

Genetics of Root Hair Formation

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Abstract There has been a great deal of recent progress in our understanding of the genetic control of root hair development, particularly in *Arabidopsis thaliana*. This chapter summarizes the genes and gene products that have been identified using forward and reverse genetic approaches. The involvement of these genes at various stages of root hair development is described, including the specification of the root hair cell type, the initiation of the root hair outgrowth, and the elongation (tip growth) of the root hair.

1 Introduction

The formation of root hairs has been used for more than a century to study fundamental problems in plant biology, using physiological, cell biological, and developmental approaches (Cormack 1935; Cutter 1978; Haberlandt 1887; Leavitt 1904; Sinnot and Bloch 1939). In the past 20 years, a great deal of attention has been devoted to using genetics to study root hair formation, particularly in the model plant species *Arabidopsis*. *Arabidopsis* root hairs are amenable to genetic dissection because (1) they are easily visible on the root surface and appear rapidly (within 3 days) after seed germination, making them one of the most convenient postembryonic cells for phenotypic analysis; (2) the entire developmental history of the *Arabidopsis* epidermis has been defined, from its embryonic origin through its mature cell features (Dolan et al. 1993, 1994; Scheres et al. 1994); (3) the root epidermal cells are generated and differentiate in a file-specific manner, which enables all stages of development to be analyzed along the root at any time; (4) the root hair cells are not required for plant viability or fertility, and so any type of mutant can be isolated and analyzed; (5) large-scale genetic screens are feasible, since large numbers of seedlings can be analyzed for their root hair phenotype; and

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(6) molecular and genomic resources are available in *Arabidopsis* for the rapid analysis of new genes and proteins.

In this chapter, we describe the genetics of root hair cell specification, root hair initiation, and root hair growth (elongation). A list of the genes identified from *Arabidopsis* is presented in Table 1.

Table 1 Genes involved in root hair formation in *Arabidopsis*

Gene ^a	Root hair mutant phenotype	Predicted product	Reference
<i>AGP30</i>	None	Arabinogalactan protein	van Hengel et al. 2004
<i>AIP1</i>	Short root hairs	Actin-interacting protein	Ketelaar et al. 2007
<i>AKT1</i>	Long root hairs	Potassium transporter	Desbrosses et al. 2003
<i>ARA6</i>	None	Rab GTPase	Grebe et al. 2003
<i>ARF1</i>	Dominant mutants have no hairs, or have short or double root hairs	ADP-ribosylation factor GTPases	Xu and Scheres 2005
<i>AtEXO70A1</i>	Reduced root hair length	Exocyst subunit Exo70	Synek et al. 2006
<i>AtIPK2a</i>	Long root hairs	Inositol polyphosphate kinase	Xu et al. 2005b
<i>AUX1</i>	Short hairs	Auxin transport	Pitts et al. 1998
<i>AXR1</i>	Bulges form but do not elongate	Subunit of RUB1-activating enzyme	Cernac et al. 1997; del Pozo et al. 2002
<i>AXR2/IAA7</i>	Dominant mutants are hairless, except where root meets hypocotyl	Repressor of auxin-responsive transcription	Nagpal et al. 2000
<i>AXR3/IAA17</i>	Dominant mutants are hairless, except where root meets hypocotyl	Repressor of auxin-responsive transcription	Leyser et al. 1996
<i>BHLH32</i>	High phosphate does not suppress root hair development	bHLH transcription factor	Chen et al. 2007
<i>BIG</i>	Short hairs in high phosphate conditions	Calossin	Lopez-Bucio et al. 2005
<i>BRISTLED1 (BST1)/DER4</i>	Short hairs, sometimes branched	Unknown	Parker et al. 2000; Ringli et al. 2005
<i>CAP1</i>	Hairs short, bulbous, occasionally branched	Actin-binding protein	Deeks et al. 2007
<i>CEN3/DER1/ACT2</i>	Short, wide hairs, some with wide bases, some hairs curled and/or branched	Vegetative actin	Ringli et al. 2002
<i>CENTPEDE1 (CEN1)</i>	Short, wide hairs, sometimes curled	Unknown	Parker et al. 2000
<i>CENTPEDE2 (CEN2)</i>	Short, wide hairs, sometimes branched and/or curled	Unknown	Parker et al. 2000

(continued)

Table 1 (continued)

Gene ^a	Root hair mutant phenotype	Predicted product	Reference
<i>COW1</i>	Short, wide root hairs, often branched at the base	Phosphatidylinositol transfer protein	Bohme et al. 2004; Vincent et al. 2005
<i>CPC</i>	Reduced root hair number	R3 Myb transcription factor	Wada et al. 2002
<i>DER2</i>	Hairs stop growing after bulge forms	Unknown	Ringli et al. 2005
<i>DER3/ENL7</i>	Hairs have wide bases and sometimes branch	Unknown	Ringli et al. 2005
<i>DER5</i>	Short, distorted hairs	Unknown	Ringli et al. 2005
<i>DER6</i>	Very short hairs	Unknown	Ringli et al. 2005
<i>DER7</i>	Hairs often short, wide, and bulbous	Unknown	Ringli et al. 2005
<i>DER8</i>	Hairs often depolarized	Unknown	Ringli et al. 2005
<i>EGL3</i>	None	bHLH transcription factor	Bernhardt et al. 2005
<i>EIN2</i>	Root hairs form further from the end of the epidermal cell	Ethylene response	Fischer et al. 2006
<i>ENL1</i>	Wavy, branched hairs	Unknown	Diet et al. 2004
<i>ENL5</i>	Short, wide, curved hairs	Unknown	Diet et al. 2004
<i>EPC1</i>	Short root hairs	Glycosyltransferase	Bown et al. 2007
<i>ETC1</i>	None	R3 Myb transcription factor	Kirik et al. 2004a
<i>ETO1-4</i>	Increased root hair length and density	Ethylene overproducer	Cao et al. 1999
<i>ETR1, ERS1, ERS2, ETR2</i>	Reduced root hair length	Ethylene receptor	Cho and Cosgrove 2002
<i>EXP18</i>	–	Expansin protein	Cho and Cosgrove 2002
<i>EXP7</i>	None	Expansin protein	Cho and Cosgrove 2002
<i>GL2</i>	Excess root hairs	Homeodomain-leucine-zipper transcription factor	Masucci et al. 1996
<i>GL3</i>	Increased root hair number	bHLH transcription factor	Bernhardt et al. 2005
<i>IAA14</i>	Dominant mutants are hairless, except where root meets hypocotyl	Repressor of auxin-responsive transcription	Fukaki et al. 2002
<i>ICR1</i>	In loss-of-function mutant hairs form closer to the root tip. Ectopic expression produces short, bulbous root hairs	Coiled-coil domain scaffold protein regulated by ROPs	Lavy et al. 2007
<i>IRE</i>	Short root hairs	Serine/threonine kinase	Oyama et al. 2002
<i>KEULE</i>	Hairs absent or stunted and swollen	Sec1 protein	Assaad et al. 2001

(continued)

Table 1 (continued)

Gene ^a	Root hair mutant phenotype	Predicted product	Reference
<i>KIP</i>	Wide hairs	SABRE-like protein	Procissi et al. 2003
<i>KJK/SHV1/AtCSLD3</i>	Hairs burst after bulge forms	ER-localized cell wall polysaccharide synthase	Favery et al. 2001
<i>LPI1</i>	Root hair length and density less affected by high phosphate	Unknown	Sanchez-Calderon et al. 2006
<i>LPI2</i>	Root hair length less affected by high phosphate	Unknown	Sanchez-Calderon et al. 2006
<i>LRX1</i>	Hairs short, swollen, or branched	Leucine-rich repeat (LRR)/extensin	Baumberger et al. 2001
<i>LRX2</i>	Some hairs short, swollen, or branched	LRR/extensin	Baumberger et al. 2003
<i>MRH1</i>	Short hairs	LRR class of receptor-like kinase	Jones et al. 2006
<i>MRH2</i>	Wavy, branched hairs	Armadillo repeat containing kinesin-related protein	Jones et al. 2006
<i>MRH3</i>	Hairs have wide bases	Inositol 1,4,5-tri-phosphate 5-phosphatase	Jones et al. 2006
<i>Myosin XIX</i>	Hairs short and slow-growing	Myosin XI	Ojangu et al. 2007
<i>OXII/AGC2</i>	Variable root hair length	Oxidative-burst-inducible kinase	Anthony et al. 2004; Rentel et al. 2004
<i>PAX1</i>	Suppressor of dominant mutations in <i>AXR3</i> , <i>pax1</i> single mutant has extra root hairs that are sometimes branched	Unknown	Tanimoto et al. 2007
<i>PFN1</i>	Overexpressing root hairs twice as long as wild type	Profilin	Ramachandran et al. 2000
<i>PGP4</i>	Long hairs	Auxin transport	Santelia et al. 2005
<i>PI-4Kβ1</i>	Double mutant with <i>PI-4Kβ2</i> has branched, wavy and bulged root hairs	Phosphatidylinositol 4-OH kinase	Preuss et al. 2006
<i>PIP5K3</i>	Short, wide hairs. Overexpressors have fat, curled or bulbous hairs	Phosphatidylinositol-4-phosphate 5-kinase	Stenzel et al. 2008
<i>PLDζ1</i>	None	Phospholipase D	Ohashi et al. 2003
<i>PRP3</i>	None	Proline-rich cell wall protein	Bernhardt and Tierney 2000
<i>RABA4b</i>	None	Rab GTPase	Preuss et al. 2004

(continued)

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Gene ^a	Root hair mutant phenotype	Predicted product	Reference
<i>RHD1/UGE4</i>	Wide swellings	UDP-d-glucose 4-epimerase	Schiefelbein and Somerville 1990; Seifert et al. 2002
<i>RHD2</i>	Hairs stop growing after bulge forms	NADPH oxidase	Foreman et al. 2003
<i>RHD3</i>	Wavy, short hairs	GTP-binding protein involved in ER–Golgi transport	Wang et al. 1997; Zheng et al. 2004
<i>RHD6</i>	Hairless	Unknown	Menand et al. 2007
<i>RHL1, RHL2, RHL3</i>	Reduced root hair density, dwarf	Topoisomerase subunits	Sugimoto-Shirasu et al. 2002, 2005
<i>RHM1/ROL1</i>	Suppressor of <i>lrx1</i>	Pectic polysaccharide rhamnogalacturonan modifying enzyme	Diet et al. 2006
<i>RPA/Ai2G35210</i>	Short, bulbous and branched root hairs	ARF GTPase-activating protein	Song et al. 2006
<i>SAR1</i>	Suppressor of <i>axr1</i>	Nucleoporin	Cernac et al. 1997
<i>SCN1</i>	Short, wide, hairs, sometimes branched	ROPGDP dissociation inhibitor	Carol et al. 2005
<i>SHV2/COBL9/DER9/MRH4</i>	Hairs stop growing after bulge forms	COBRA-like protein	Jones et al. 2006
<i>SHV3/MRH5</i>	Hairs stop growing after bulge forms	Glycerophosphoryl diester phosphodiesterase (GPDH)-like protein	Jones et al. 2006
<i>SIMK</i>	Overexpression increases root hair length	Mitogen-activated protein kinase	Samaj et al. 2002
<i>SIZ1</i>	Long root hairs very near root tip	SUMO E3 ligase	Miura et al. 2005
<i>SOS4</i>	Bulges form but do not elongate	Pyridoxal kinase	Shi and Zhu 2002
<i>TIP1</i>	Wide swellings; short, wide hairs, branched at base	ANK protein S-acyl transferase	Hemsley et al. 2005
<i>TRH1</i>	Hairs stop growing after bulge forms. Some cells with multiple bulges	Potassium carrier required for auxin transport	Rigas et al. 2001
<i>TRY</i>	None	R3 Myb transcription factor	Schellmann et al. 2002
<i>TTG</i>	Excess root hairs	WD-repeat protein	Galway et al. 1994
<i>WER</i>	Excess root hairs	R2R3 Myb transcription factor	Lee and Schiefelbein 1999
<i>WRKY75</i>	Increased root hair density	Transcriptional repressor	Devaiah et al. 2007

^aMultiple names for the same gene are given when these are used in the literature

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Emons, A.M.C.; Ketelaar, T. (Eds.)

2009, XIV, 346 p. 43 illus., 2 illus. in color., Hardcover

ISBN: 978-3-540-79404-2