

学位論文（要約）

Molecular basis of haustorium development
in Orobanchaceae parasitic plants

（ハマウツボ科寄生植物における吸器発生機構の分子基盤）

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*These chapters will be published in 5 years

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List of abbreviations

35S terminator	cauliflower mosaic virus 35S terminator
3'UTR	3' untranslated region
AFB	AUXIN-RELATED F-BOX
ARF	AUXIN RESPONSE FACTOR
ATHB15	ARABIDOPSIS HOMEODOMAIN PROTEIN 15
ATHB8	ARABIDOPSIS HOMEODOMAIN PROTEIN 8
Aux/IAA	AUXIN/INDOLE-3-ACETIC ACID
AUX/LAX	AUXIN1/LIKE-AUX1
bp	base pair(s)
CASP1	CASPARIAN STRIP MEMBRANE DOMAIN PROTEIN 1
cDNA	complementary DNA
CDR	CONSTITUTIVE DISEASE RESISTANCE
CHPAA	3-chloro-4-hydroxyphenylacetic acid
cm	centimeter
Col-0	Columbia-0
C-terminal	carboxy-terminal
CYCB1;2	CYCLIN B 1;2
DEG	differentially expressed gene
DEX	dexamethasone
DMBQ	2,6-dimethoxy-1,4-benzoquinone
DMSO	dimethylsulfoxide
DNA	deoxyribonucleic acid
DNase	deoxyribonuclease
dpi	days post infection
dT	thymidine
EDTA	ethylenediaminetetraacetic acid
ER	endoplasmic reticulum
FAA	formalin-acetic acid-alcohol
GFP	Green Fluorescent Protein
GLP	GERMIN-LIKE PROTEIN
GO	gene ontology
GR	glucocorticoid receptor
GUS	β -glucuronidase

HIF	haustorium inducing factor
hpi	hours post infection
HSL	HAESA-LIKE
HSP	HEAT SHOCK PROTEIN
IAA	indole-3-acetic acid
IPA	indole-3-pyruvic acid
kbp	kilo base pairs
l	liter
M	molar
M phase	mitotic phase
mg	milligram
min	minute(s)
ml	milliliter
mM	millimolar
MP	MONOPTEROS
mRFP	monomeric red fluorescent protein
MS medium	Murashige and Skoog medium
NLS	nuclear localization signal
NPA	1-N-naphthylphthalamic acid
°C	degree Celsius
<i>P. japonicum</i>	<i>Phtheirospermum japonicum</i>
PBS	phosphate buffered saline
PCIB	p-chlorophenoxyisobutyric acid
PCR	Polymerase Chain Reaction
PGP	P-GLYCOPROTEIN
pH	negative decimal logarithm of the H ⁺ concentration
PIN	PIN-FORMED
QC	quiescent center
RAM	Root Apical Meristem
RNA	ribonucleic acid
RNase	ribonuclease
RT	reverse transcription
SAM	shoot apical meristem
sec	second(s)
spp.	species

SV40	simian virus 40
SYP122	SYNTAXIN OF PLANTS 122
TAA1	TRYPTOPHAN AMINOTRANSFERASE OF ARABIDOPSIS 1
TAR	TAA RELATED
TDIF	Tracheary Element Differentiation Inhibitory Factor
TDR	TDIF RECEPTOR
TIBA	2,3,5-Triiodobenzoic acid
TIR1	TRANSPORT INHIBITOR RESPONSE 1
v/v	volume per volume
WOX	WUSCHEL-RELATED HOMEODOMAIN
YFP	yellow fluorescent protein
YUC	YUCCA
μ	micro
μg	microgram
μl	microliter
μM	micromolar
μm	micrometer

Abstract

Parasitic plants invade other plants to retrieve nutrients. In particular, genus *Striga* (family: Orobanchaceae) threatens food security through infects food crops such as maize, sorghum, and upland rice. Currently, no efficient countermeasures exist against these noxious weeds because we still lack a clear understanding of the molecular mechanisms underlying plant parasitism. To address this issue, the facultative parasite *Phtheirospermum japonicum* (family: Orobanchaceae) was established as a model plant to study parasite-host interactions at the molecular level. Upon host recognition, parasitic plants, including those in the Orobanchaceae family, develop an invading organ called the haustorium. The haustorium in Orobanchaceae attaches to host roots, penetrates into host cell layers, eventually reaching the vasculature tissue and forming a parasite-host connection via the xylem bridge. During this developmental course, the radial pattern in parasitic root tissues is remarkably reorganized. I successfully developed cell-type-specific markers and observed their expression patterns during tissue reorganization. Interestingly, vascular-meristem-like cell development was observed in the central region of the haustorium. Further clonal analysis showed that various cell types initiated cell division simultaneously and differentiated into vascular-meristem-like cells, which eventually became the source of xylem cells, thus dictating xylem bridge formation. In addition, I performed tissue-specific transcriptome analysis coupled with laser microdissection and identified the first molecular markers for the parasite-specific intrusive cell that develops at the haustorium interface and has a unique morphological feature. Gene ontology analysis suggested that peroxidase activity may be an important factor at the interface region. Because local auxin gradients can lead to organogenesis and vascular patterning, I investigated whether auxin is a primary factor driving haustorium development. To examine auxin gradient dynamics, I next tracked the expression of synthetic auxin response promoter DR5 throughout haustorium development. Strong DR5 expression was observed on the surface of the haustorium

emerging site facing the host root. This strong expression was also maintained at the growing haustorium apex. During the late stage of haustorium development, DR5 expression patterns coincided with the location of xylem bridge formation. To clarify these dynamics, I explored the expression pattern and subcellular localization of PIN and AUX/LAX proteins (respectively auxin efflux and influx carriers). The expression of these proteins and DR5 were similar, suggesting that auxin transport mediators contribute to shaping auxin gradients during haustorium development. Application of auxin transport inhibitors demonstrated that auxin efflux activity is not important for haustorium initiation *per se*, but is crucial for xylem bridge formation. Based on these data, I propose a model of haustorium development regulated by the auxin transport network.

Chapter I: General introduction

Parasitic plants evolved an ability to acquire nutrients from other plant species. Among variety of species of parasitic plants, *Striga* spp. in Orobanchaceae family threatens food security by infecting food crops such as maize, sorghum and land rice mainly in Africa. Devastating damage caused by *Striga* infection was estimated at 1 billion USD annually, affecting more than 100 million people in Africa (Spallek et al., 2013). Currently, there are no efficient and feasible countermeasures against these noxious weeds due to the lack of understanding on the molecular mechanism of plant parasitism. One important feature which has been successfully employed by *Striga* during host plant parasitization is to germinate in close proximity to host plants. This is achieved by sensing a host root-derived chemical, strigolactone. Strigolactone was originally identified as a germination stimulant for *Striga* seeds (Cook et al., 1966). More than 40 years later, the rediscovery of strigolactone as a plant hormone, which regulates shoot branching, has driven strigolactone research in various model plants (Umehara et al., 2008), leading to identifications of its signaling pathway and components (Reviewed in; Smith and Li, 2014). These new insights gained, in turn, led to the discovery of convergent evolution of strigolactone perception in parasitic plants in Orobanchaceae (Conn et al., 2015). Another important aspect of *Striga* infection is the development of a specialized organ, the haustorium. Nutrient transfer from host plants relies on making new vascular connection to host plants through the haustorium. Only parasitic plant develops haustorium, thus non parasitic model plants cannot be used for to study haustorium. For decades, botanists have scrutinized haustorium structure with various microscopy techniques (*i.e.*, optical or electron microscopy) to understand how parasitic plants reach host vasculatures to steal nutrients. As a result, similarities and differences across haustoria in various species are well characterized. However, molecular mechanisms underlying plant parasitism remain largely unknown. Fortunately, rapid advancements in DNA sequencing technology have vastly increased genome and transcriptome accessibility in

multiple organisms, including parasitic plants and especially the Orobanchaceae family. With currently available transcriptomic and genomic data, we can apply molecular biological techniques to investigations on the genetic factors behind plant parasitism. Recently, facultative parasitic plant *Phtheirospermum japonicum* is studied as a model plant for plant parasitism in Orobanchaceae. *P. japonicum* is self-compatible plants and grows easily in the laboratory conditions with relatively short life cycle (~ 3 months), which facilitate genetics. Furthermore, the transformation method with *Agrobacterium rhizogenes* was established (Ishida et al., 2011). Draft genome is available as well (Conn et al., 2015). In this thesis, I aim to explore and understand haustorium development using *P. japonicum*.

Chapter II: Molecular analysis of haustorium development

*本章については、5年以内に雑誌等で刊行予定のため、非公開。

Chapter III: Auxin transport network underlies xylem bridge formation in parasitic plants

*本章は雑誌等で発表予定の未発表データを含むため、非公開。

Chapter IV: Concluding remarks

My aim in this study was to clarify haustorium developmental mechanisms using a facultative parasitic plant, *P. japonicum*. I incorporated multidisciplinary approaches, including molecular biology, plant physiology, and cell biology. As a result, I have successfully elucidated haustorium developmental mechanisms with respect to cell fate transition and auxin involvement.

In Chapter II, I described haustorium developmental dynamics using live imaging techniques. With cell-type specific markers, I tracked major tissue reorganization during haustorium development. Two cell fate transitions were highlighted during this reorganization process. First, vascular-meristem-like cells (origin of vascular tissues) were developed in the haustorium central region. Based on clonal analysis, this shift is most likely achieved through re-differentiation of multiple cell types located within the haustorium central region. This re-differentiation represents non-specific cell fate transition, which depends on the cells' relative positions within haustorium tissue. Second, intrusive cells were specifically differentiated from the epidermal cells. This re-differentiation represents specific cell fate transition. To better understand the mechanism behind intrusive cell re-differentiation, I performed transcriptome analysis using laser capture microdissection and successfully identified a unique transcriptome for intrusive cells. The upregulated genes in these cells should be a promising target for further functional analyses of haustorium in the future.

In Chapter III, I assessed the role of auxin in haustorium development. Based on DR5 expression patterns, I found that auxin distribution is dynamically changed during haustorium development. To elucidate these dynamics, I investigated auxin transporters and demonstrated that PjPIN2, PjPIN3, and PjLAX1 were predominantly expressed at the haustorium apex during early development. Their subcellular localizations suggest a major contribution to auxin maxima establishment in the epidermis at the haustorium initiation site. In later developmental stages,

PjPIN1, PjPIN3, PjLAX2, and PjLAX5 distinctly overlapped with DR5 expression pattern, coinciding with the xylem-bridge-formation site. Analysis of auxin efflux inhibitors also clearly demonstrated the importance of auxin efflux for xylem vessels connections during later development, but also showed that efflux was less critical for haustorium initiation and vascular-meristem-like cell differentiation in the earlier stages. This pattern is in contrast with stem-cell organ initiation (e.g., for lateral root, leaf, and flower), where organogenesis is arrested upon treatment with an auxin transport inhibitor, due to the lack of auxin maxima. Nonetheless, auxin maxima are involved in vascular-meristem-like cell specification, as its disruption alters haustorium shape and broadening vascular-meristem-like cell domain. These data suggest that auxin positively regulates vascular-meristem-like and xylem cell differentiation. Moreover, multiple transporters tightly control auxin distribution during haustorium formation.

Given that auxin function is conserved across species, parasitic plants may have adapted the auxin signaling pathway for haustorium development. However, we currently do not know how auxin signaling performs such different functions in the formation of other organs versus the haustorium. These processes may involve existing signaling components that undergo convergent evolution to specifically permit auxin responses upon haustorium formation in parasitic plants.

Supplementary Table 1: List of primers used in Chapter II

name	sequence	purpose
HB15pro-f1	TTGGTCTCAACATggagCCGATTGCTTGTITTTGATG	promoter
HB15pro-r1	TTGGTCTCAACAaaaatAGAAGGCATGGGGGGA	
HB15pro-f2	TTGGTCTCAACATatTTCTCTTTCTCTGCTCATTT	
HB15pro-r2	TTGGTCTCAACAacattCTCAGTCCTTAATTA	
PjWOX4-ggf1	TTGGTCTCAACATggagTTCACCGGTCCGGTTTTTAA	promoter
PjWOX4-ggr1	TTGGTCTCAagccACTTTTACCACCAATCT	
PjWOX4-ggf2-2	TTGGTCTCAagctCTCATATTCTTAAAAATGAGA	
PjWOX4-ggr2-2	TTGGTCTCAACAagtgcTCTCATTAAACAGCTGAATG	
PjWOX4-ggf3	TTGGTCTCAACATgacACACCACATATCCGTATC	
PjWOX4-ggr3	TTGGTCTCAgtagTAATTAGATGGTGGGGGG	
PjWOX4-ggf4	TTGGTCTCActacAGACCACTTTCCCATTTTTC	
PjWOX4-ggr4	TTGGTCTCAACAacattTTTATGATGGGGGCAAAAT	
PjTDR-ggf1	TTGGTCTCAACATggagTGATCTCTGCACAAAGCTAG	promoter
PjTDR-ggr1	TTGGTCTCAACAagggtTTATGTGTAGGAAATGT	
PjTDR-ggf2	TTGGTCTCAACATccccACACTCGATCTTTTTTAT	
PjTDR-ggr2	TTGGTCTCAACAacattGGTTTAGGGGATGGGTT	
PjCASP1pro-ggf1	TTGGTCTCAACATggagACGGCCGCAAAATGATG	promoter
PjCASP1pro-ggr1	TTGGTCTCAACAcaatACAATAGAGCAGCCAGT	
PjCASP1pro-ggf2	TTGGTCTCAACATattGTACGTCGTGATCCTTG	
PjCASP1pro-ggr2	TTGGTCTCAACAacattCTTCTTTTCTTTTGGTTA	
Venus-NTf1	TTGAAGACAAAATGtgagcaaggcgga	coding region
Venus-NTr1	TTGAAGACAAACCTTTGtacagctcgtccatgcc	
PjCASP1-ggf3	TTGAAGACAAaggtATGGAGAAAAGTGAATCAACC	coding region
PjCASP1-ggr3	TTGAAGACAAaagcTTAATGTTTTTTAGAGCTATAGCC	
PjCASP1-ggf4	TTGAAGACAAgctTCGAACAAAAAAGATATATTA	3'UTR region
PjCASP1-ggr4	TTGAAGACAAATGACGGGCTTTTCGAG	
PjCASP1-ggf5	TTGAAGACAAAGTCATCCAGCCCGGAAA	
PjCASP1-ggr5	TTGAAGACAAagcgGCCAAAATCGGGAA	
AtCO2-ggf1	TTGAAGACAAAGGAGagattggccctttg	promoter
AtCO2-ggr1	TTGAAGACAAACATtattcgttataactagggttc	
PjIRX3-ggf1	TTGAAGACAAaggagTTGACCTGTGTGCCGGA	promoter
PjIRX3-ggr1	TTGAAGACAAcattGGTGGTGGTGGTGTCGAG	
PjHSL1pro-f1	TTGGTCTCAACATggagATCTAATAACCCACGATCGCA	promoter
PjHSL1pro-r1	TTGGTCTCAACAacgacCGCTGACAACCCGAC	
PjHSL1pro-f2	TTGGTCTCAACATgtcagCTGAAGTCGTGGCAT	
PjHSL1pro-r2	TTGGTCTCAACAacattGCGACGGCTCAGGG	
PjGLP-f1	TTGGTCTCAACATggagTATCAGCTCTCATCTAC	promoter
PjGLP-r1	TTGGTCTCAACAacagAAGGAAAAAAGGGGA	
PjGLP-f2	TTGGTCTCAACATctgtTTTCTTTTCTCTTCCG	
PjGLP-r2	TTGGTCTCAACAacattAGTCTTTGTTAATGGGTGTG	
PjODR1-ggf1	TTGGTCTCAACATggagGGAACCCGCGAGAGATATA	promoter
PjODR1-ggr1	TTGGTCTCAACAaagtTGAGTCCATATGTGAGAG	
PjODR1-ggf2	TTGGTCTCAACATactCTCACAGTCTACTCAAC	
PjODR1-ggr2	TTGGTCTCAACAacattGATGATAAGATTGTATGATACAC	
PjACT-ggf1	TTGGTCTCAACATggagCTCGCTGGTTTTCTTTTAA	promoter
PjACT-ggr1	TTGGTCTCAACAaagtTTTGAATGGCAATGAG	
PjACT-ggf2	TTGGTCTCAACATatctAAAATCACTCCCAAT	
PjACT-ggr2	TTGGTCTCAACAacattCTTATTCTGAGGAACAAA	
AtSYP122-ggf1	TTGGTCTCAACATatccATGAACGATCTTCTCTCCG	coding region
AtSYP122-ggr1	TTGGTCTCActcCGTTTACAACCTCCACG	
AtSYP122-ggf2	TTGGTCTCAaggaCCTTAAAGAGCTAGATCG	
AtSYP122-ggr2	TTGGTCTCAACAaagcTTAGCGTAGTAGCCGCG	
XVE-ggf1	TTGAAGACAAaatgaaagcgttaacgg	coding region
XVE-ggr1	TTGAAGACAAccaatcatcaggatctcta	
XVE-ggf2	TTGAAGACAAatgactcgtctggcgtcca	3'UTR region
XVE-ggr2	TTGAAGACAAaagctcagactgtgcaaggga	
OLexA-ggf1	TTGAAGACAAggagctcagacagcttgcat	promoter
OLexA-ggr1	TTGAAGACAAcattgactgcttcagcctg	
NLS-f1-NT1	TTGAAGACAAccatGCCTCCAAAGAAGAAAGTaatgTTGTCTTCAA	signal peptide
NLS-r1-NT1	TTGAAGACAAcattACTTTTCTTTTCTTTTGGAGGcatgTTGTCTCAA	
LoxmC-f	TTGGTCTCAACATccatAACTTCGTATAGCATACATTATACGAAGTATATGGTGAGCAAGGGCG	add loxP site
LoxmC-r	TTGGTCTCAACAActtgTACAGCTCGTCCA	
LoxSYPter-f	TTGGTCTCAACATatccATGAACGATCTTCTC	add loxP site
LoxSYPter-r	TTGGTCTCAACAacattATAACTTCGTATAATGTATAGCTATACGAAGTTATcgcctcgttttactctat	
PjACT-ggff	TTGAAGACAAaggagCTCGCTGGTTTC	promoter
PjACT-ggfr	TTGAAGACAAatggCTCTTATTCTGAGGAACAAAA	
RT primer	TATAGAATTCGCGGCCGCTCGCGATAATACGACTCACTATAGGGCGTTTTTTTTTTTTTTTTTTTTTTTTTTTT	whole transcript amplification
Tagging	TATAGAATTCGCGGCCGCTCGCATTT	
PCR primer	GTATAGAATTCGCGGCCGCTCGCGAT	

Supplementary table 2: List of primers used in Chapter III

name	sequence	purpose
Venus-linker-f	TTGGTCTCAACATggagGTGGAGGTGGAGCTgtgagcaaggcgagg	coding region
Venus-linker-r	TTGGTCTCAACAAGccCCAGCGGCCGACGACACCAGCCTTgtacagctctcc	
PIN1-gg1	TTGGTCTCAACATggagATAGGCATAAGGTGATTTGGGA	promoter
PIN1-gg2	TTGGTCTCAACAActtgTACATTTGTAAGT	
PIN1-gg3	TTGGTCTCAACATcaagACTGGGCCATTAG	
PIN1-gg4	TTGGTCTCAACAActtCTTTTTTTATTTTTTTTT	
PIN1-gg5	TTGGTCTCAACATaatgATAACACCGTGGATTCT	coding region
PIN1-gg6	TTGGTCTCAACATccAGCGGCTGGCGGCCGT	
PIN1-gg7	TTGGTCTCAAGaaACCGAGGCCGAGAT	
PIN1-gg8	TTGGTCTCAACAActccGTAGATGTCCGACCTGGA	
PIN1-gg11	TTGGTCTCAACATggccTCCCGCGGTTGGTCCGGC	
PIN1-gg12-3	TTGGTCTCAACAActcagaCCAATTAAGCTGGAGTAAGTG	
PIN1-gg13-3	TTGGTCTCAACATTTGACTTGGTCACTGATTTCAATTCAGGTTCAATTC	
PIN1-gg14-2	TTGGTCTCAACAAAAGCTCATAGCCCC	
PIN1-gg15	TTGGTCTCAACATgcttACGAACTTCGAATGGCCAT	3'UTR + terminator
PIN1-gg16	TTGGTCTCAACAActcGAAAGTTATGAGTTCCTCCCA	
PIN2-gg1	TTGGTCTCAACATggagAATCTTCTAACCTACGTTG	promoter
PIN2-gg2	TTGGTCTCAACAActcAGGAAATTTATATATAAAGG	
PIN2-gg3	TTGGTCTCAACATcttCTCATGGTCTTATTAACATTA	
PIN2-gg4	TTGGTCTCAAGagGAGGGGCAAGTGG	
PIN2-gg5	TTGGTCTCAActtTCTCTCTCTCTACATACAAACCCCTACCCTCTACAAACCCCTCCAACTCTTTCTTTCTTT	
PIN2-gg6	TTGGTCTCAACATcattTTTTTTCTTTTCTTTTAAATTTAGTTTAAACAAATGGCGTCTGTAAGAAAGAAAGAGTTGG	
PIN2-gg7	TTGGTCTCAACATaatgATCAGGAAAGGACA	coding region
PIN2-gg8	TTGGTCTCAgaaATCCGCCACGAAGGG	
PIN2-gg9	TTGGTCTCAActcGCGGTCGCCCTCCT	
PIN2-gg10	TTGGTCTCAActcGGGAACTGGTCCGT	
PIN2-gg11	TTGGTCTCAgaaCCGCCGGCTCCATC	
PIN2-gg12	TTGGTCTCAACAActcTGAAGTTGCAGCAATATCT	
PIN2-gg13	TTGGTCTCAACATggccAGAGGTATATATGGTATTTTTATTT	
PIN2-gg14	TTGGTCTCAActcCATTCTGTTTTCCCA	
PIN2-gg15	TTGGTCTCAActcCACAAGGAGATTGAA	
PIN2-gg16	TTGGTCTCAActcACCAATAAGGCTATAAG	
PIN2-gg21	TTGGTCTCAActcCGTTTCTATTGAGTCTTATGAGACCAA	
PIN2-gg22	TTGGTCTCAActcAGACCTGAATAAGGAGTGAAGACCAA	
PIN2-gg17-2	TTGGTCTCAActcCGATTTATCTAATTTTGTGG	
PIN2-gg18	TTGGTCTCAACAActcTTAAACCCCAAGTAGCAC	
PIN2-gg19	TTGAAGACAActcGATTTGTTGGCAGAATAGA	3'UTR + terminator
PIN2-gg20	TTGAAGACAActcCACATTTGAGTCTTTGGCC	
PIN3-ggf13	TTGGTCTCAACATggagCACCCCAAAAAAGAGTAGA	promoter
PIN3-ggr1	TTGGTCTCAACAActcCGAACCTAAAATGA	
PIN3-ggf2	TTGGTCTCAACATggacGCCATTCCAAAAA	
PIN3-ggr2	TTGGTCTCAACAActcTTGTTTTCTCTCTGTTTCTC	
PIN3-ggf3	TTGGTCTCAACATaatgATATCTGGCACGA	coding region
PIN3-ggr3	TTGGTCTCAActcTCCCAATCTCGG	
PIN3-ggf4	TTGGTCTCAActcGGCAAGCTCCAGTCCACA	
PIN3-ggr4	TTGGTCTCAActcCCCTGCTGATGATT	
PIN3-ggf5	TTGGTCTCAActcAAGACTAATTACGACGCGAA	
PIN3-ggr5	TTGGTCTCAACAActcTTCGGTATCCCAATTTTG	
PIN3-ggf6	TTGGTCTCAACATggccGGTGAATATTTATTTATTATCTT	
PIN3-ggr6	TTGGTCTCAActcAACGACCAATGA	
PIN3-ggf7	TTGGTCTCAActcTTCGTTTAGGTAAGAAGATAATACA	
PIN3-ggr7	TTGGTCTCAActcCAACAGCAATGGAAG	
PIN3-ggf8	TTGGTCTCAActcCTGTTACCCTCCT	
PIN3-ggr8	TTGGTCTCAACAActcCAACAAGTACTATCGAAGAA	
PIN3-ggr9	TTGAAGACAActcCTTTCTAAGTAGTAATCGG	3'UTR + terminator
PIN3-ggr93	TTGAAGACAActcACCTTATCTCCCAAGGTA	
PIN4-ggf1	TTGGTCTCAACATggagCAAAAGCCCAAAATCCAC	promoter
PIN4-ggr1	TTGGTCTCAACAActcATTGGATCACAAAAA	
PIN4-ggf2	TTGGTCTCAACATcgtTGGTCCGATTACATAT	
PIN4-ggr2	TTGGTCTCAACAActcTTTTCTTATCACTGTATATGC	
PIN4-ggf3	TTGGTCTCAACATaatgATAAGCTGGCACGAT	coding region
PIN4-ggr3	TTGGTCTCAAGccGTCTCCGGAACTGCTC	
PIN4-ggf4	TTGGTCTCAAGccGCCTCCATCGTGTCTCAAGGTCGAGTCcgacTGAGACCAA	
PIN4-ggr4	TTGGTCTCAActcGACTCGACCTTGAACGACACGATGGAGGCggccTGAGACCAA	
PIN4-ggf5	TTGGTCTCAActcGTCGTTTTCGCTCGACGGCCAGGATTTCTcgaaTGAGACCAA	
PIN4-ggr5	TTGGTCTCAActcAGGAAATCTGGCCGTCGAGCGAAACGACgacTGAGACCAA	
PIN4-ggf6	TTGGTCTCAActcAGCCAGCCTCAGATCG	
PIN4-ggr6	TTGGTCTCAACAActcTTAGCCTCTCCATTCTGA	
PIN4-ggf7	TTGGTCTCAACATggccGGTGAAGTACTATATTTAATTTG	
PIN4-ggr7	TTGGTCTCAACAActcAGCACCAACTTTT	
PIN4-ggf8	TTGGTCTCAACATcaagTAGTTGGGGTCTTA	
PIN4-ggr82	TTGGTCTCAACAActcTTACCCAGTACTAAGAATTGC	

PIN4-ggf92	TTGAAGACAAgcttGCAAACCTCCACCCACACA	3'UTR + terminator
PIN4-ggr92	TTGAAGACAaagcCACCACCACAACCTAAACATACC	
PIN9-gf1	TTGAAGACAaggagTTCTTCAAGGTGAGTGGC	
PIN9-gr1	TTGAAGACAacattCTTTGGTTTTCTTTTTT	
PIN9-ggf1	TTGGTCTCAACATggagTTCTTCAAGGTGAGTGGC	promoter
PIN9-ggr2	TTGGTCTCAACAaagcTGAGGCCTTTTGAG	
PIN9-ggf2	TTGGTCTCAACATgcttTTAATTTCTTTGTCTGCC	
PIN9-ggr1	TTGGTCTCAACAacattCTTTGGTTTTCTTTTTT	
PIN9-ggf3	TTGGTCTCAACATaatgATATCACTCACAGACCTC	coding region
PIN9-ggr3	TTGGTCTCAACAactccGAAATCTCCGATCTCGA	
PIN9-ggf4	TTGGTCTCAACATggccTCGGCGGctctTGAGACCAA	
PIN9-ggr4	TTGGTCTCAagagCGCCGCGAagccATGTTGAGACCAA	
PIN9-ggf5	TTGGTCTCAactcCACCAGAGCCGGC	
PIN9-ggr5	TTGGTCTCAACAacgacAACATAAACCCAAAATTCAG	
PIN9-ggf6	TTGGTCTCAACATgtcgTCTATTGTACATGCTTCCT	
PIN9-ggr6	TTGGTCTCAtaaaGACCACGTTAGCC	
PIN9-ggf7	TTGGTCTCAtttaGTCTCGTTCAAGTAATAATTT	
PIN9-ggr72	TTGGTCTCAACAaagcTGCCCTGAACATT	
PIN9-ggf8	TTGAAGACAagcttTACCACAGGGATT	3'UTR + terminator
PIN9-ggr8	TTGAAGACAaccAAAAACAGCAAGG	
PIN9-ggf9	TTGAAGACAagggtTCTAACAGAGAAAATAGAGG	
PIN9-ggr9	TTGAAGACAaagcCTCCTACATTGTCTATCTT	
LAX1-ggf1	TTGGTCTCAACATggagTAGATTGAGATGCCGAGCC	promoter
LAX1-ggr1	TTGGTCTCAACAaagAGAAAGGAAAAAGGGGAC	
LAX1-ggf2	TTGGTCTCAACATctttTACTCACTCTCACTCCCT	
LAX1-ggr2	TTGGTCTCAACAacattCGTTTTTCGAAATTTCTTTCTCT	
LAX1-ggf3	TTGGTCTCAACATaatgTCGTCCGAGAAACAAGC	coding region
LAX1-ggr3	TTGGTCTCAACAattgAAGCTAACGCCTTCTTTT	
LAX1-ggf4	TTGGTCTCAACATCAAagtgcgaagggcggag	
LAX1-ggr4	TTGGTCTCAACAagattCTTGTacagctctccatg	
LAX1-ggf5	TTGGTCTCAACATaatcACGTCAATCAGGTTTTCTG	
LAX1-ggr5	TTGGTCTCAACAagggtGAAAACATAGAGTGTGGC	
LAX1-ggf6	TTGGTCTCAACATaccTAACCTTACCCTCG	
LAX1-ggr6	TTGGTCTCAACAaagcTTAATGGTGGGGTGGGGC	
LAX1-ggf7	TTGAAGACAagcttTCGGATTGGGATTTCTCAAC	3'UTR + terminator
LAX1-ggr7	TTGAAGACAaagcATTAGGGTTGAGCACGGT	
LAX2-ggf1	TTGGTCTCAACATggagATTTTCATGGCTTTTGGG	promoter
LAX2-ggr1	TTGGTCTCAACAAtccaCCTTGTATTGCTTT	
LAX2-ggf2	TTGGTCTCAACATtgaGTCTATTGATTTAGGGAG	
LAX2-ggr2	TTGGTCTCAACAacattGTTTTGTTTTTTCTTTCACTC	
LAX2-ggf3	TTGGTCTCAACATaatgGAGTCTCTGATAAGGTT	coding region
LAX2-ggr3	TTGGTCTCAACAactcTCTGAAATCAGCTTCTCTCT	
LAX2-ggf4	TTGGTCTCAACATggccAGCCATGTTATTCAAGTTTTT	
LAX2-ggr4	TTGGTCTCAaagcACCGTGGTTGCACAAC	
LAX2-ggf5	TTGGTCTCAgttcATTCCTTCATTCCAC	
LAX2-ggr5	TTGGTCTCAACAagatGACAAATTAGCAAACAATAGTAC	
LAX2-ggf6	TTGGTCTCAACATatctTAATATTACAAAAATCTTTGTG	
LAX2-ggr6	TTGGTCTCAACAAtgaTCTCTCTGCCCAA	
LAX2-ggf7	TTGGTCTCAACATtcatGCACGCAATGTGG	
LAX2-ggr7	TTGGTCTCAaagcACGATGGCCAGGAACCA	
LAX2-ggf8	TTGGTCTCAgttcCCGTTCTTCGGCCCTA	
LAX2-ggr8	TTGGTCTCAACAaagcTCAAGGGGGCTGAGGA	
LAX2-ggf9	TTGAAGACAagcttCATTATTCAACCATGGTGTAC	3'UTR + terminator
LAX2-ggr9	TTGAAGACAaagcGTTGGTGAGAATGATAT	
LAX4-ggf1	TTGGTCTCAACATggagCGAGAGTTOCCATATC	promoter
LAX4-ggr1	TTGGTCTCAACAagttAATTTCTGATTGGTGC	
LAX4-ggf2	TTGGTCTCAACATtaacGGTGAATTTGAATCT	
LAX4-ggr2	TTGGTCTCAatcgTCTTCGTTTTGGTGAATGAG	
LAX4-ggf3	TTGGTCTCAacgaGAACGAGAATCAAAT	
LAX4-ggr3	TTGGTCTCAACAacattGTCTTGGATTTCTTTT	
LAX4-ggf4	TTGGTCTCAACATaatgTCTGCTCAGAAGCAA	coding region
LAX4-ggr4	TTGGTCTCAACAactccTTAAAGCTAACACCTTCTTTTT	
LAX4-ggf5	TTGGTCTCAACATggccAACCATGTTATTCAAGTTCGT	
LAX4-ggr5	TTGGTCTCAACAagtaAGTCGAGTAAATGGAA	
LAX4-ggf6	TTGGTCTCAACATtactGCCAACCGATCTCG	
LAX4-ggr6	TTGGTCTCAACAaaacCCCCCCEAAAAA	
LAX4-ggf7	TTGGTCTCAACATgtttGGGAATCTATGGTCA	
LAX4-ggr7	TTGGTCTCAaagACAGCTCATATCAGACATA	
LAX4-ggf8	TTGGTCTCActtgTAGTTGCCTCCAAAATTTGG	
LAX4-ggr82	TTGGTCTCAACAaagcTCAATGGTGGGGTGGTAA	

LAX4-ggf9	TTGAAGACA ^{gctt} CAACAGCTCATATTCGTTTC	3'UTR + terminator
LAX4-ggr9	TTGAAGACA ^{agcg} GGACATGATTAGGATTTA	
LAX5-ggf13	TTGGTCTCAACAT ^{ggag} TTGGGTCTTGAAGTTAATGGG	promoter
LAX5-ggr12	TTGGTCTCAACA ^{atcgg} GTGCGATTGAATAT	
LAX5-ggf22	TTGGTCTCAACAT ^{ccga} GTGTTTGGAAAGAGA	
LAX5-ggr23	TTGGTCTCA ^{ttta} AAAGCTATGGGTAGGC	
LAX5-ggf23	TTGGTCTCA ^{aaa} GTCTCTCTGATTTTTCAAAGTT	
LAX5-ggr2	TTGGTCTCAACA ^{catt} TTTTTTTCTCTTCACAA	
LAX5-ggr3	TTGGTCTCAACAT ^{aatg} TTCCCAATAACAAG	coding region
LAX5-ggr3	TTGGTCTCAACA ^{actcc} CCTGAAGCTAACATTCTCTTT	
LAX5-ggr4	TTGGTCTCAACAT ^{ggcc} AAGCATATTATCCAGGtctTGAGACCAA	
LAX5-ggr4	TTGGTCTCA ^{aga} CCTGGATAATATGGTT ^{ggcc} ATGTTGAGACCAA	
LAX5-ggr5	TTGGTCTCA ^{tctt} ACCCTTCACTATTTTTTTTCAA	
LAX5-ggr5	TTGGTCTCAACA ^{aggc} CGTGGCAAGGGGAGAA	
LAX5-ggf6	TTGGTCTCAACAT ^{tctc} CGTTATCGCGATGCA	
LAX5-ggr62	TTGGTCTCAACA ^{aagc} TCAGTGCTTTGCTGGTGG	
LAX5-ggr7	TTGAAGACA ^{gctt} TGAGACCGGCCGCCTT	3'UTR + terminator
LAX5-ggr7	TTGAAGACA ^{agcg} CTGGGTGATTTGTAACGGTTT	
LAX3-ggf13	TTGAAGACA ^{aggag} TTCCGAGAGGTAGAGTT	promoter
LAX3-ggr1	TTGAAGACA ^{catt} TTGCTAGCTGTTTA	
LAX3-ggf2	TTGGTCTCAACAT ^{aatg} GCTTCAGAGAAAGTT	coding region
LAX3-ggr2	TTGGTCTCAACA ^{actcc} TCTAAAATCAACCTTCTCTCTC	
LAX3-ggf3	TTGGTCTCAACAT ^{ggcc} AACCATGTAATTCAGGTATTT	
LAX3-ggr3	TTGGTCTCAACA ^{atagc} TGATGGGAGTGTTA	
LAX3-ggf4	TTGGTCTCAACAT ^{gcta} GTGCTGTTTATTGGCC	
LAX3-ggr4	TTGGTCTCAACA ^{aagc} CAACAACAAAACCC	
LAX3-ggf5	TTGAAGACA ^{gctt} TGGGTTTGGAGGGT	3'UTR + terminator
LAX3-ggr5	TTGAAGACA ^{agcg} CCACCTAATAAATGCCCACTCA	
DR5-f	TTGAAGACA ^{aggag} GTATCCGAGCCGAGG	promoter
DR5-r	TTGAAGACA ^{catt} GGTGGATCCGATCGAT	
AtPGP4-f1	TTGGTCTCAACAT ^{GGAGggttaaggattggctctat}	promoter
AtPGP4-r1	TTGGTCTCAACA ^{AGTCAcgcattactctctg}	
AtPGP4-f2	TTGGTCTCAACATT ^{GACcattcctccctgg}	
AtPGP4-r2	TTGGTCTCAACA ^{CATT} agagttccagatacct	
AtRPS5a-ff	TTGAAGACA ^{aggag} ATTCAGTTGCAG	promoter
AtRPS5a-fr	TTGAAGACA ^{AATGGctgtgtagagagaaaca}	
MPpro-f1	TTGGTCTCAACAT ^{ggag} CCCGTCTCAATTTTTCTTCT	promoter
MPpro-r1	TTGGTCTCAACA ^{Aggag} AATGTGAAAGTTGAAAAG	
MPpro-f2	TTGGTCTCAACAT ^{ctcc} AAACGAATAACGACAT	
MPpro-r2	TTGGTCTCAACA ^{catt} TTATCTATTACTTAATCCCC	
YUC3-f1	TTGGTCTCAACAT ^{aatg} AATCATTGCGTGCCGCC	coding region
YUC3-r1	TTGGTCTCAACA ^{Aaccg} TTGACCAGCTCAACTC	
YUC3-f2	TTGGTCTCAACAT ^{cgg} TGACCTTCTCCAAGTTG	
YUC3-r2	TTGGTCTCAACA ^{Aagc} TAGGAATTATGGATACAGGGCT	
GR-ggf1	TTGGTCTCAACAT ^{cgat} ATTAGCAAGCCACTG	ligand binding domain
GR-ggr1	TTGGTCTCAACA ^{Aagc} TCATTTTTGATGAAACAGAAGCT	
HSPter-f	TTGAAGACA ^{AGCT} TTatagaagatgaagatgaatatt	3'UTR + terminator
HSPter-r	TTGAAGACA ^{AAAGCG} gcctcgtttactctat	
Ter-ggf1	TTGGTCTCAACAT ^{atcg} ATACATAACTTCGTATAATGTATGCTATACGAAGTTATCTCTAGCTAGAGTCGATCGA	add LoxP site
Ter-ggr1	TTGGTCTCA ^{gaga} TCTGGATTTTAGTACTGGA	
Ter-ggf2	TTGGTCTCA ^{tctc} TAGCTAGAGTCGATCGACA	
Ter-ggr2	TTGGTCTCAACA ^{catt} ATAACTTCGTATAGCATACATTATACGAAGTTATATCTGGATTTAGTACTGGATT	
Lox4x-f1	TTGGTCTCAACAT ^{ccat} AACTTCGTATAATGTATGCT	increase spacer region
Lox4x-r1	TTGGTCTCA ^{atat} CTGGATTTTAGTACTGGA	
Lox4x-f2	TTGGTCTCA ^{ATAT} atgaagatgaagatgaatatt	
Lox4x-r2	TTGGTCTCAACA ^{AATCG} cctcgtttactctat	
Lox4x-f3	TTGGTCTCAACAT ^{CGAT} atgaagatgaagatgaatatt	
Lox4x-r3	TTGGTCTCA ^{AGCG} cctcgtttactctat	
Lox4x-f4	TTGGTCTCA ^{cgct} CTAGCTAGAGTCGATCGACA	

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