig; **1840.** Available: https://archive.org/details/nomenclatorbota00heyngoog

36. **Holl F, Heynhold G**. Flora von Sachsen. Verlag von Justus Naumann. Dresden; **1842.** Available: https://books.google.com.au/books/about/Flora_von_Sachsen.html?id=pEI-AAAAcAAJ&redir_esc=y

37. **ABRC**. Arabidopsis Natural Accessions (Ecotypes). **TAIR**. **2018;** Available: https://www.arabidopsis.org/abrc/catalog/natural_accession_5.html

38. **Meyerowitz EM**. Arabidopsis Thaliana. **Annu Rev Genet**. **1987;**21: 93–111. Available at doi:10.1146/annurev.ge.21.120187.000521

39. **Somerville CR**. Arabidopsis blooms. **Plant Cell**. **1989;**1: 1131–1135. Available: https://www.ncbi.nlm.nih.gov/pmc/articles/PMC1459042/pdf/hw1131.pdf

40. **Pennisi E**. Arabidopsis Comes of Age. **Science**. **2000;**290: 32–35. Available at doi:10.1126/science.290.5489.32

41. **Meyerowitz EM**. Prehistory and history of Arabidopsis research. **Plant Physiol**. **2001;**125: 15–9. Available at doi:10.1104/pp.125.1.15

42. **Leonelli S**. Arabidopsis, the botanical Drosophila: from mouse cress to model organism. **Endeavour**. **2007;**31: 34–8. Available at doi:10.1016/j.endeavour.2007.01.003

43. **Leonelli S**. Growing Weed, Producing Knowledge An Epistemic History of Arabidopsis thaliana. **Hist Philos Life Sci**. **2007;**29: 193–224. Available: https://www.jstor.org/stable/23334228

44. **Koornneef M, Meinke D**. The development of Arabidopsis as a model plant. **Plant J**. **2010;**61: 909–21. Available at doi:10.1111/j.1365-313X.2009.04086.x

45. **Krämer U**. Planting molecular functions in an ecological context with Arabidopsis

276 thaliana. **Elife**. **2015;**4: 1–13. Available at doi:10.7554/eLife.06100
277 46. **Provart NJ, Alonso JM, Assmann SM, Bergmann DC, Brady SM, Brkljacic J, et al.**
278 50 years of Arabidopsis research: highlights and future directions. **New Phytol**. **2016;**209:
279 921–944. Available at doi:10.1111/nph.13687
280

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