

This Week's Citation Classic™

Hager A, Menzel H & Krauss A. Versuche und Hypothese zur Primärwirkung des Auxins beim Streckungswachstum. (Experiments and hypothesis concerning the primary action of auxin in elongation growth.) *Planta* 100:47-75, 1971. [Inst. Botany, Univ. Münster, Federal Republic of Germany]

The paper describes a mechanism whereby the growth hormone auxin can change properties of the plant cell wall and thereby induce enhanced elongation. The hormone is assumed to cause an increase of H^+ -concentration in the cell wall compartment via an activation of ATP-dependent proton pumps in the plasmalemma. The increased H^+ -level, in turn, leads to an increase of wall plasticity and thus to increased cell elongation. [The *SCI*[®] indicates that this paper has been cited in over 215 publications since 1971]

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"This paper was preceded by some controversy. I was working at the Botanical Institute of the University of Munich as a *Wissenschaftlicher Assistent* and, in 1962, I produced a so-called *Habilitationsschrift*, an extensive scientific paper, which had to be submitted to the Faculty of Natural Sciences of the University of Munich. A positive vote on this *Schrift* by the professors on the faculty is necessary —according to German academic customs —to obtain the *venia legendi*, i.e., the permission to lecture at the university.

"In this *Habilitationsschrift*, entitled 'Analyses of cell elongation mechanisms inducible by H^+ -ions',¹ I showed, among other things, that the growth of sunflower stem sections or oat coleoptiles can be stimulated when transferred into acidic buffers (pH 4-5), even without addition of the growth hormone auxin. I proposed the term 'acid growth' (*Säurewachstum*)¹ for this kind of elongation, which was thought to be caused by pH-dependent changes of cell wall properties and which could be induced also under anaerobic conditions.

"Within the faculty, the opinions of the referees concerning these results were rather controversial. Some considered the findings as artifacts or else as of no relevance for the explanation of biological growth processes, others showed a sort of benign indulgence, and finally some thought the results to be very interesting. In the end, however, the work was judged positive and I got my *Habilitation*.

"In 1970, after more experimental results, obtained in collaboration with Anne Krauss and Helga Menzel, doctoral students at this time, I dared to propose that a pH-decrease in the cell wall is an essential step in the auxin chain of action and that this pH-decrease is caused by an active export of H^+ -ions from the cytoplasm into the wall. The driving force for this H^+ -secretion could be ATP-dependent H^+ -pumps in the plasmalemma; the activity of the pumps could be controlled by auxin. I presented these ideas for the first time in a plenary lecture at the meeting of the Deutsche Botanische Gesellschaft in Erlangen, in 1970, and published them in *Planta* in 1971.

"These ideas stimulated many research groups to test them critically and to do further experiments. In this connection, I would like to mention R. Cleland and D.L. Rayle; without their intensive research, the acid growth hypothesis would not have obtained acceptance so rapidly. The work of E. Marrè", P.M. Ray, M.L. Evans, Y. Masuda, L.N. Vanderhoeff, R. Hertel, and many others can also be referred to in this context.

"However, it was not until the early 1980s that we could clearly demonstrate the transmembrane transport of protons and the postulated ATP-dependent proton pumps.^{2,3}

"I think the reason why this paper has been quoted so often may be the new approaches offered for an analysis of the molecular mechanism of action of the well-known growth hormone auxin; the proposed hypothesis could explain a 40-year-old finding,⁴ namely, an auxin-induced cell wall softening.

"On the other hand, it was shown for the first time that the mechanism proposed by the hypothesis of Mitchell^{5,6} (ATP = ΔpH) does play a role not only in energy coupling at the membranes of 'procaryotic' mitochondria and chloroplasts but also at membranes of the eucaryotic ('host') cell where it can control growth processes."

1. Hager A. *Untersuchungen über einen durch H^+ -Ionen induzierbaren Zellstreckungsmechanismus*. Habilitationsschrift. Munich: University of Munich, Faculty of Natural Sciences, 1962.
2. Hager A, Frenzel R & Laible D. ATP-dependent proton transport into vesicles of microsomal membranes of *Zea mays* coleoptiles. *Z. Naturforsch. Sect. C* 35:783-93, 1980.
3. Hager A & Helmle M. Properties of an ATP-fueled, Cl⁻-dependent proton pump localized in membranes of microsomal vesicles from maize coleoptiles. *Z. Naturforsch. Sect. C* 36:997-1008, 1981.
4. Heyn A N J. Der Mechanismus der Zellstreckung. *Rec. Trav. Bot. Néerl.* 28:133-244, 1931.
5. Mitchell P. Chemiosmotic coupling in oxidative and photosynthetic phosphorylation. *Biol. Rev. Cambridge Phil. Soc.* 41:445-502, 1966.
6. Citation Classic. Commentary on *Biol. Rev. Cambridge Phil. Soc.* 41:445-502, 1966. *Current Contents* (16): 14, 17 April 1978.