

Seminar

Molekulare Mechanismen der Signaltransduktion

08.05.13 – MQ

- Background Auxin

- Einstieg in genetische Studien zum Auxin Signaling:

1. Estelle and Somerville, (**1987**) Auxin resistant mutants of *Arabidopsis thaliana* with an altered morphology. **Molecular and General Genetics** 206:200

2. Lincoln et al., (**1990**) Growth and development of the axr1 mutants of Arabidopsis. **Plant Cell** 2:1071

3. Leyser et al., (**1993**) Arabidopsis auxin-resistance gene AXR1 encodes a protein related to ubiquitin-activating enzyme E1. **Nature** 364:161

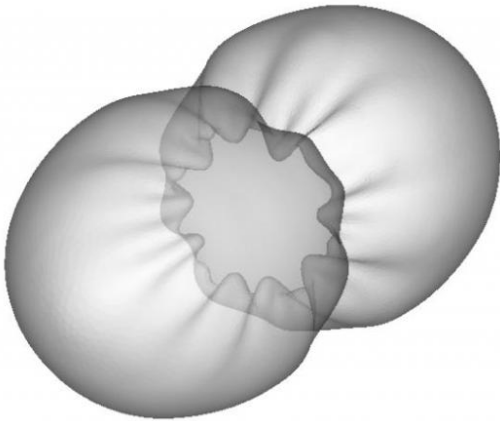
- Terminvergabe

Introduction

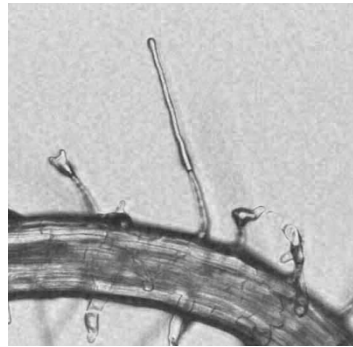
Definition:

Hormones are chemical signals that are produced in one part of the body, transported to other parts, bind to specific receptors, and trigger responses in target cells and tissues.

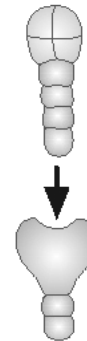
- Hormone (greek) → to excite
- In general, plant hormones control plant growth and development by affecting the division, elongation, and differentiation of cells.



cell division



cell
elongation

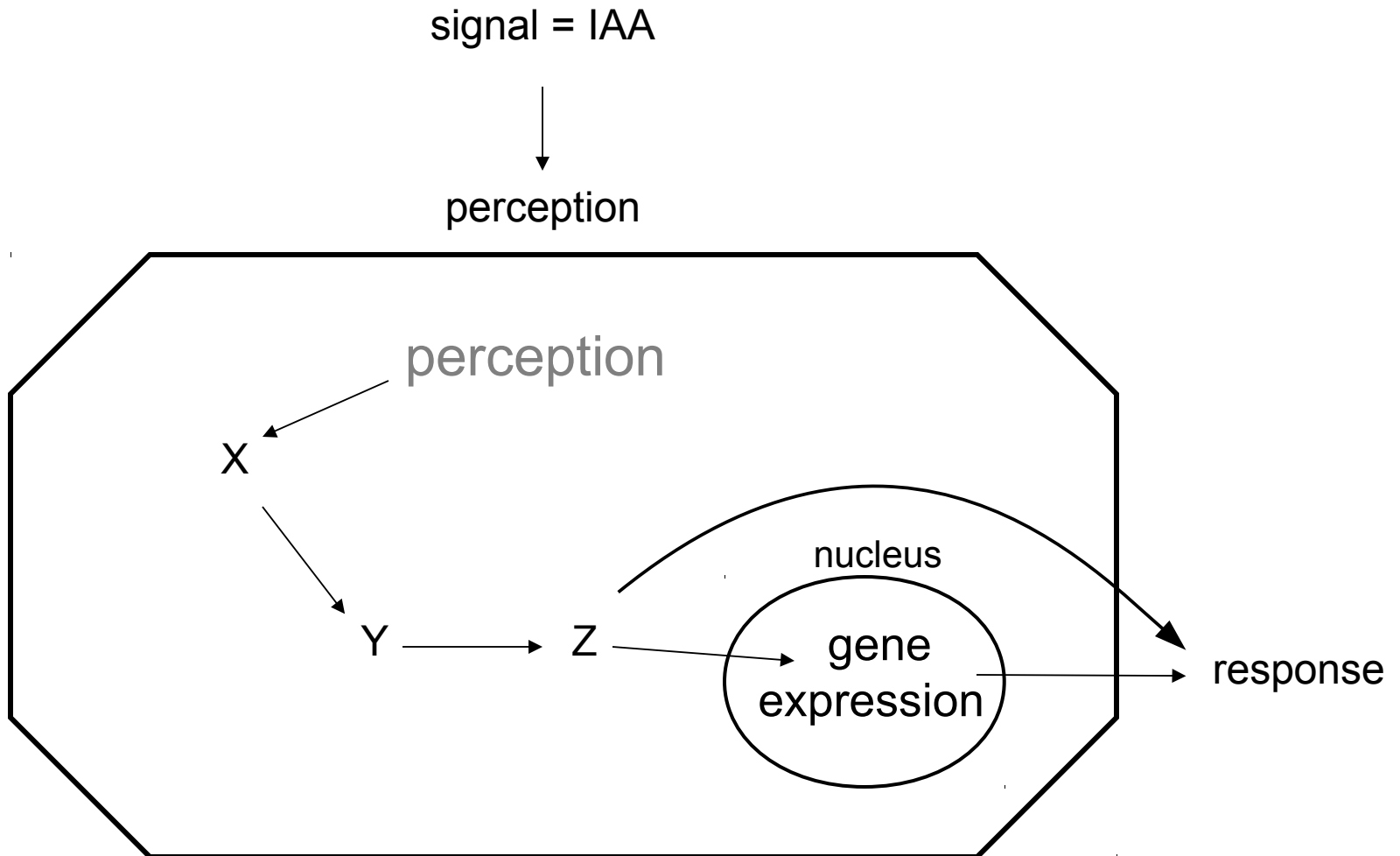


cell
differentiation

→ **Aim of this seminar:** Elucidate the transduction pathway of the signaling molecule/hormone auxin from perception to cellular/morphological responses

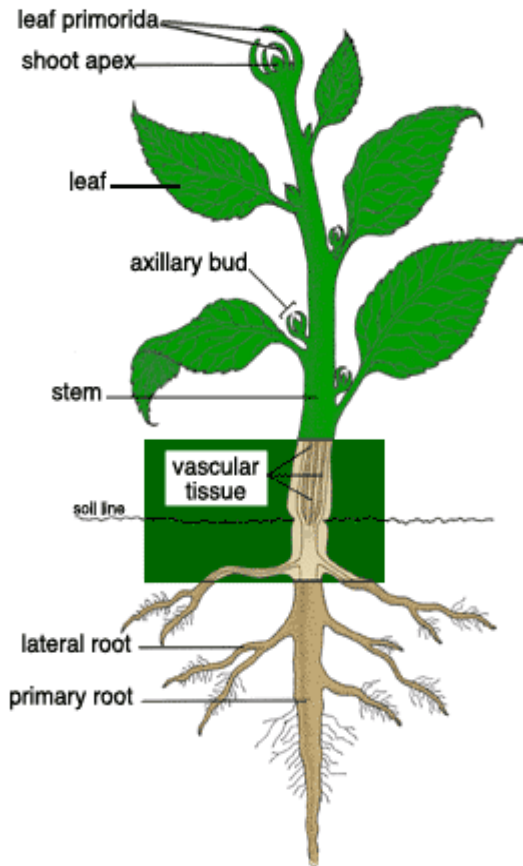
Excluding: biosynthesis, metabolism, transport

Black box of signaling



Auxin History I - 1758-1880

By definition hormones need to move between organs
→ transport system in plants?



1758

Henri Louis Duhamel du Monceau

→ two streams of sap moving in opposite directions are responsible for establishing correlations between organs



1880

Julius von Sachs

→ proposed a first coherent framework of root-forming, flower-inducing, and other special substances, which move in different directions through the plant to control its growth and development

The vasculature!
Alternatively: movement by diffusion

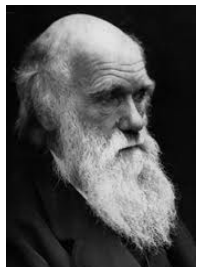
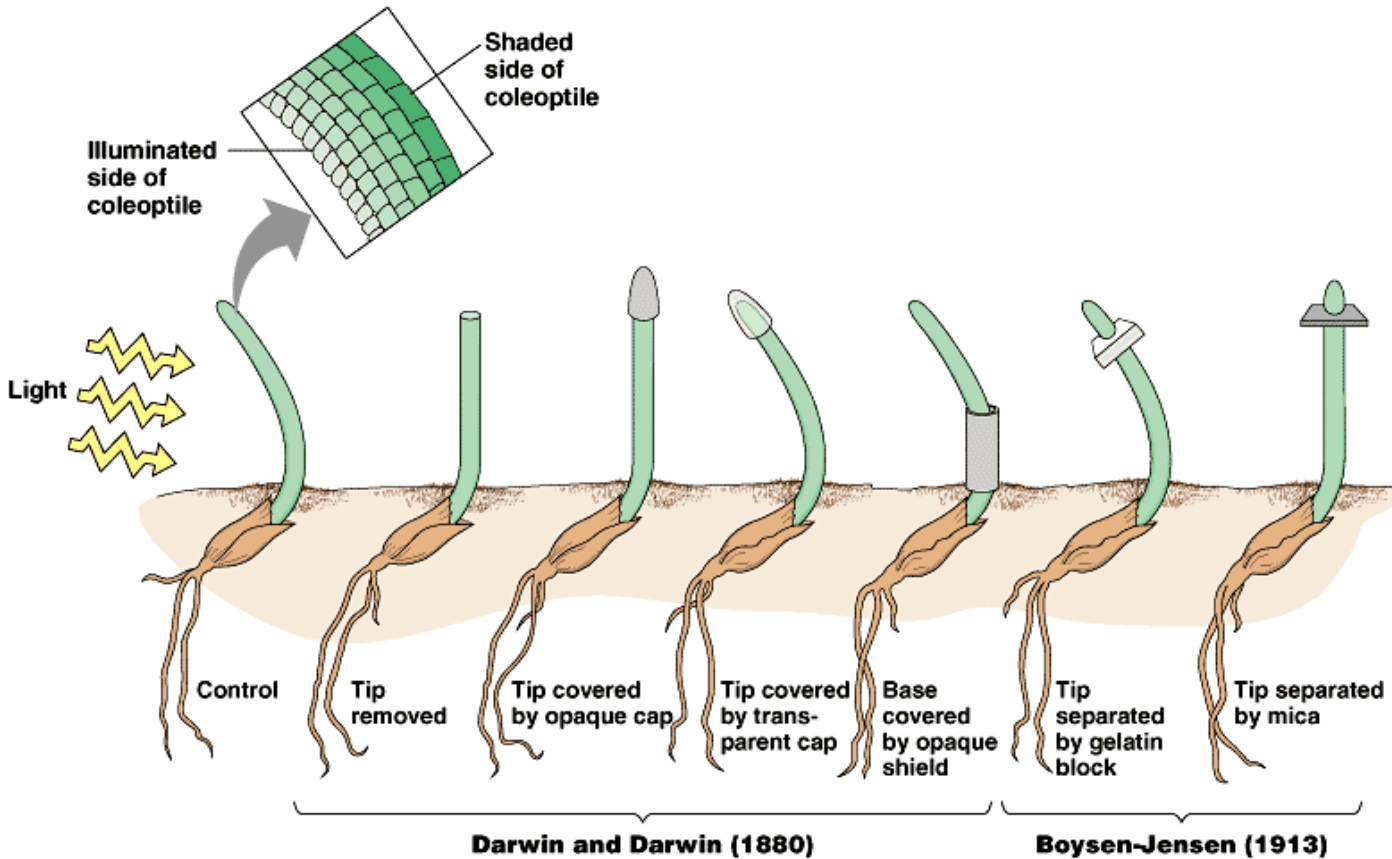
Auxin History II - 1880-1935



Canary grass
(*Phalaris canariensis*)



Oat
(*Avena ssp*)



“When seedlings are freely exposed to a lateral light some influence is transmitted from the upper part of the coleoptile that acts on the lower part of the coleoptile”
 “*The Power of Movement in Plants*”
 (1880) by Darwin and Darwin.

Peter Boysen-Jensen demonstrated that the signal was a mobile chemical substance

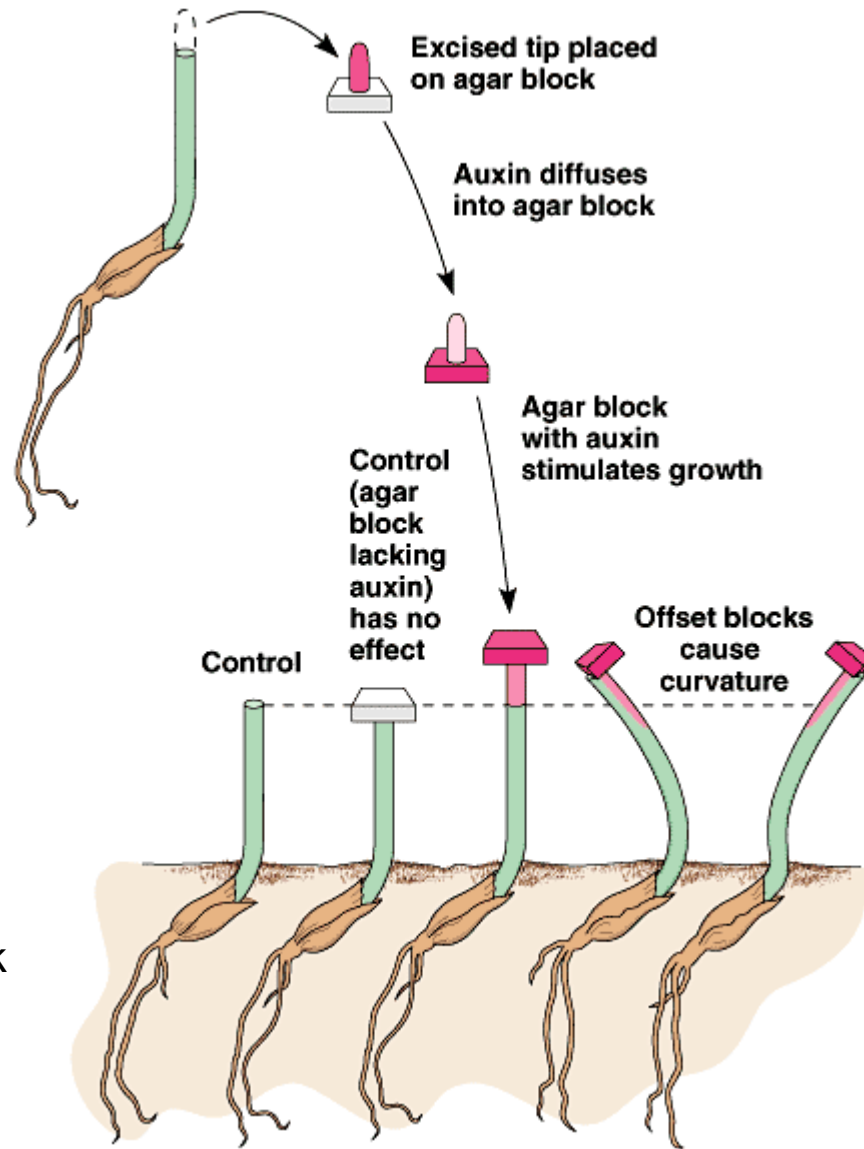
Auxin History II - 1880-1935



Frits W. Went - 1958

In 1926, F.W. Went extracted the chemical messenger for phototropism, naming it **auxin** → *auxano* (greek) = to grow

→ an asymmetrical distribution of auxin moving down from the coleoptile tip causes cells on the dark side to elongate faster than cells on the brighter side.



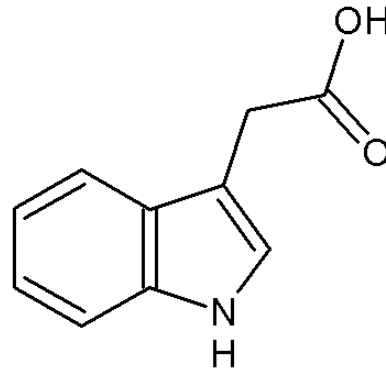
Auxin History II - 1880-1935



Kenneth V. Thimann
1960

Supplement to "Nature," January 19, 1935

**Identity of the Growth-Promoting and Root-
Forming Substances of Plants**



IAA
indole-3-acetic acid

→ the principal auxin in all plant species

Auxin History III - 1935-1985

THE NEW PHYTOLOGIST

VOL. XXXIV, No. 5

4 DECEMBER, 1935

ACTIVATION OF CAMBIAL GROWTH BY PURE HORMONES

By R. SNOW

Fellow of Magdalen College, Oxford

+ IAA

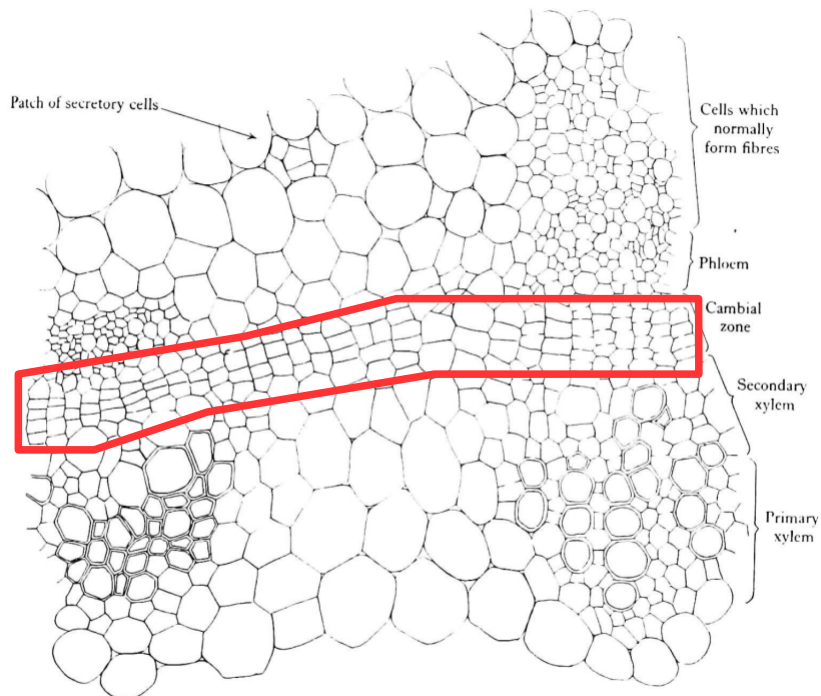


Fig. 4, Exp. 3* Experimental plant no. 1. Section at 10 mm. below top, and 5 mm. below zone covered by gelatins and auxin-*a*. $\times 202$.

*Sunflower seedlings

- IAA

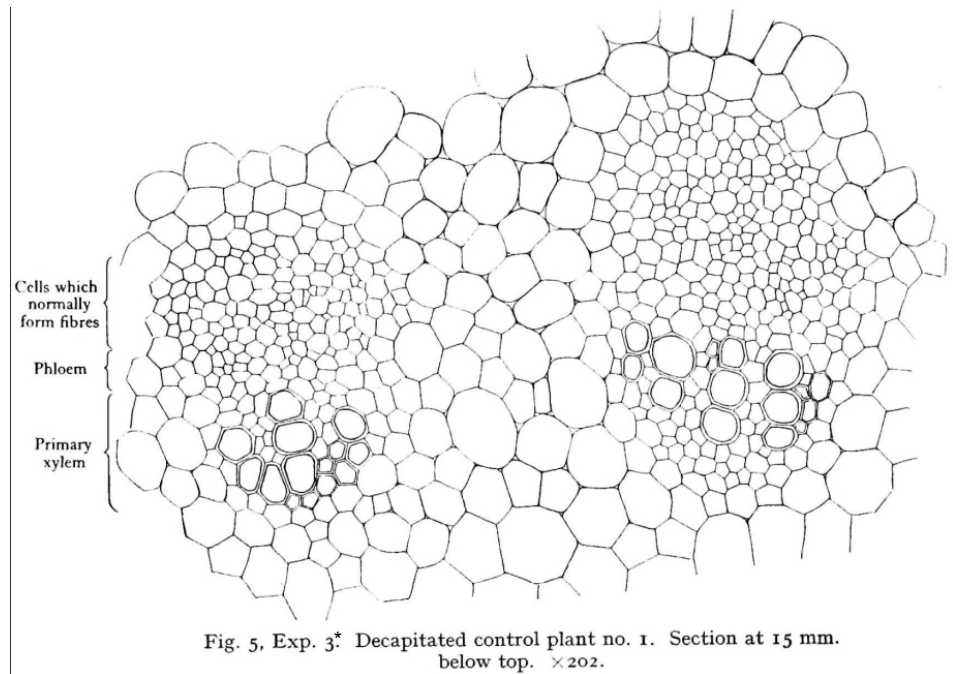


Fig. 5, Exp. 3* Decapitated control plant no. 1. Section at 15 mm. below top. $\times 202$.

*Sunflower seedlings

Auxin History III - 1935-1985

Changes Induced by Indoleacetic Acid in Nucleic Acid Contents and Growth of Tobacco Pith Tissue¹

Julius Silberberger, Jr., and Folke Skoog

Department of Botany,
University of Wisconsin, Madison

SCIENCE, Vol. 118

October 16, 1953

Auxin treatment increases the
level of nucleic acids!



Gene activation?

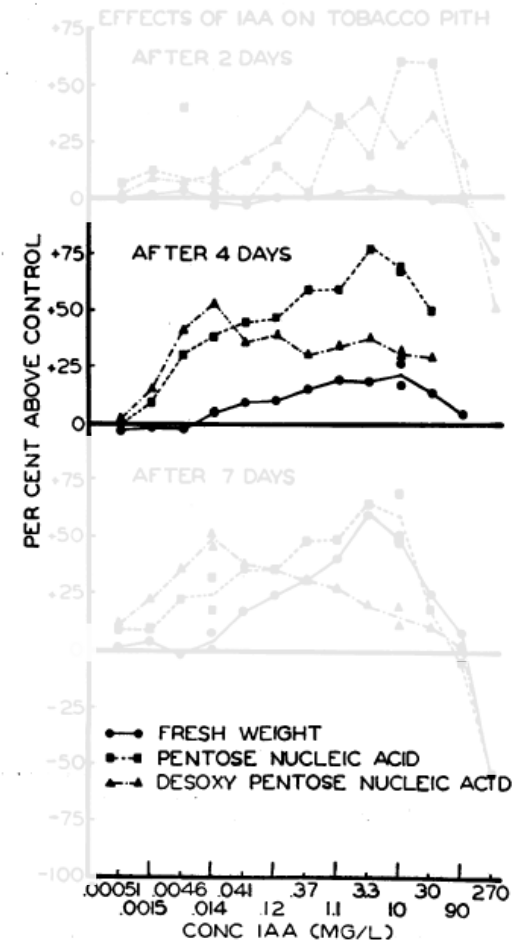


FIG. 1. Changes as per cent of controls in fresh weight; DNA content, and PNA content in excised tobacco pith tissue disks cultured on a sucrose agar medium with serial concentrations of IAA for 2, 4, and 7 days.

Support: Inhibitors of RNA and protein biosynthesis prevent cell elongation (Key, 1969, Annu Rev Plant Physiol)



Gene activation hypothesis: Auxin regulates the synthesis of specific RNAs required for cell growth

Auxin History III - 1935-1985

J. Mol. Biol. (1985) **183**, 53–68

Rapid Induction of Specific mRNAs by Auxin in Pea Epicotyl Tissue

Athanasios Theologis†, Thanh V. Huynh and Ronald W. Davis

*Department of Biochemistry
Stanford School of Medicine
Stanford University, Stanford, CA 94305, U.S.A.*

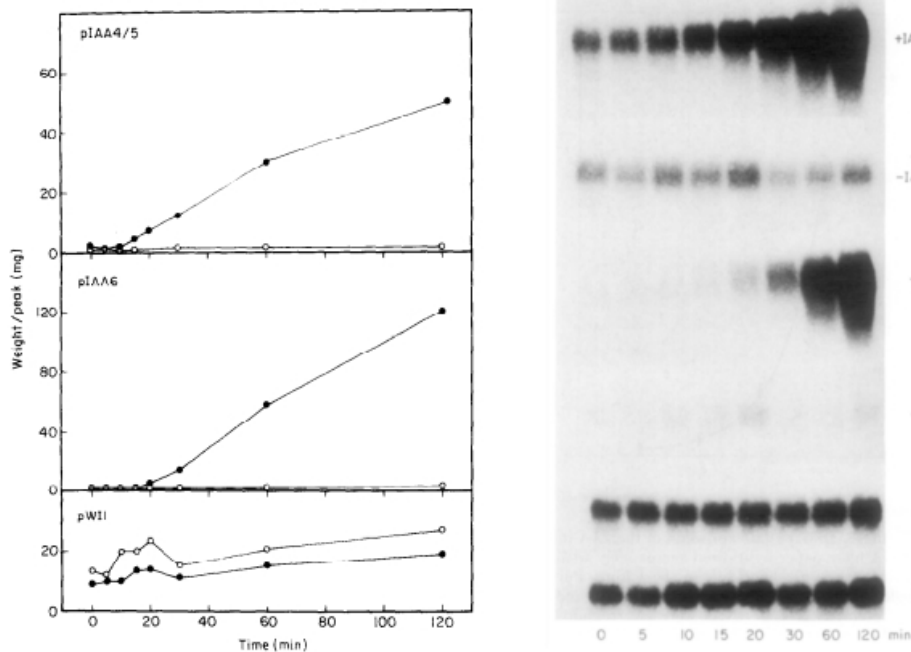
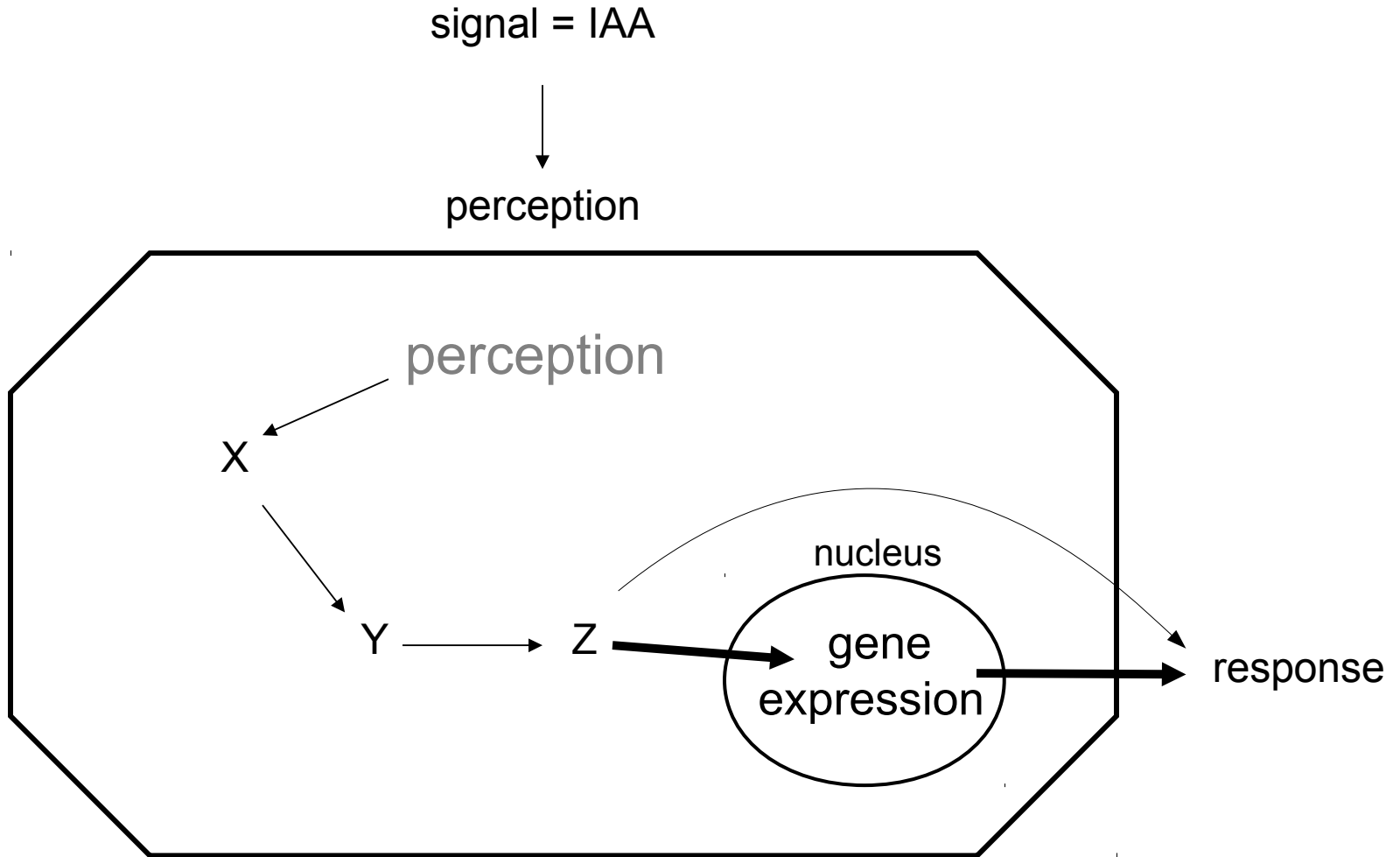


Figure 3. Induction kinetics of the IAA-inducible mRNAs. Endogenous IAA-depleted pea segments were treated with or without 20 μ M-IAA. Poly(A)⁺ RNA was isolated at various time intervals from 2 g fresh weight (100 segments) of control or IAA-treated tissue: 20 μ g of poly(A)⁺ RNA from 0, 5, 10, 15, 20, 30, 60 and 120 min incubations were electrophoretically separated and transferred to aminophenylthioether paper as described in Materials and Methods. Time-points are indicated at the bottom of respective lanes on the right-hand side of the Figure. Two RNA papers were prepared, one contained the IAA mRNAs (+IAA) and the other the control mRNAs (–IAA). The filters were successively hybridized to ³²P-labeled pIAA4/5, pIAA6 and pW11 plasmid DNAs (top, middle, bottom right) after previous removal of the radioactive probe as described in Materials and Methods. The autoradiograms of these papers are shown on the right-hand side of the Figure, and were scanned in a Joyce–Loebl recording densitometer. The areas under the curves were quantitated by weighing, and the results are shown on the left-hand side of the Figure. (●) With IAA; (○) without IAA.

← Rapid induction of mRNAs after 10–15 min of IAA application

↓
The most likely scenario:
Auxin regulates cell growth indirectly by controlling *de novo* expression of genes required for that process.

Black box of signaling



Gene activation hypothesis suggests the 'nuclear route'

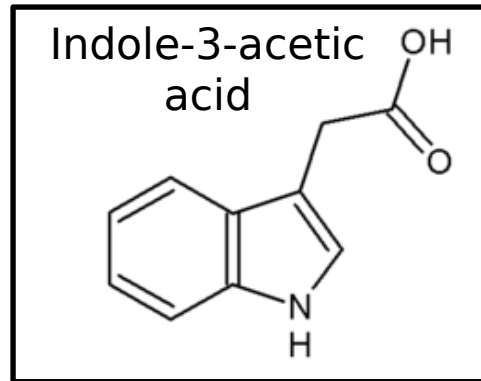
Arabidopsis thaliana



- Small size (30 cm)
- Rapid life cycle (6-8 weeks)
- Prolific seed production (5000 seeds/plant)
- Sequenced genome (125 Mb; ~28,000 genes)
- Easily transformable
- Tremendous community resources

A power multicellular eukaryotic model system

Auxin regulates plant development

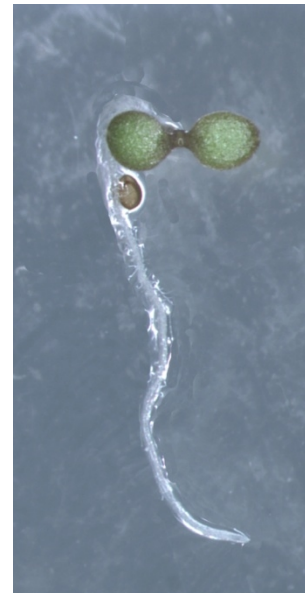


▷ Embryonic patterning

Growth & Apical dominance

Root development

Tropic growth responses

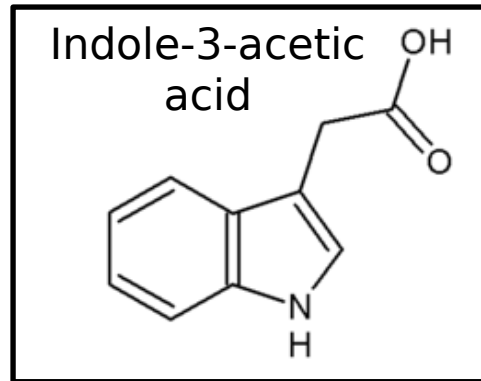


wild-type



bdl axr1
mutant

Auxin regulates plant development



Embryonic patterning

▷ Growth & Apical dominance

Root development

Tropic growth responses

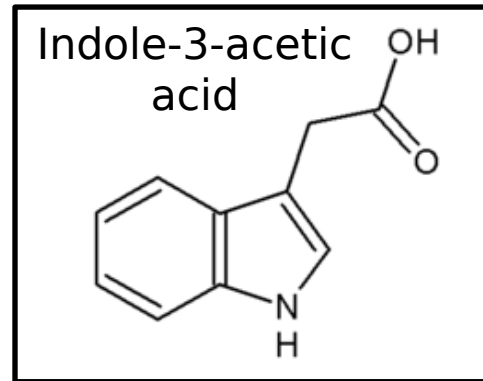


wild-type



axr6-3 mutant

Auxin regulates plant development



Embryonic patterning

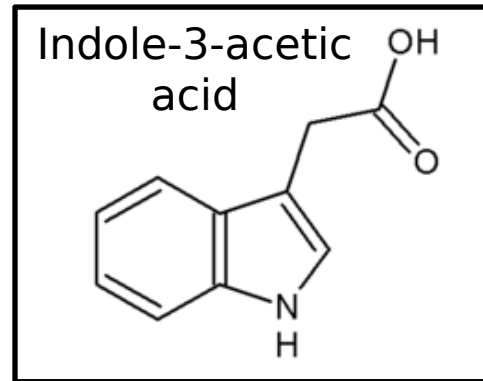
Growth & Apical dominance

▷ Root development

Tropic growth responses



Auxin regulates plant development



Embryonic patterning

Growth & Apical dominance

Root development

▷ Tropic growth responses



wild-type *aux1* mutant

Auxin-resistant mutants of *Arabidopsis thaliana* with an altered morphology

Mark A. Estelle* and Chris Somerville

MSU-DOE Plant Research Laboratory, Michigan State University, East Lansing, MI 48824, USA

Aim:

- Isolation of mutants with increased auxin resistance
- Identification of signaling elements that regulate auxin response

What was known?

- Auxin induces cell extension
- Auxin induces cell division
- Auxin induces cell differentiation

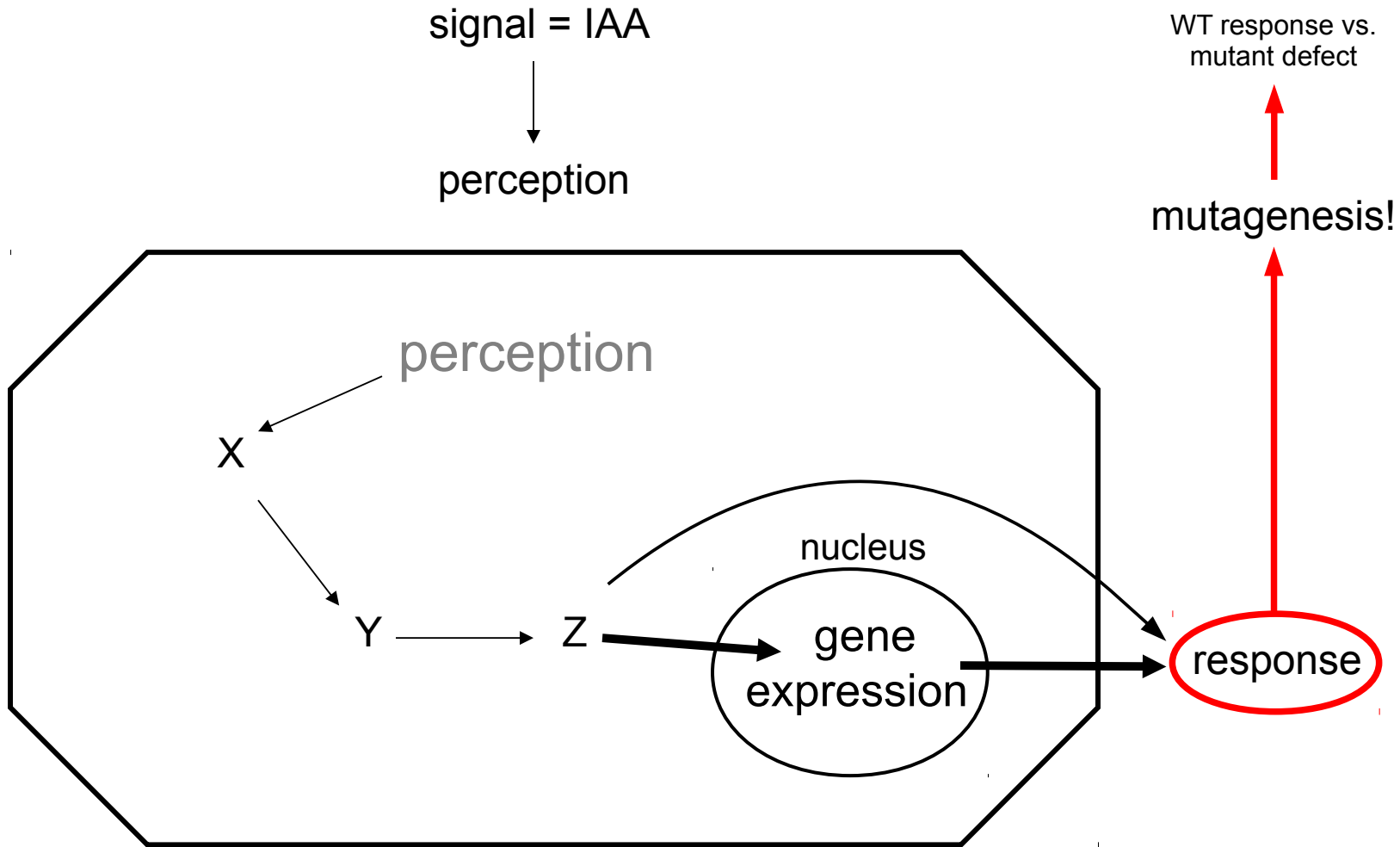


Depends most likely on *de novo* gene expression/protein synthesis

What was NOT known?

- enzymes of auxin biosynthesis
- auxin transport facilitators
- auxin signaling elements
- *Arabidopsis* genome sequence

Black box of signaling



Genetic approach?

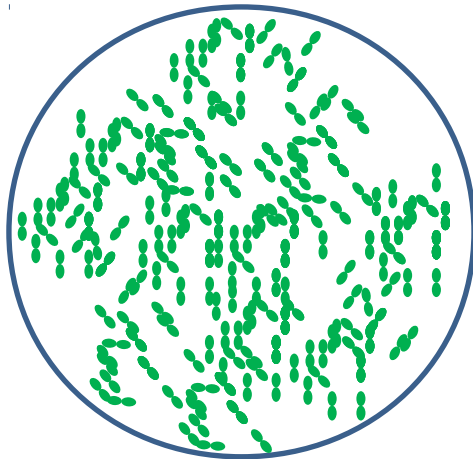
Mutagenesis

Prerequisite:

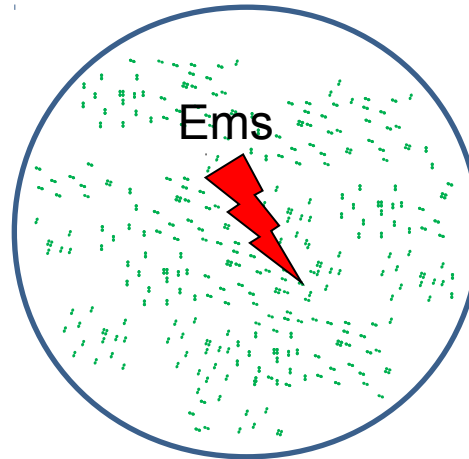
- Phenotype associated with trait of interest

└─▶ Seedling development → screen for mutants defect in wild-type response

Germination:

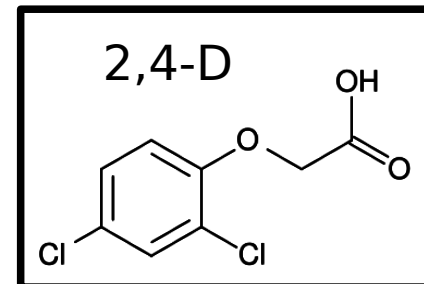
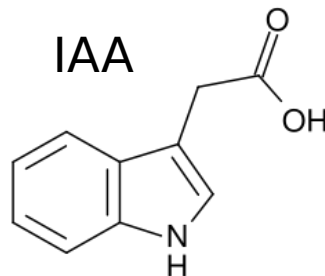


-
auxin



+
auxin

Ems = ethyl methanesulfonate
↓
Substitution G/C to A/T



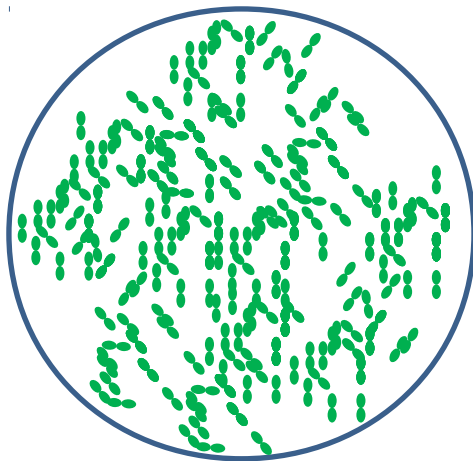
Mutagenesis

Prerequisite:

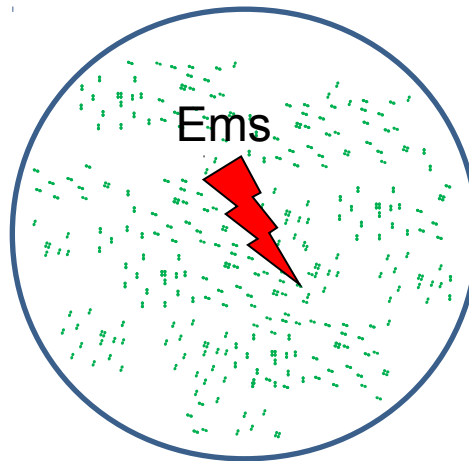
- Phenotype associated with trait of interest

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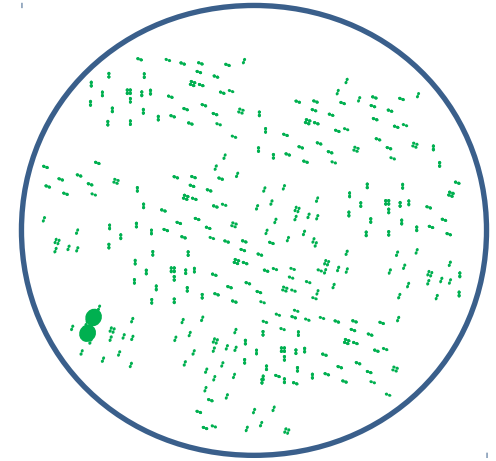
Germination:



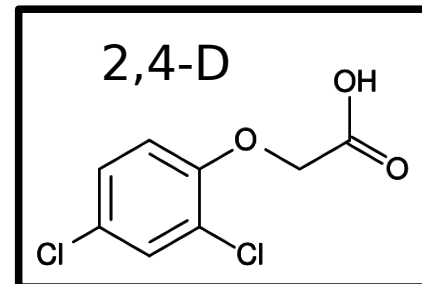
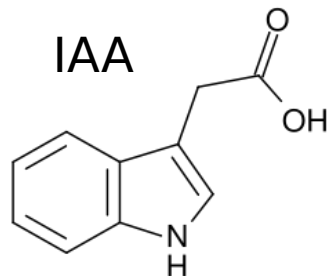
-
auxin



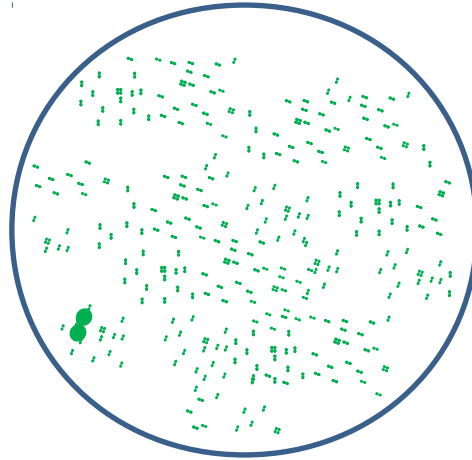
+
auxin



+
auxin



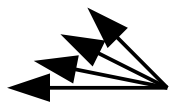
Mutant/Gene nomenclature



+
auxin

Same mutant screen,
different genes:

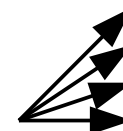
axr1
axr2
axr3
axrx



Name of the mutant: *auxin resistant 1 - axr1*

alleles:

axr1-1
axr1-2
axr1-3
axr1-x

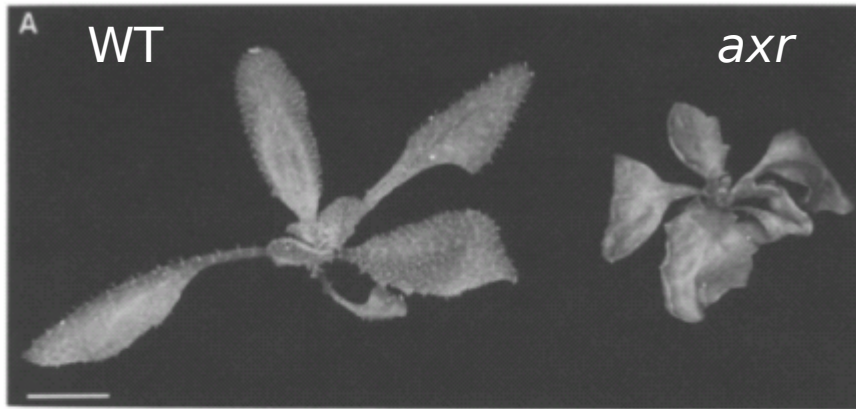


Name of the gene: *AUXIN RESISTANT 1 - AXR1*

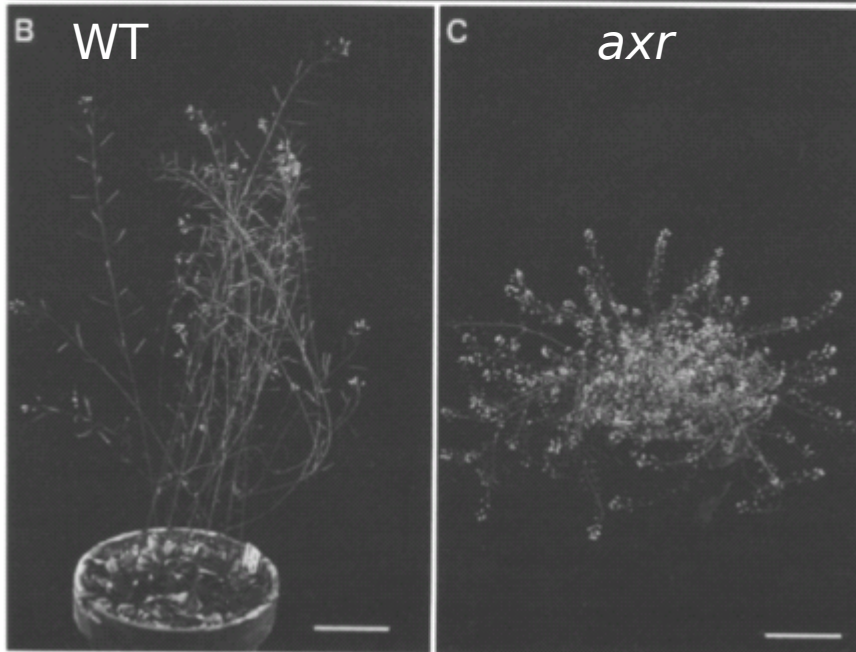


Name of the protein: *AUXIN RESISTANT 1 - AXR1*

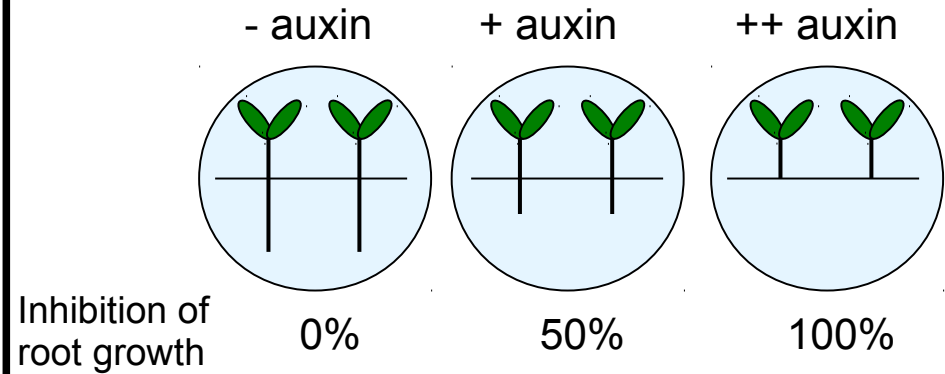
Phenotypes



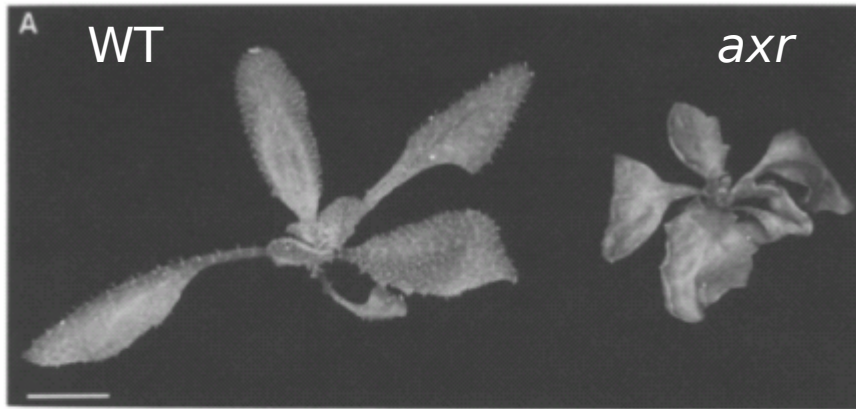
- rosette smaller, short petioles, crinkled leaves
- roots thinner, not as highly branched
- 25-30 inflorescences compared to 1-5 in WT
→ apical dominance
- pollen fertility reduced → stamen shorter



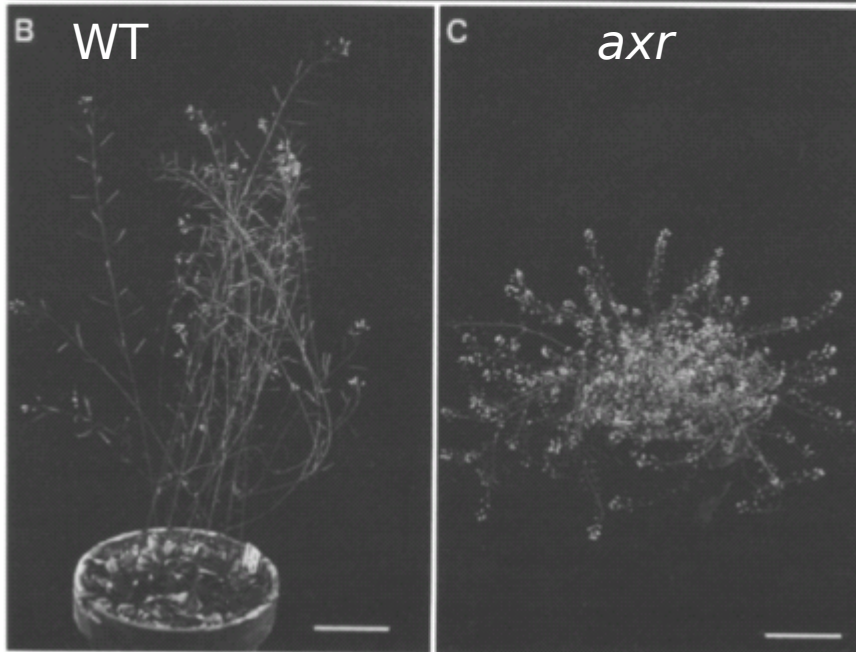
Auxin response assay – root growth inhibition:



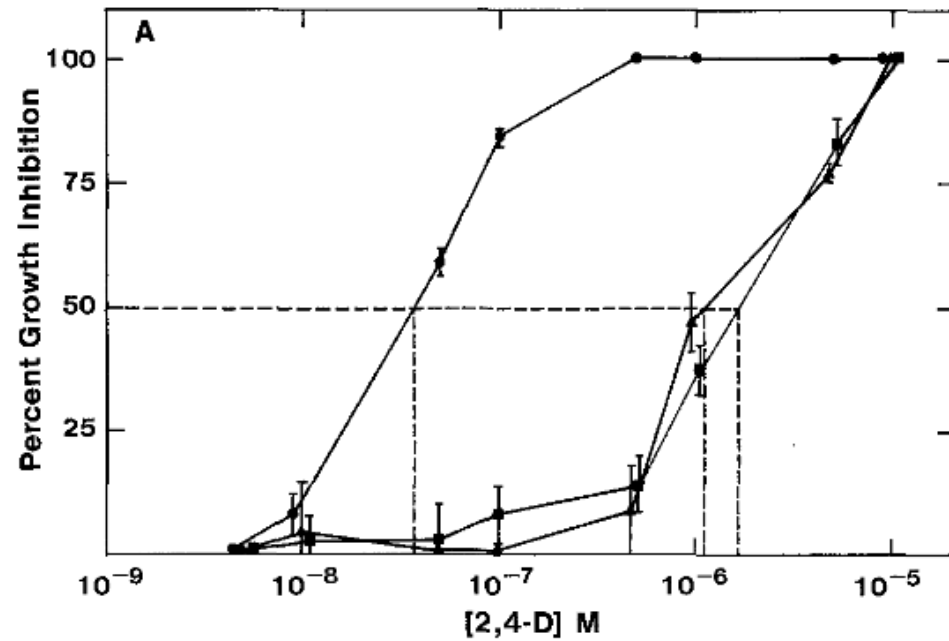
Phenotypes



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- pollen fertility reduced → stamen shorter



Root growth inhibition on auxin media:



Auxin-resistant mutants of *Arabidopsis thaliana* with an altered morphology

Mark A. Estelle* and Chris Somerville

MSU-DOE Plant Research Laboratory, Michigan State University, East Lansing, MI 48824, USA

Conclusion:

- Defects associated to auxin action at every developmental stage**
 - AXR1 must be elemental for auxin response across tissues and developmental stages**
 - but mutants viable → loss-of-function, not null alleles!**

“...An attractive possibility is that the *AXR1* gene codes for an auxin receptor...”

Growth and Development of the *axr1* Mutants of *Arabidopsis*

Cynthia Lincoln, James H. Britton, and Mark Estelle¹

Department of Biology, Indiana University, Bloomington, Indiana 47405

Aims:

- Further characterization of *axr* mutants**
- Genetic mapping of the underlying gene**

Isolation of additional mutants with *axr1*-like phenotype:

Table 1. Recovery of *axr1* Mutants^a

M2 population	Mutagen	Selection	Mutants recovered
A ^b	EMS	2,4-D	<i>axr1-1</i>
			<i>axr1-2</i>
			<i>axr1-3</i> ←
			<i>axr1-4</i>
			<i>axr1-5</i>
			<i>axr1-6</i>
B ^b	EMS	2,4-D	<i>axr1-7</i>
			<i>axr1-8</i>
			<i>axr1-9</i>
			<i>axr1-11</i>
			<i>axr1-12</i> ←
			<i>axr1-15</i>
C ^c	EMS	2,4-D	<i>axr1-16</i>
			<i>axr1-17</i>
			<i>axr1-18</i>
			<i>axr1-19</i>
			<i>axr1-20</i>
			<i>axr1-21</i>
C ^c	EMS	IAA	<i>axr1-22</i>
D ^c	γ	2,4-D	<i>axr1-23</i> ←

^a A total of 470,000 seeds from four distinct M2 populations was screened for mutants that were able to elongate roots on either 5 μM 2,4-D or 50 μM IAA.

^b Estelle and Somerville (1987).

^c This study.

Isolation of additional mutants with *axr1*-like phenotype:

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A ^b	EMS	2,4-D	<i>axr1-1</i> <i>axr1-2</i> <i>axr1-3</i> <i>axr1-4</i> <i>axr1-5</i> <i>axr1-6</i>
B ^b	EMS	2,4-D	<i>axr1-7</i> <i>axr1-8</i> <i>axr1-9</i> <i>axr1-11</i> <i>axr1-12</i> <i>axr1-15</i>
C ^c	EMS	2,4-D	<i>axr1-16</i> <i>axr1-17</i> <i>axr1-18</i> <i>axr1-19</i> <i>axr1-20</i> <i>axr1-21</i>
C ^c	EMS	IAA	<i>axr1-22</i>
D ^c	γ	2,4-D	<i>axr1-23</i>

^a A total of 470,000 seeds from four distinct M2 populations was screened for mutants that were able to elongate roots on either 5 μ M 2,4-D or 50 μ M IAA.

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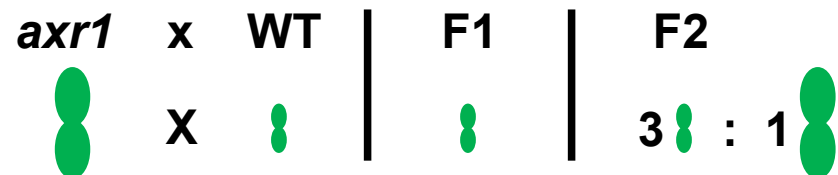
Segregation analysis:

Table 2. Genetic Segregation of 2,4-D Resistance in *axr1* Lines

Cross	Number of Plants		χ^2 ^a
	Resistant	Sensitive	
<i>axr1-19</i> \times wild-type F1	0	23	2.07 ^b
F2	186	493	
<i>axr1-21</i> \times wild-type F1	0	51	1:12 ^b
F2	82	281	
<i>axr1-22</i> \times wild-type F1	0	22	2.83 ^b
F2	56	216	
<i>axr1-23</i> \times wild-type F1	0	33	0.683 ^b
F2	117	383	

^a χ^2 was calculated based on an expected ratio of three sensitive to one resistant.

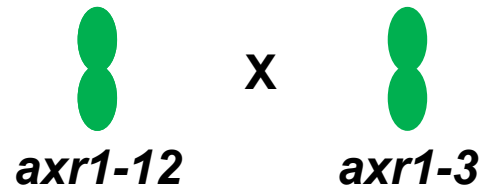
^b $P > 0.05$.



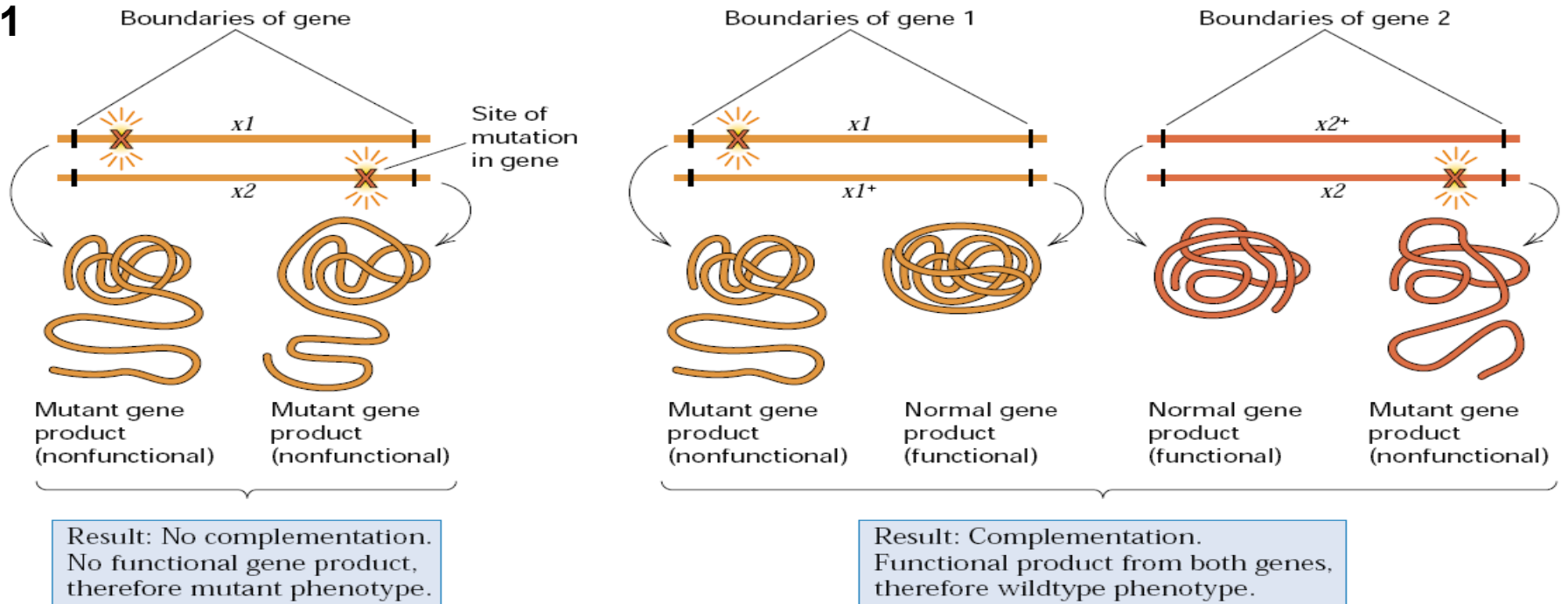
***axr1*-like mutant phenotypes are inherited recessively
→ typical for loss-of-function alleles**

axr mutations in the same gene?

P



F1



Mutant phenotype
→ same gene/allelic



WT phenotype
→ different genes

Complementation test

Table 3. Complementation Analysis of *axr1* Lines

Cross	Number of Plants	
	Resistant	Sensitive
<i>axr1</i> -12 × <i>axr1</i> -3	33	0
<i>axr1</i> -19 × <i>axr1</i> -3	21	0
<i>axr1</i> -20 × <i>axr1</i> -3	13	0
<i>axr1</i> -22 × <i>axr1</i> -3	24	0
<i>axr1</i> -23 × <i>axr1</i> -3	39	0



axr1-x mutations are alleles in the same gene

Morphology:

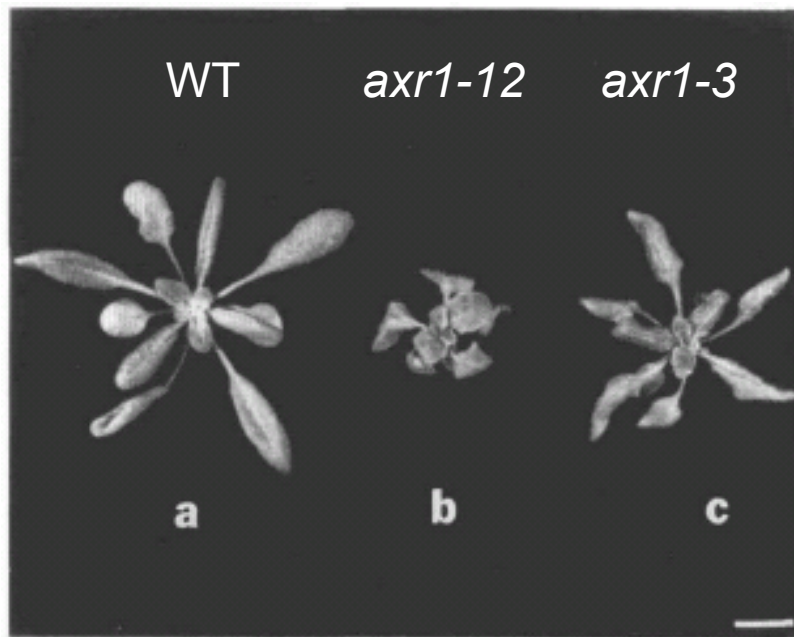


Figure 1. Phenotype of Wild-Type and Mutant Rosettes.

Rosettes were photographed when the plants were 3 weeks old.

(a) Wild type.

(b) *axr1-12/axr1-12*.

(c) *axr1-3/axr1-3*.

Bar = 1 cm.

→ Allelic differences also in root growth assays

Alleles show different expression of morphological and response defects



Figure 2. Comparison of Mature Wild-Type and Mutant Plants.

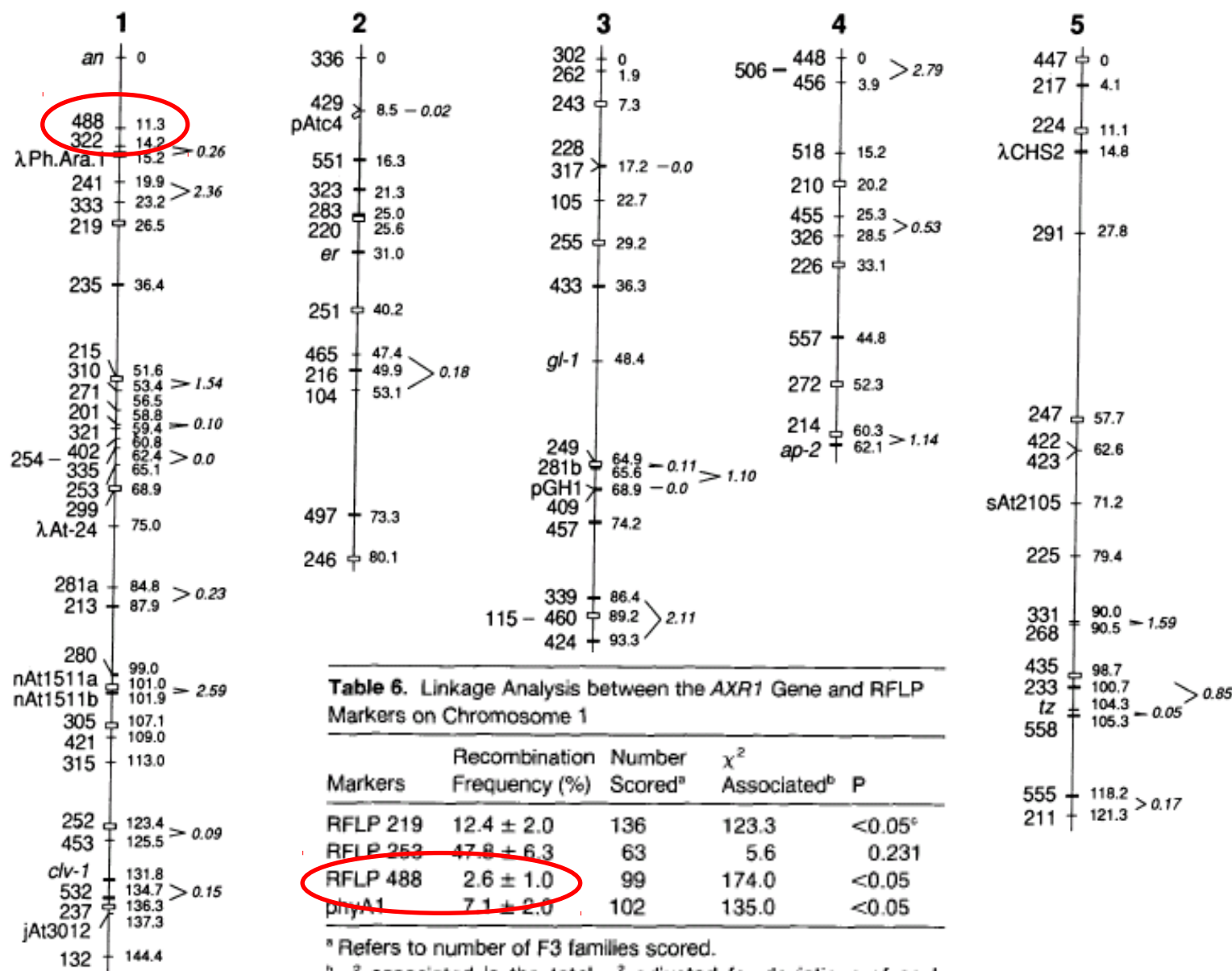
Wild-type and mutant plants were photographed when 7 weeks old.

(a) Wild type.

(b) *axr1-12/axr1-12*.

(c) *axr1-3/axr1-3*.

Bar = 3 cm.



Growth and Development of the *axr1* Mutants of *Arabidopsis*

Cynthia Lincoln, James H. Britton, and Mark Estelle¹

Department of Biology, Indiana University, Bloomington, Indiana 47405

Conclusion:

- ***axr1* mutants represent different alleles in the same gene**
- **'weak and strong' alleles**
- **essential function in growth related processes throughout developmental stages is confirmed**
- ***AXR1* gene maps to the top of chromosome 1**

***Arabidopsis* auxin-resistance gene *AXR1* encodes a protein related to ubiquitin-activating enzyme E1**

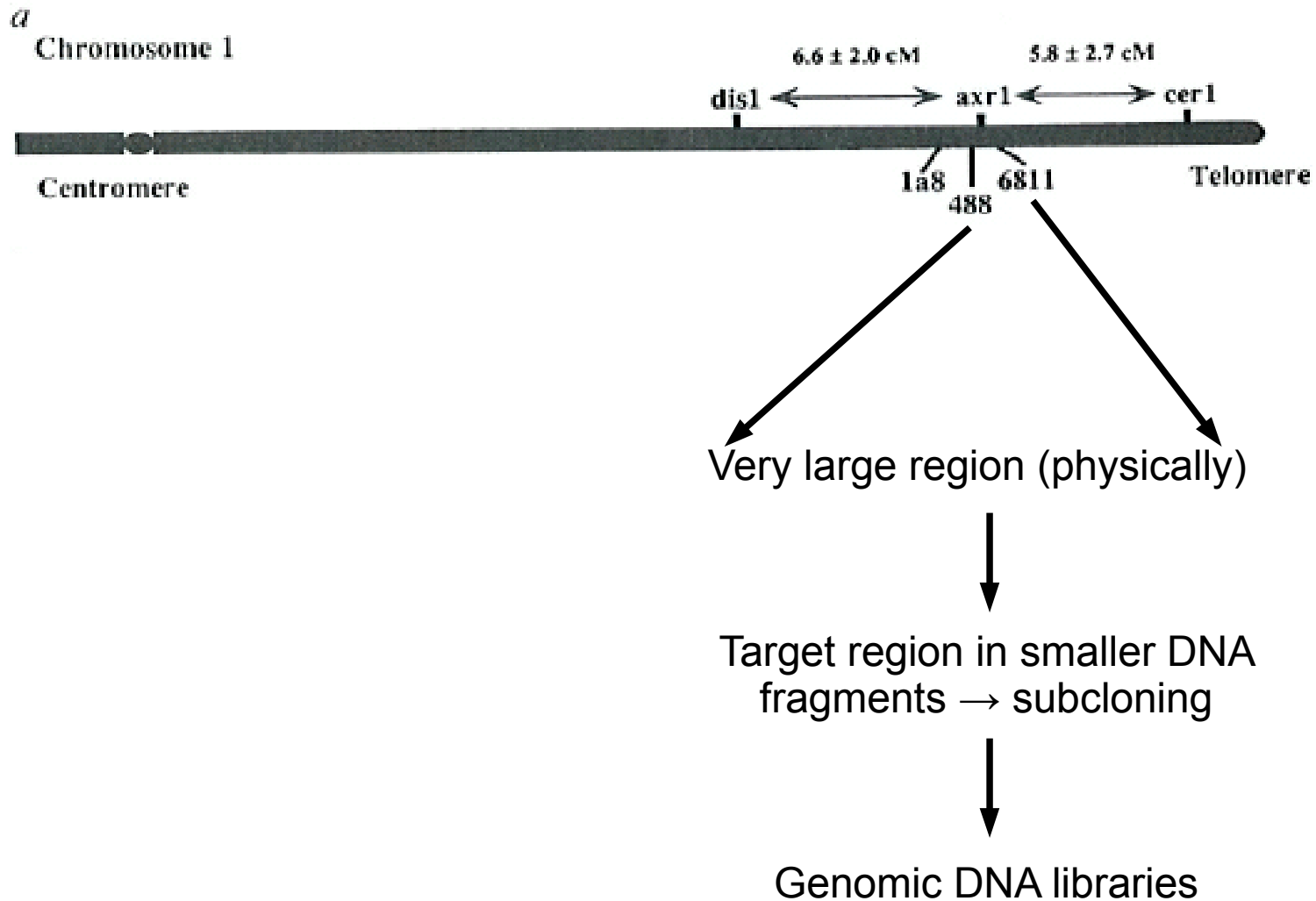
**H. M. Ottoline Leyser, Cynthia A. Lincoln*,
Candace Timpfe, Douglas Lammer,
Jocelyn Turner & Mark Estelle†**

Department of Biology, Indiana University, Bloomington,
Indiana 47405, USA

Aim:

- Fine-mapping and cloning of *AXR1*

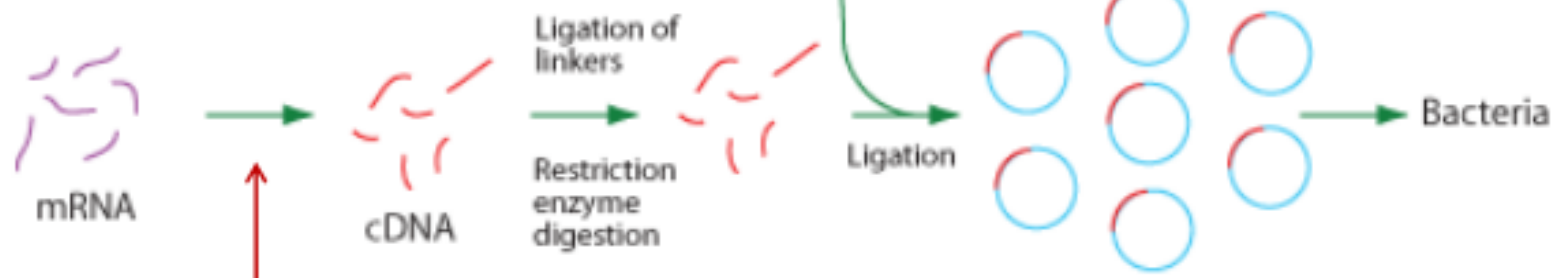
AXR1 - Chromosome Walking



Genomic Library



cDNA Library

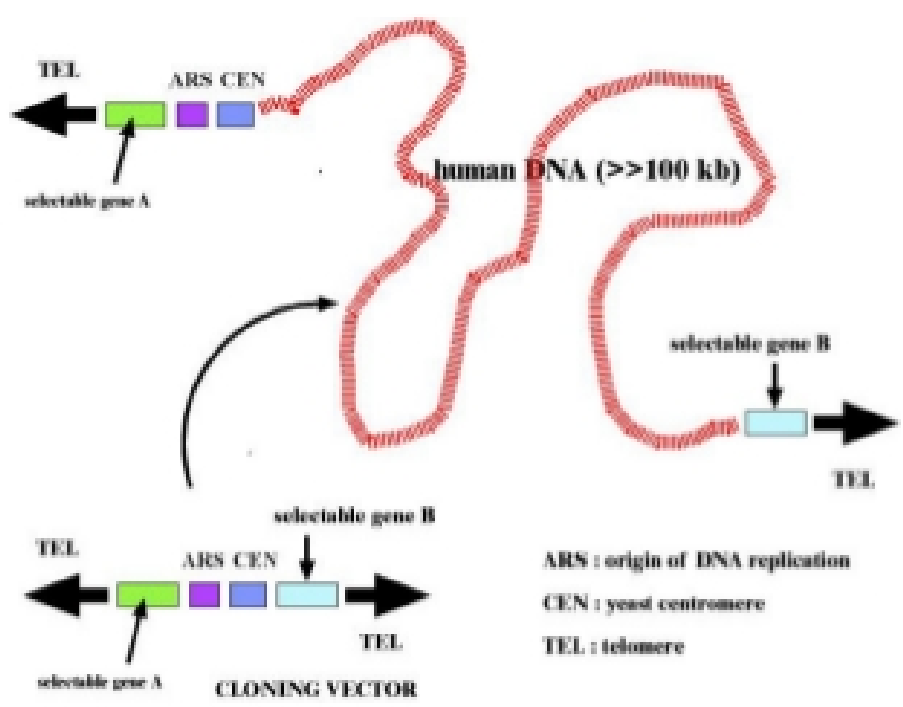


Reverse Transcription

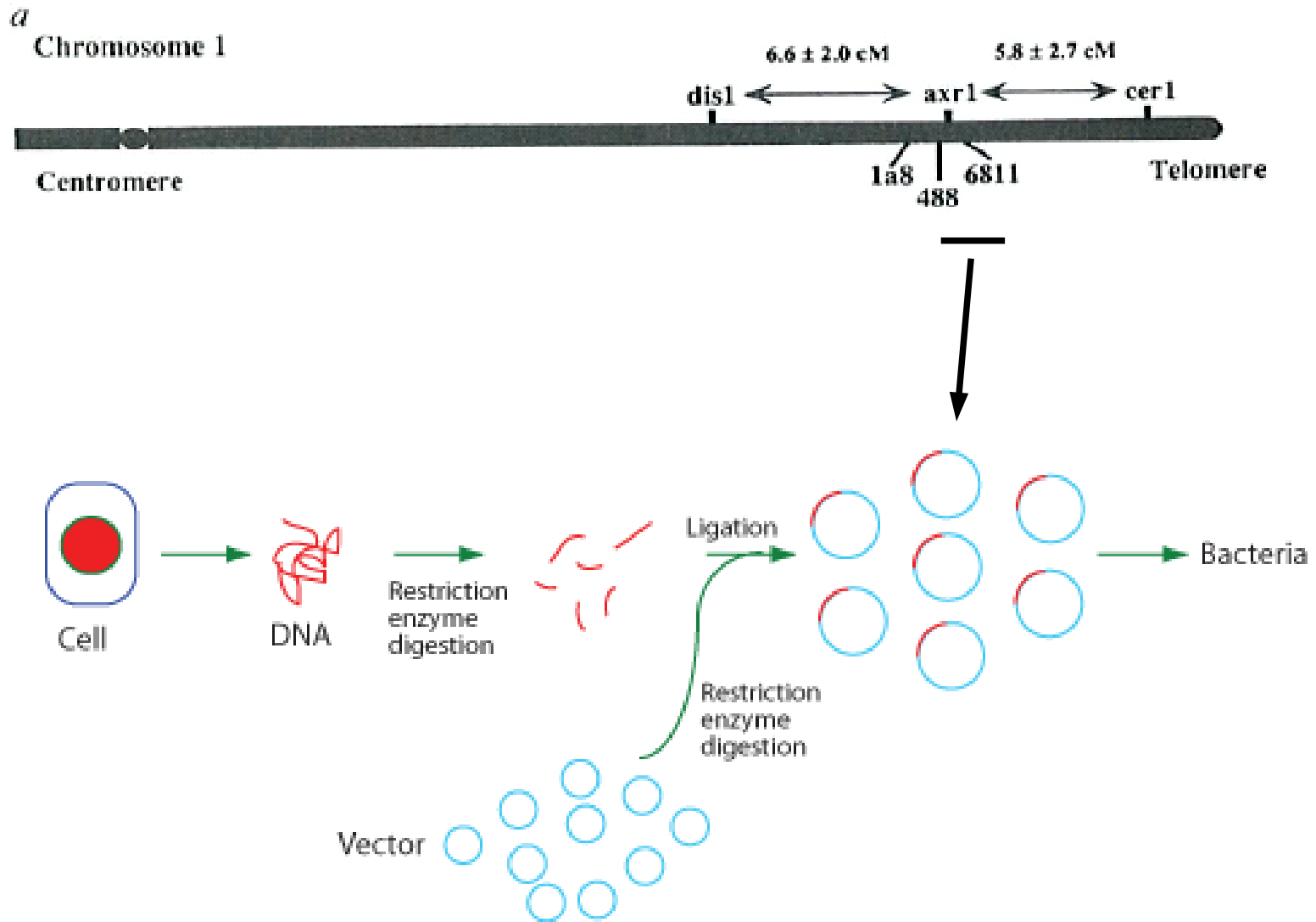
Vectors for cloning of large DNA fragments – YACs, cosmids, ...

Approximate maximum length of DNA that can be cloned into vectors

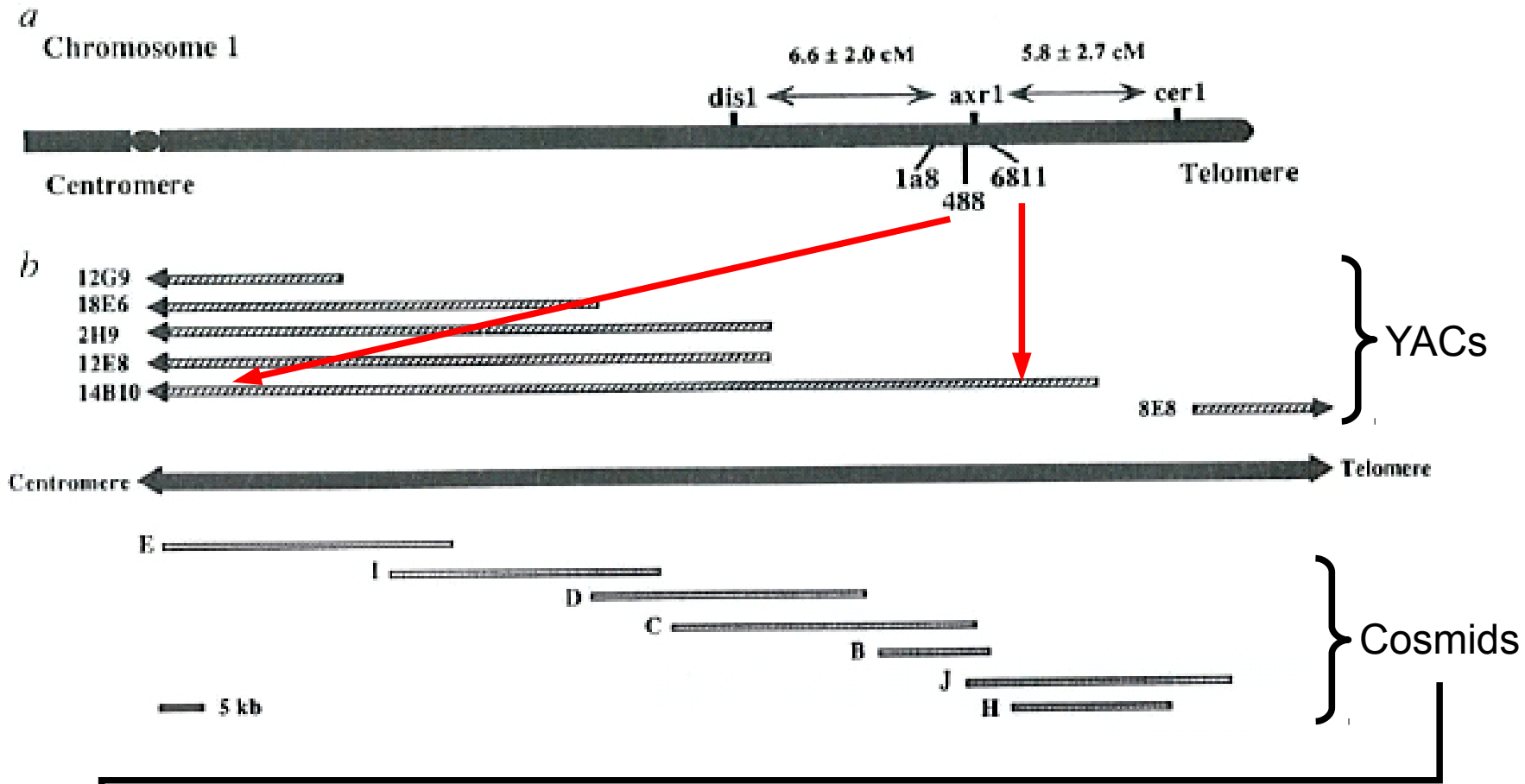
Vector type	Cloned DNA (kb)
Plasmid	20
lambda phage	25
Cosmid	45
BAC (bacterial artificial chromosome)	300
YAC (yeast artificial chromosome)	1000



AXR1 - Chromosome Walking



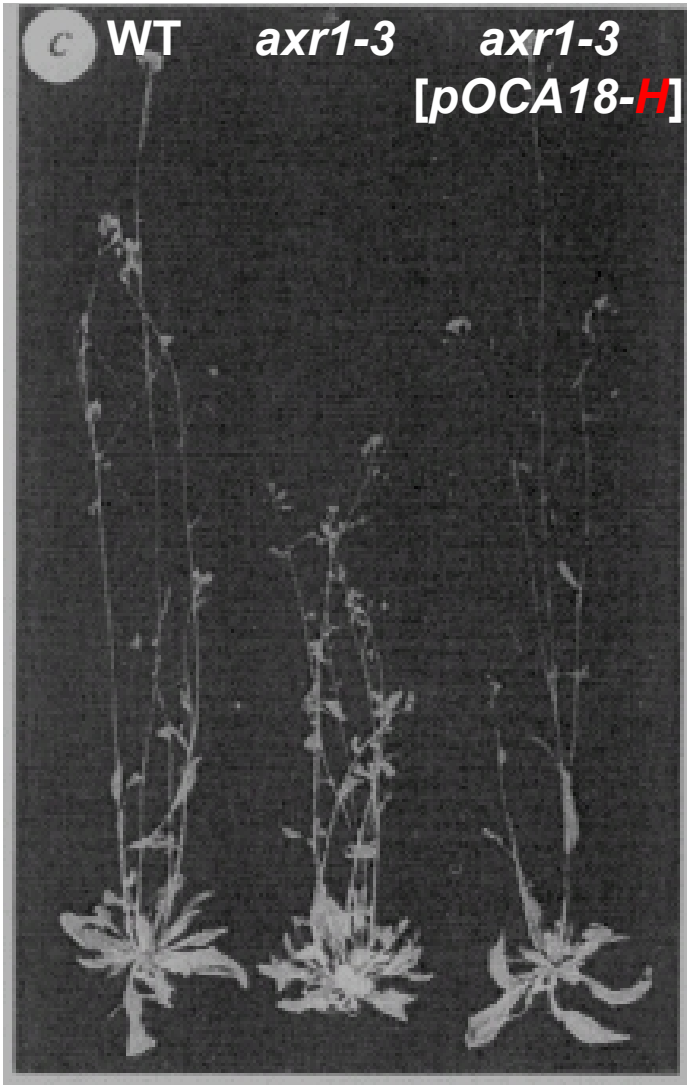
AXR1 - Chromosome Walking



Transform cosmid clones E – H by agrobacterium transformation into *axr1-3* mutants

Check for restoration of the WT phenotype

Transgenic complementation analysis



→ Cosmid **H** can restore the wild type phenotype in the mutant background

↓
Cosmid **H** contains the ***AXR1*** gene

Transgenic complementation analysis

Cosmid **H** contains the *AXR1* gene



Screen cDNA library with cosmid **H**

→ Which genes are located on cosmid **H**?



2 cDNAs identified

→ *AXR1* candidates



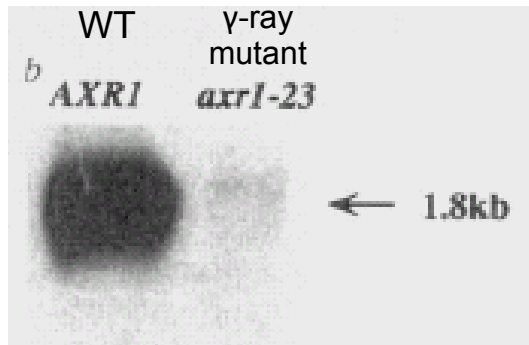
Northern Blot

→ How much transcript (1.8 kb mRNA) is present in the *axr1-23* deletion mutant?



None!

→ 1.8 kb transcript represents the *AXR1* gene



Sequencing of the *AXR1* gene in *axr1-3* and *axr1-12* mutants

234
 1 ATGCGAGCGAGTAAAGAGCTCCAGGAGACATGTTGGAAGAAGAGCCAAACATGCTAGAACCTAAAGCCAGGTACGCTCGCTCAGGATTTGGAGGCGAGG
 1 M Q A G C G R R R A H V E E E P T N V E P K T R Y D S Q L R I N G E V S
 281
 14 TAGGTCAGGCGCTCTGGCAAGCAAGGAGTAATCTGCTTACTCAATGTTGGCCCTACTGGTTCCGAGGCTTTGCAAGCACTCTGCTACTGAGTGGTGGTGGTGGTAC
 14 G Q A A L E E A S I C L L N C G P T G S E A L K N L V L G G V G S
 328
 47 CATCACCGCTGTGTTGATGGATCTAAGGTTCAATTCTGGTCACTCTGGGAAACAATCTCTGTTGGTGGATGGGAAGAGTGGTGGCCCAATCAAAAGCTAAATCTCT
 47 I T V V D G S R V Q F S D L G N H F M V D A K S V G Q S E A K S V
 375
 120 TGTGGCTTCTCTCAAGAGGCTTAATTAATCTGTTTAAGCCCAATCTTATTTGAGGAGATTCGAGACAGCTTGATTACTACTAAGCCAGCTCTCTCTCTCTCTCT
 120 C A F L Q R L N D S V M A K F S E E M P D T L I T T M P S F P S Q S
 422
 461 TCACTCTGTTTATATGCTCACTCAAGCTGGTGGAAAGATTCAATGTTCAAACTTGATAGAAATTTGGAGAGTCAAAAGCTTAAGTTGGTTTGGTGGCTCTTA
 461 T L V T A T Q L V E D S M L K L D R I K D A N V R L V L V R S Y
 468
 501 TGGCTTGGTGGCTTGGTGGCTATCTCTGTAAGGAGGACCCCAATTTGACTCAAAACCTGATCACTTTCTTGGAGAGCTGGGCTGAAATATCCATGG
 501 C L A G F V R I E V K E H P I I O S E P D R P L D D L R L N N P W
 515
 601 CTGGAATTAAGAGCTTTGTGGAGACCAATTCATCTGAATGTTTCAGAGCCGCGCGCTGCACATAGGCATACCTTCAGCTGCTCATTTCTGTAAGATGG
 601 P E L K S F Y E T I D L N V S E P R A A H R K I P Y V V I L V S H A
 621
 701 CTGAGGAGTGGCTGCAATCCCATAGTGGTAACTCTCTCACTCAGGAGGAGGAGAAAGAGTTTAAGGATTTGGTTAAGTCCAGAGTATATCTACGGA
 701 F E H A Q S H S G N L P S T H E E E K S E P K D L V A S E M Y S T D
 721
 801 TGAAGATAATTAAGAGAGGCTTTGAAGCGCTTTTCAAAAGTTTITGCTCTCTCGAGCACTCAAGCTCAAGAGTTCAAAAGTAAATTAATGATAGTCTGCT
 801 E D N Y K E A I E A A F K V F A P H G E S S R E V Q E L I N D S C A
 821
 901 GAAGTGAATTCGAATTCCTCAGCTTTTGGGCTTAAGTATGAGTCTCTGTAAGGAGTTTGGTTTAAATTAAGGCTGGTGGAGAGCAAGCCCTTGAAGGTTCTA
 901 E V M S H S S A F W V M V A A L K E F V L M E G G G E A P L E G S I
 921
 1001 TACTAGATATGCTCTCTTCACAGCAAGCACTATATCAATTTGCGAGAAATCTCTTTTGAAGCAAGGAGAGCTGATTTTCTGTCATGAGGAGACCGAGTTAA
 1001 P D M T S T E R F I N L Q N I V L A K A E A D F L V I E E R V K T
 1021
 1101 AAACCTTTTAAACCAAACTCTGGAGAGCTGAGGAGATCTCAAAAGCAACATCTACAGCTTTCTGCAAGAAATGCAAGGAACTTAAATTTGTCACATAT
 1101 N I L K K I G H D P K S I P K P T I K S F C R N A S E L E L C S Y
 1121
 1201 CGTATGGTACAGGAGAGCTTTCAGAAAGCTCTCTCTGAACTCAAAATTTGAAGTATTTAGCGGAGGAGGATTACAGCTGCTGCAATGGGATTTTATATCTCT
 1201 R M V E D E K F R N P S V T E I L K T L A D E D Y S G A H G F Y I L L
 1221
 1301 TTMAAGCTGAGAGAGATTTGCTGCTCAACTATATACAGTCTTCTGGGAGTTTGAATGAGAGGATGAGATGAGGAGATTTCTCGATTAAAGAACTACTGCTCT
 1301 R A A D R R F A A R Y N K F P G Q F D G G H D E D I S R L E T T A L
 1321
 1401 GAGCTCTCTGAGGAGTTGGGCTGGAAGGCTCACTACTCTAGATGACCTTATCCATGAGAGTGGTGGCTTTGGTGGCTCGAGAGATTCAGTGGTGGTCT
 1401 S L L T D L C C N G S V L P D D L E H E M C R P G A S E I E V V S
 1421
 1501 GCGTTTGTGAGGAGATTCGATCTCTCAAGAGCTCAATAGCTTTGTCAAGAGGAGTTGGTTCGAGTGTGGGAGCTTACATCTTCAAGTGGATTCGATCAGA
 1501 A F V C C I A K Q E V E L V T K D F V P M L G T Y I F R G E D R K
 1521
 1601 AGTCTCAATTATGGAATTTGTGAGAGATCTTTGCTTAAACACATTCGATTTGAAGACAGAGAGAGAGCTCTATCATATATTTCTCTGATTAAGAGATA
 1601 R Q L L R L
 1621
 1701 ATCTTTTGGTACTACTAGAGAAACAAATTTTCAATGACAGTTTCACTGAGAGCA 1755

***axr1-3* = G461A**
Cysteine → Tyrosine

***axr1-12* = C1246T**
Glycine → STOP

AXR1 function?

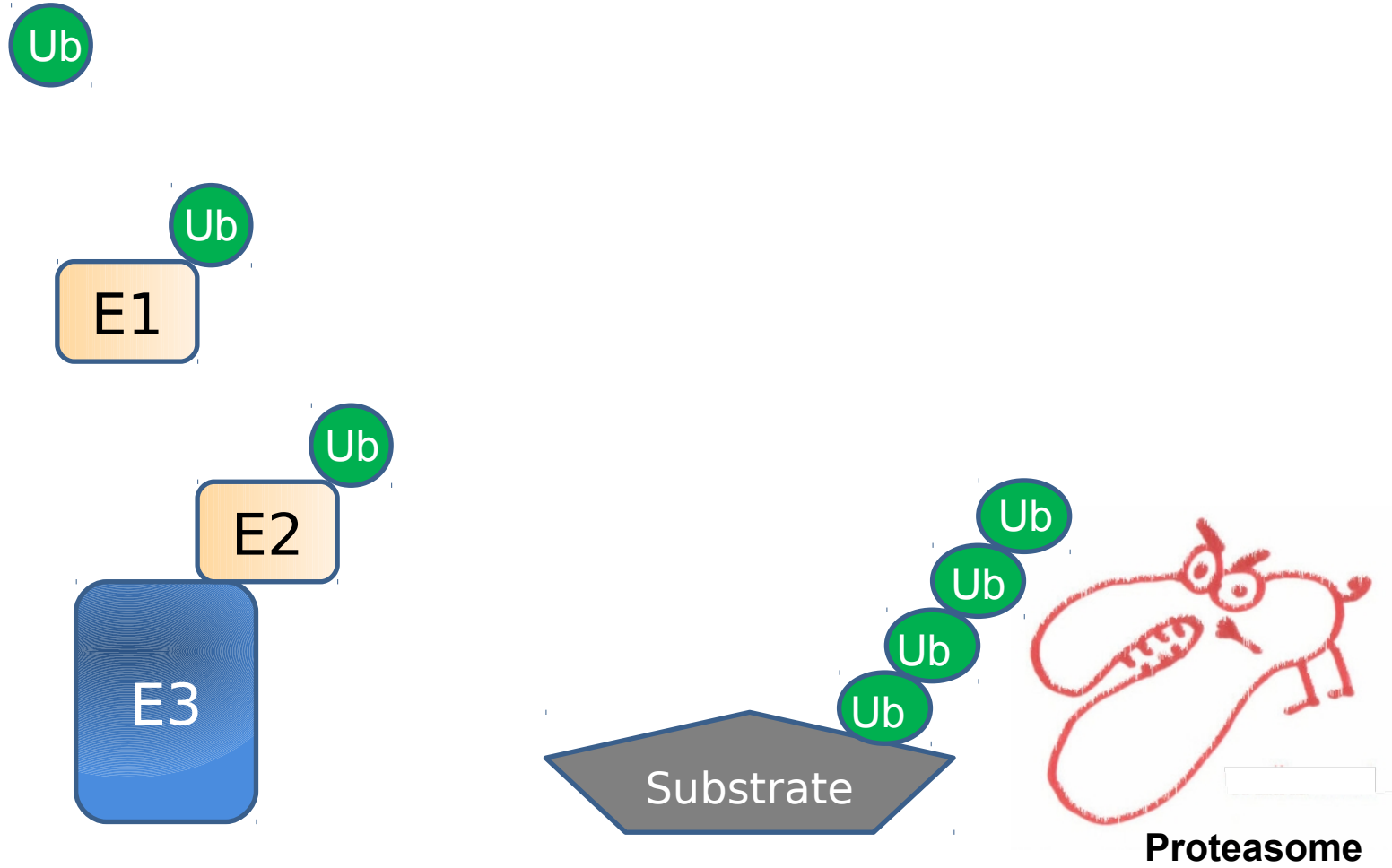
Sequence similarity searches with Genbank database:

human	M	S	S	P	L	K	R	R		R	V	S	S	P	P	P	R	P	G		S	N	G	E	P	A	Q	E	V	L		E	I	V	G	E	Y	P	T	R	G		M	A	K	N	G	S	E	A	D	I		D	E	G	L	Y	S	H	Q	L	Y		60																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																									
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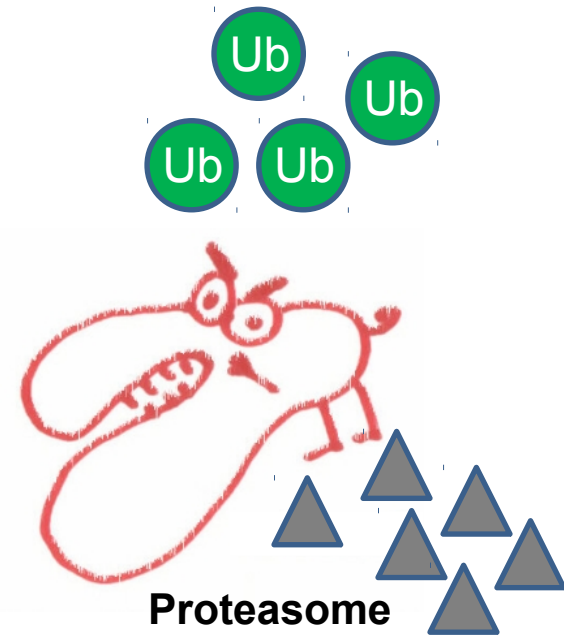
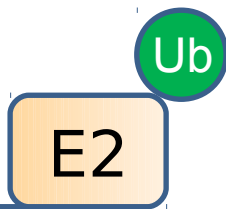
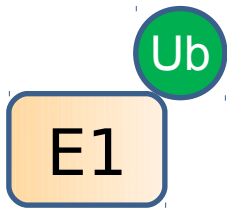
AXR1 Protein: 540 AS, ca. 60 kD

Similarity to human and yeast E1 ubiquitin activating enzymes

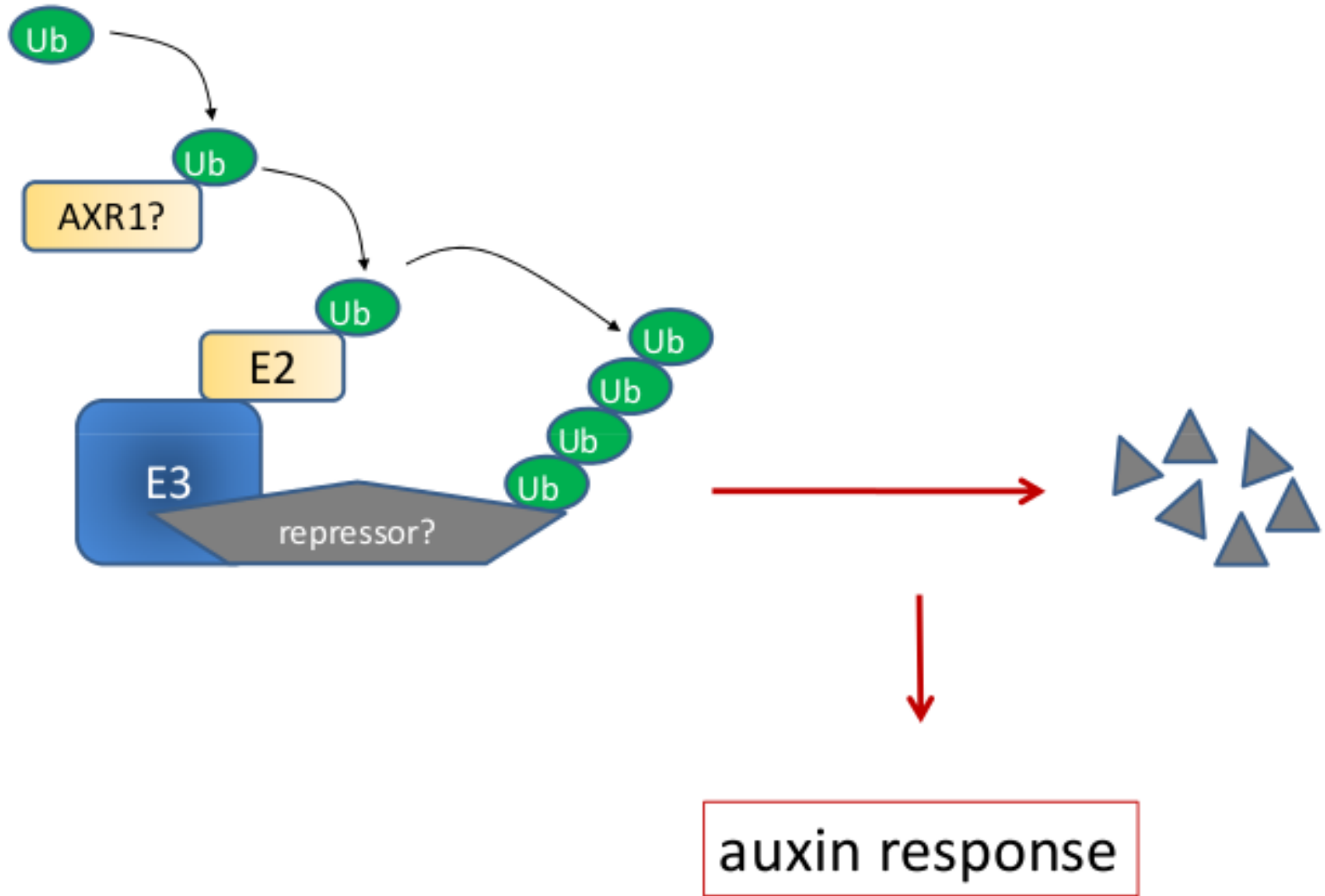
The ubiquitin system



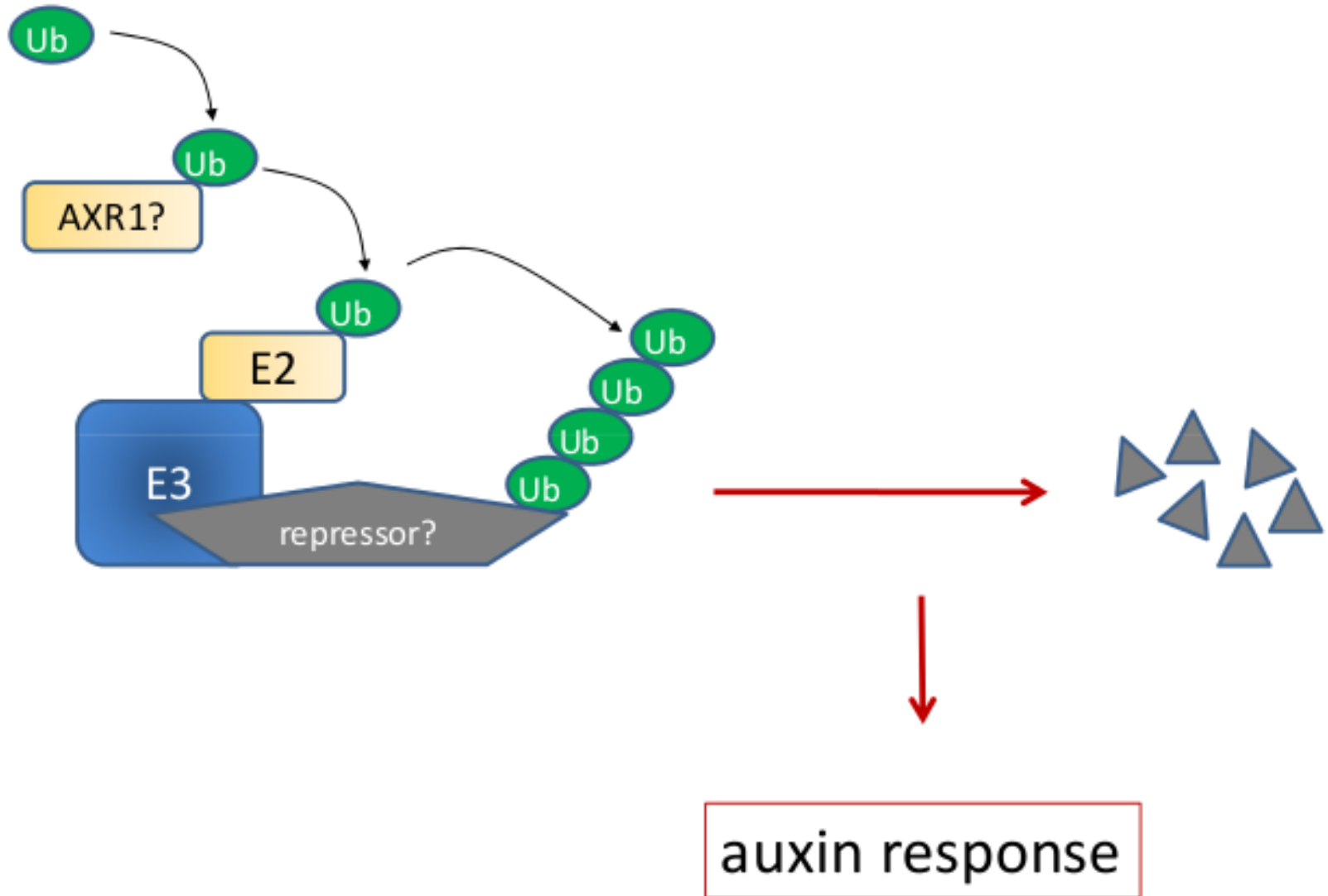
The ubiquitin system



Preliminary model of auxin signaling



Preliminary model of auxin signaling



How could protein degradation be associated with the gene activation hypothesis?

Allgemeines zur Struktur von Papers + Wie präsentieren?

Wie ist ein Paper strukturiert?

- Abstract
 - Zusammenfassung
- Introduction
 - Einleitung und State of the art
 - Zielstellung der Arbeit
- Results
- Discussion
 - Ergebnisse werden evaluiert und in Zusammenhang mit Daten aus der Literatur gebracht
 - Conclusions = Big picture
- Material and Methods
 - Was wurde womit wie gemacht
- References
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Wie präsentiere ich ein Paper?

- Hintergrund/Einleitung mit **Ausgangsmodel**
- Zielstellung
- Ergebnisse (anhand der Abbildungen)
 - Wenn nötig, neue Methoden erklären
- Diskussion
 - Big picture
- Fazit
 - Welche Erkenntnisse sind hinzugekommen
 - **Model erweitern**

Termine

datum	autoren	titel	link	wer stellt vor?
08.05.	Estelle and Somerville (1987)	Auxin-resistant mutants of Arabidopsis thaliana with an altered morphology	Mol Gen Genet 206:200 full text pdf B	marcel pdf
	lincoln et al. (1990)	Growth and development of the axr1 mutants of Arabidopsis	Plant Cell 2:1071 full text pdf B + glossar	marcel
	leyser et al. (1993)	Arabidopsis auxin-resistance gene AXR1 encodes a protein related to ubiquitin-activating enzyme E1	Nature 364:161 abstract B + glossar	marcel
15.05.	Abel et al. (1994)	Early auxin-induced genes encode short-lived nuclear proteins.	PNAS 91:326-330 B + glossar	carolin
	Ballas et al. (1993)	Identification of the Auxin-responsive Element, AuxRE, in the Primary indoleacetic Acid-inducible Gene, PS-IAA4/5, of Pea (Pisum sativum)	J Mol Biol 233:580 B + glossar	luz
22.05.	Ulmasov et al. (1997)	ARF1, a transcription factor that binds to auxin response elements.	Science 276:1865 B + glossar	x + y
29.05.	Ruegger et al. (1998)	The TIR1 protein of Arabidopsis functions in auxin response and is related to human SKP2 and yeast Grr1p	Genes & Development 12:198 full text pdf B + glossar	x + y
05.06.	Gray et al. (1999)	Identification of an SCF ubiquitin-ligase complex required for auxin response in Arabidopsis thaliana	Genes & Development 13:1678 full text pdf B + glossar	x + y
12.06.	Gray et al. (2001)	Auxin regulates SCFTIR1-dependent degradation of AUX/IAA proteins	Nature 414:271 abstract B + glossar	x + y
19.06.	Hamann et al. (1999)	The auxin-insensitive bodenlos mutation affects primary root formation and apical-basal patterning in the Arabidopsis embryo	Development 126: 1387-1395 abstract B	x + y
	Hamann et al. (2002)	The Arabidopsis BODENLOS gene encodes an auxin response protein inhibiting MONOPTEROS-mediated embryo patterning	Genes Dev 16: 1610-1615 B	x + y
25.06.	Kepinski and Leyser (2005)	The Arabidopsis F-box protein TIR1 is an auxin receptor	Nature 435:446 abstract B + glossar	x + y
	Callis (2005)	news and views zu den beiden papers (= kommentar)	news and views B	
03.07.	Dharmasiri et al. (2005)	Plant development is regulated by a family of auxin receptor F box proteins	Dev Cell 9(1):109-119 abstract B	x + y
10.07.	Tan et al. (2007)	Mechanism of auxin perception by the TIR1 ubiquitin ligase	Nature 446:640 abstract B + glossar	x + y
	Guilfoyle (2007)	news and views zum paper (= kommentar)	news and views B	
17.07.	Calderon-Villalobos et al. (2012)	A combinatorial TIR1/AFB-Aux/IAA co-receptor system for differential sensing of auxin	Nat Chem Biol. 8(5):477-85 B	x + y ... dazu pizza und schlussbesprechung
	Vanneste and Friml (2012)	news and views zum paper (= kommentar)	news and views B	