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Appendix D

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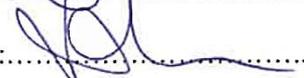
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**A molecular genetic analysis of the requirement of TOR kinase  
signalling for plant growth**

A thesis presented in partial fulfilment of the requirements for the degree

Doctor of Philosophy

in

Plant Biology

at Massey University, Palmerston North, New Zealand.

Daniel Rexin

2015



## Abstract

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Eukaryotes have developed a highly complex mechanism to incorporate signals from nutrient, energy, stress, developmental, and environmental cues to modulate their growth. To promote this growth, eukaryotes have to coordinate the expansion in cellular mass and size through macromolecular synthesis with the increase in cell number through division. This demands a complex orchestration of a plethora of cellular processes such as transcription, protein synthesis, metabolism and cell wall synthesis. The TARGET OF RAPAMYCIN (TOR) pathway was identified as a central integrator of this growth-regulating mechanism. Components of this pathway, including the TOR kinase and its interaction partners REGULATORY-ASSOCIATED PROTEIN OF TOR (RAPTOR) and LETHAL WITH SEC 13 PROTEIN 8 (LST8), are highly conserved among eukaryotes. This includes plants, for which the adaptation to changing environmental conditions is particularly important given their sessile lifestyle and highly plastic development.

This work sought to further expand the knowledge of how TOR function was adapted to suit the requirements of plants. Therefore, I analysed genetic knock-out mutants of *raptor* in *Arabidopsis thaliana*, which resulted in a severe reduction of growth but did not cause an early developmental arrest as reported by previous studies. Detailed analysis of these mutants further revealed defects in the development of trichomes, gametophytes, and the polar extension of root hairs and pollen tubes. Potential causes for these defects were indicated by lower DNA content and limited ROS accumulation in *raptor* mutants. High similarities between *raptor* and *lst8* mutants indicated that the formation of TOR complexes as found in other eukaryotes might not be functionally conserved in plants.

Further, I adapted a CRE//ox system for the induction of mosaic deletions of RAPTOR, which indicated no tissue-specific requirement for RAPTOR functions within the root of *A. thaliana*, but demonstrated a role in the regulation of meristem size.

To conclude, this data presents further evidence for an altered requirement of RAPTOR and LST8 function for TOR signalling in plants compared to fungi and animals. This thesis revealed novel functions of TOR in plant development, ROS homeostasis and endoreduplication. It further draws attention to the connection with other signalling pathways to regulate growth and development in plants.

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## Abbreviations

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°C	Degrees Celsius
μE	Micro-Einstein
μm	Micro-meter
μM	micro-molar
4E-BP	4E-BINDING PROTEIN
ABA	Abscisic acid
ABRC	Arabidopsis Biological Resource Center
Akt	s. PKB
amiRNA	artificial microRNA
AML1	ARABIDOPSIS MEI2-LIKE 1
AMPK	AMP-ACTIVATED PROTEIN KINASE
APC/C	Anaphase promoting complex/cyclosome (APC/C)
APR2	ADENOSINE 5'-PHOSPHOSULFATE REDUCTASE
ATG	AUTOPHAGY-RELATED
ATP	Adenosine triphosphate
AVO	ADHERES VORACIOUSLY TO TOR2
bp	Nucleotide base pairs
Ca <sup>2+</sup>	Calcium
CDC	CELL DIVISION CYCLE
CDK	CYCLIN-DEPENDENT KINASE

cm	Centi-meter
Col-0	Columbia-0
CTAB	Cetyltrimethyl ammonium bromide
DAG	Days after germination
DAI	Days after induction
ddH2O	Double-distilled water
DEPTOR	DEP DOMAIN-CONTAINING MTOR-INTERACTING PROTEIN
DEX	Dexamethasone
DNA	Deoxyribonucleic acid
EdU	Ethynyl deoxyuridine
eIF2	EUKARYOTIC INITIATION FACTOR 2
eIF3h	EUKARYOTIC TRANSLATION INITIATION FACTOR 3h
eIF4E	EUKARYOTIC TRANSLATION INITIATION FACTOR 4E
FAT	FRAP, ATM, TRAPP2
FATC	FAT, C-terminal
FKBP12	FK506 BINDING PROTEIN
FLC	FLOWERING LOCUS C
FRB	FKBP12-rapmycin binding
FT	FLOWERING LOCUS T
g	Gram
GAP	GTPase activating protein
GEF	GUANINE NUCLEOTIDE EXCHANGE FACTOR
GFP	GREEN FLUORESCENCE PROTEIN
GL	GLABRA

GOI	Gene of interest
GUS	$\beta$ -glucuronidase
h	Hour(s)
H <sub>2</sub> O <sub>2</sub>	Hydrogen peroxide
HEAT	Huntingtin, Elongation factor 3, A subunit of protein phosphatase 2a, and TOR1
hiTAIL-PCR	High-efficiency thermal asymmetric interlaced PCR
HM	Hydrophobic motif
HSp	Heat shock promoter
kbp	1000bp
KOG1	KONTROLER OF GROWTH
LD	Long day
LD	Long day (16h light 8h dark)
LRX1	LEUCINE-RICH REPEAT/EXTENSIN 1
LST8	Lethal with SEC 13 protein 8
LTP1	LIPID TRANSFER PROTEIN 1
MEI2	MEIOSIS REGULATOR-2
mg	Milli-gram
MIPS1	MYO-INOSITOL-1 PHOSPHATE SYNTHASE 1
mL	Milli-liter
mm	Milli-meter
mRNA	Messenger ribonucleic acid
MS	Murashige and Skoog
mTOR	Mechanistic/Mammalian TOR
n	Sample size

NiR	NITRITE REDUCTASE
nm	nano-meter
NR	NITROGEN REDUCTASE
PA	Phosphatidic acid
PCG1 $\alpha$	PEROXISOME PROLIFERATOR-ACTIVATED RECEPTOR (PPAR)- $\gamma$ coactivator
PDK1	PHOSPHOINOSITIDE-DEPENDENT KINASE 1
PI	Phosphatidylinositol
PI(3,4,5)P <sub>3</sub>	Phosphatidylinositol 3,4,5-triphosphate
PI3K	PHOSPHATITYLINOSITOL-30-KINASE
PI-3P	Phosphatidylinositol 3-phosphate
PIKK	Phosphatidylinositol 3-kinase-related kinase
PIN	PIN-FORMED
PKC	PROTEIN KINASE C
PLD	PHOSPHOLIPASE D
PP2A	PROTEIN PHOSPHATASE 2A
PRAS40	PROLINE-RICH AKT SUBSTRATE OF 40KDA
PTEN	PHOSPHATASE AND TENSIN HOMOLOG
RAG	RAS-RELATED GTPASE
RAM	Root apical meristem
RAPTOR	REGULATORY-ASSOCIATED PROTEIN OF TOR
RBR1	RETINOBLASTOMA-RELATED 1
RD	Regulatory domain
RHEB	RAS HOMOLOG ENRICHED IN BRAIN

RHO1	RAS HOMOLOG 1
RiBi	Ribosome biogenesis
RICTOR	RAPAMYCIN-INSENSITIVE COMPANION OF MTOR
RNA	Ribonucleic acid
RNC	RAPTOR N-terminal conserved
RNC/C	RAPTOR N-terminal Conserved / putative Caspase
ROM2	RHO1 MULTICOPY SUPPRESSOR 2
ROS	Reactive oxygen species
RRM	RNA-recognition motifs
RT	Room temperature
RTG	Retrograde response pathway
S6K	40S RIBOSOMAL PROTEIN S6 KINASE
SD	Short day
SD	Short day (10h light 12h dark)
SEM	Scanning electron microscope
SFP1	SPLIT FUNGER PROTEIN 1
SNRK1	SNF1-RELATED KINASE-1
STAT3	SIGNAL TRANSDUCER AND ACTIVATOR OF TRANSCRIPTION 3
TAG	Triacylglyceride
TAP	TWO A PHOSPHATASE ASSOCIATED PROTEIN
TCA	Tricarboxylic acid cycle
TCO89	89-KDA SUBUNIT OF TOR COMPLEX ONE
TM	Turn motif
TOR	TARGET OF RAPAMYCIN

TORC	TOR complex
TOS	MTOR signalling motif
TPR	Tetratricopeptide repeat
TSC	TUBEROUS SCLEROSIS
U2AF	U2 AUXILIARY FACTOR
ULK1	UNC51-LIKE KINASE 1
uORF	Upstream open reading frame
VPS34	VACUOLAR PROTEIN-SORTING DEFECTIVE 34
Wat1p	WD repeat-containing protein
WOX5	WUSCHEL-RELATED HOMEODOMAIN 5
Wt	Wild type

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