

# Peach (*Prunus persica*) TAC1 protein interaction with a LIGHT HARVESTING CHLOROPHYLL A/B BINDING (LHCB) homolog and transcriptomic analyses reveal connections to photosynthesis

Jessica M. Waite<sup>1</sup>, Erik Burchard<sup>2</sup>, Chris Dardick<sup>2</sup>, Courtney A. Hollender<sup>3§</sup>

<sup>1</sup>USDA ARS Tree Fruit Research Laboratory

<sup>2</sup>USDA ARS Appalachian Fruit Research Station

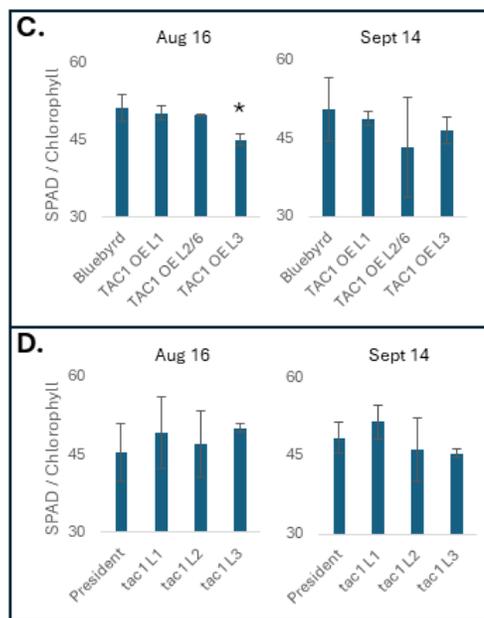
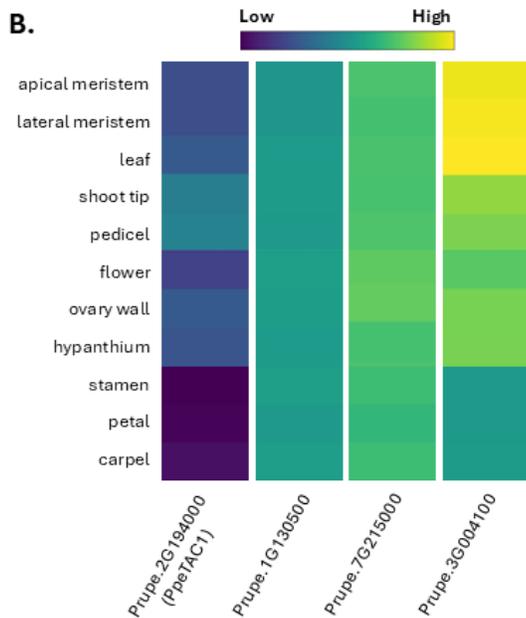
<sup>3</sup>Michigan State University Department of Horticulture

<sup>§</sup>To whom correspondence should be addressed: [chollend@msu.edu](mailto:chollend@msu.edu)

## Abstract

Plants receive and interpret external light, gravity, and temperature cues to both set and change the angles of their lateral organs for optimal growth and development. In recent years, the roles of the IGT/LAZY protein family in integrating light and gravity cues have become increasingly apparent. Here we investigated protein-protein interactions for peach (*Prunus persica*) TAC1 (PpeTAC1). *TAC1* is a light-regulated IGT/LAZY family member involved in maintaining outward growth of lateral branches in numerous plant species. Using a yeast-two-hybrid screen with a peach library, we identified three candidate protein interactors, including a LIGHT HARVESTING CHLOROPHYLL A/B BINDING (LHCB) family protein. We found that neither *TAC1* silencing nor *PpeTAC1* overexpression in plum (*P. domestica*) altered chlorophyll content, despite a recent finding that *LAZY1*-silenced plum trees have chlorotic leaves due to reduced chlorophyll. However, we identified multiple differentially expressed chloroplast-, photosynthesis-, and light-related genes between *tac1* mutant and standard peaches. Collectively, we identified connections between *PpeTAC1* and chloroplasts, photosynthesis-related machinery, and light. This data supports a role for the TAC1 protein as an integrator of light perception into mechanisms controlling lateral organ orientation in concert with or in parallel to the LAZY/DRO gravitropic-response pathway.

A. PpeTAC1 Interactors	# Colonies	Closest <i>A. thaliana</i> Homolog	E-value	Description
Prupe.3G004100	20	AT1G29930	2.14e-130	CAB1, LHCB1.3   chlorophyll A/B binding protein 1
		AT1G29920	3.36e-130	CAB2, LHCB1.1   chlorophyll A/B-binding protein 2
		AT1G29910	3.36e-130	CAB3, LHCB1.2   chlorophyll A/B binding protein 3
		AT2G34420	9.22e-129	LHCB1.5   photosystem II light harvesting complex gene B1B2
		AT2G34430	1.37e-128	LHCB1.4   light-harvesting chlorophyll-protein complex II subunit B1
Prupe.1G130500	2	AT3G06790	1.56E-78	plastid developmental protein DAG [MORF3, MULTIPLE ORGANELLAR RNA EDITING FACTOR 3
Prupe.7G215000	1	AT2G19740	1.08E-46	EL31Z, RIBOSOMAL PROTEIN EL31Z
		AT5G56710	8.84E-46	EL31X, RIBOSOMAL PROTEIN EL31X
		AT4G26230	2.77E-45	EL31Y, RIBOSOMAL PROTEIN EL31Y



E. Name	Fold change	Closest <i>A.t.</i> homolog	<i>A.t.</i> gene name	Involved in:
Prupe.1G021600	-35.93	AT3G22840	ELIP1	Chlorophyll binding, photoprotection (Heddad et al. 2006)
Prupe.2G215400	-11.7	AT5G36700	ATPGLP1	Photorespiration (Schwarte et al. 2007)
Prupe.1G291100	-5.33	AT2G26710	BAS1	Photoreceptor and brassinosteroid signaling (Neff et al. 1999)
Prupe.1G291800	-4.5	AT2G26710	BAS1	Photoreceptor and brassinosteroid signaling (Neff et al. 1999)
Prupe.1G311400	-3.89	AT5G38430	RBCS1B	Rubisco small subunit, photosynthesis (Berardini et al. 2015)
Prupe.6G129600	-2.66	AT3G52740	BIC1	Cryptochrome function (Wang et al. 2017)
Prupe.1G021800	-2.51	AT3G22840	ELIP1	Chlorophyll binding, photoprotection (Heddad et al. 2006)
Prupe.1G021400	-2.44	AT3G22840	ELIP1	Chlorophyll binding, photoprotection (Heddad et al. 2006)
Prupe.3G080900	-2.24	AT5G17870	PSRP6	Plastid-specific ribosomal protein precursor (Berardini et al. 2015)
Prupe.2G039900	2.01	AT1G60500	DRP4C	Dynamin related protein (Berardini et al. 2015)
Prupe.3G100300	2.15	AT1G80920	J8	Chloroplast stroma, light regulated (Berardini et al. 2015)
Prupe.8G162800	2.23	AT2G17880	DJC24	Chaperone DnaJ-domain superfamily (Berardini et al. 2015)
Prupe.2G157700	2.4	AT2G45770	CPFTSY	Integration of LHC proteins into thylakoids (Yuan et al. 2002)
Prupe.2G284600	2.53	AT5G66520	CREF7	PPR protein involved in chloroplast mRNA editing (Berardini et al. 2015)
Prupe.5G148400	2.58	AT1G08510	FATB	Fatty acid synthesis in plastids (Berardini et al. 2015)
Prupe.2G288700	3.16	AT2G29760	OTP81	Chloroplast RNA editing (Berardini et al. 2015)
Prupe.1G364400	3.33	AT4G36040	DJC23	Chaperone DnaJ-domain superfamily (Berardini et al. 2015)
Prupe.6G309400	6.02	AT1G56600	AtGolS2	Stress protection from light, drought, heat (Benedito dos Santos et al. 2020)
Prupe.5G130700	8.21	AT1G32640	AtMYC2	Photoreceptor and multiple hormone signaling (Song et al. 2022)

**Figure 1. PpeTAC1 connections with photosynthesis- and plastid-related genes, as shown through yeast-two-hybrid interactions, co-expression, and comparative transcriptomics:**

**A.** Candidate protein interactor results from a yeast-two-hybrid screen using peach TAC1 (PpeTAC1) as bait. Peach gene IDs from the *Prunus persica* v2.0 assembly (Verde et al. 2017) are reported along with the number of yeast colonies from which

each interactor was identified. Closest *Arabidopsis thaliana* homologs for each gene, as well as E-values and brief protein descriptions are also shown. **B.** Gene expression of *PpeTAC1* and the three identified interactors across multiple types of aerial tissues. Heatmap visually demonstrates that all genes are co-expressed at similar (medium expression) levels in shoot tips and pedicel tissues. Co-expression also occurs for shoot meristems and some floral tissues, but with a greater range of expression. Scale is based on normalized, log transformed transcript read counts. **C and D.** Chlorophyll measurements in plums (*Prunus domestica*) with *PpeTAC1* overexpressed (C) or *TAC1* silenced (D) exhibited no major changes in chlorophyll content compared to controls. Error bars represent standard deviation for three trees of each line. Asterisk (\*) indicates significance ( $p \leq 0.05$ ) according to a Student's t-test. **E.** Chloroplast-, photosynthesis-, and light-related differentially expressed genes from a transcriptomic comparison between *Ppetac1* mutant and standard peaches. *P. persica* genome v2.0 gene IDs and fold change in *Ppetac1* relative to standard trees are reported, along with closest *Arabidopsis* homologs and a short description of known processes that these genes are involved in.

## Description

Members of the *IGT/LAZY* gene family, including *TILLER ANGLE CONTROL 1 (TAC1)*, *LAZY*, and *DEEPER ROOTING (DRO)* genes, have emerged as key players in integrating light and gravity cues to set the orientation of plant organ growth (Kawamoto et al. 2022, Waite et al. 2021, Waite et al. 2018). The *IGT/LAZY* genes in peach (*Prunus persica*) were identified when a transposon insertion in *PpeTAC1* was determined to cause a columnar peach growth habit resulting from a narrow branch angle phenotype (Dardick et al 2013). Silencing of *TAC1* via RNAi in plum (*Prunus domestica*) phenocopied the peach columnar growth habit while overexpression resulted in wider branch growth angles (Hollender et al 2018). The upright branch angle phenotype of *tac1* loss-of-function or silenced plants across species supports its role in promoting wide branch angles, which is opposite to *lazy1* mutants with wide to weeping branch growth (Xu et al. 2017, Hollender et al. 2018, Hollender et al. 2020, Li et al 2022a, Kawamoto and Morita 2022, Kohler et al. 2024). While *TAC1* plays a key role in setting the angle of lateral branch growth, or gravitropic set point angle, it was not required for gravitropic reorientation responses in *Arabidopsis thaliana* (*arabidopsis*) (Hollender et al. 2020). In contrast, research over the past few decades has determined that *LAZY* and *DRO* clade proteins are central to organ reorientation in response to changes in gravity (Kawamoto and Morita 2022, Yoshihara et al. 2020). Mechanistically, *DRO* proteins have been shown to direct the asymmetric auxin transport associated with gravitropic responses in *arabidopsis* roots. *DRO1*, 2, and 3, are also referred to as *LZY3*, 4, and 2 in Nishimura et al. 2023, and *LAZY4*, 3, and 2 in Yoshihara and Spalding 2017, respectively. Gravitimulation leads to their phosphorylation and binding to amyloplasts during the sedimentation process, followed by the recruitment of *RCC1*-like domain (RLD) proteins to the plasma membrane, which regulate PIN-dependent auxin transport (Furutani et al. 2020, Nishimura et al. 2023, Chen et al. 2023, Kulich et al 2023). Specific amino acid alterations to *LAZY1* domain II, or the *IGT* domain, was also shown to reverse gravitropism in *arabidopsis* branches (Yoshihara et al. 2020). Significantly less is known about how *TAC1* functions in branch angle and orientation control. *TAC1* proteins contain four out of five conserved domains found in *LAZY* proteins (domains I-IV). However, they lack the C-terminal EAR-like CCL domain V, which is important for *LAZY* and *DRO* protein interactions with RLD proteins (Waite and Dardick 2021).

In addition to their roles in gravitropism, multiple lines of evidence connect *IGT/LAZY* family members with light signaling. *AtTAC1* expression is light-dependent and treatments with photosynthesis inhibitors drastically reduce its expression and lead to a narrow branch angle phenotype (Waite et al. 2018). Additionally, in rice, *OsTAC1* expression responds to photoperiod, which contributes to altered plant architecture (Wang et al. 2023). LC-MS/MS screens for protein-protein interactors of *IGT* family members *DRO1* and *DRO3* revealed multiple light- and photosynthesis-related candidates: *LIGHT HARVESTING CHLOROPHYLL A/B BINDING* protein, *LHCB4.1*, and two proteins associated with Photosystem I (*PSI*) (Furutani et al. 2020). *LAZY* and *DRO* genes are also required for light-induced changes to lateral organ angles, and *AtDRO1* expression is light regulated via repression by *PHYTOCHROME INTERACTING FACTORS* in the hypocotyl and promotion by *ELONGATED HYPOCOTYL 5 (HY5)* in the root (Waite et al. 2024a, Yang et al. 2020).

To better understand *TAC1* function in trees, we developed a yeast-two-hybrid (Y2H) library of peach proteins to identify putative protein interactors for *PpeTAC1* protein (Prupe.2G194000). The *PpeTAC1* bait vector was transformed into yeast, mated with the Y2H prey library, and plated on appropriate selective media. Positive colonies were selected, re-plated on higher stringency media, and plasmids from surviving colonies were sequenced to determine the identity of candidate interacting proteins. We found 23 putative interactors with the *PpeTAC1* bait. Sequencing results identified three distinct genes (Fig. 1A). Prupe.3G004100, whose closest *arabidopsis* homologs belong to the *LIGHT HARVESTING CHLOROPHYLL A/B BINDING 1 (LHCB1)* protein family, accounted for 20 of the 23 interactions (Fig. 1A). *LHCB1* proteins are important for photosynthesis, through regulation of photosystem efficiency and photoprotection (Dall'Osto et al. 2015). They are synthesized in the cytosol before being post-translationally imported to the chloroplast thylakoid membrane, where they form parts of a modular light harvesting complex (LHC) antenna system that surrounds photosystem II (*PSII*) reaction centers

(Dall’Osto et al. 2015, Pietrykowska et al. 2014). Two additional interactors were identified, accounting for 3 of the 23 interactions, Prupe.1G130500 and Prupe.7G215000 (Fig. 1A). Prupe.1G130500 is most closely related to MULTIPLE ORGANELLAR RNA EDITING FACTOR 3 (MORF3), and Prupe.7G215000 to ribosomal proteins in the L31e family. MORF proteins are involved in RNA editing in mitochondria and plastids, changing cytidines to uridines, largely in mRNA coding regions (Takenaka et al. 2012). MORF3 is required for this process in mitochondria, whereas MORF2 and MORF9 carry this out in chloroplasts. Arabidopsis homologs of Prupe.7G215000, EL31Y, X, and Z, belong to the L31e family of cytoplasmic ribosomal proteins, and form part of the large 60S ribosomal subunit (Scarpin et al. 2022). To address whether interactors are expressed in a similar spatiotemporal context, we analyzed tissue-specific expression across published datasets (see methods). Transcripts from these datasets were collectively normalized such that transcriptomic comparisons could be made. We found that *PpeTAC1* was expressed at similarly high levels to all interactors in shoot tips and flower pedicels (Fig. 1B). Co-expression, but to a lesser degree occurred in apical and lateral meristems, and some floral tissues (Fig. 1B).

To further investigate the connection between *TAC1* and chloroplasts, we next tested whether chlorophyll levels were altered in plum trees with *TAC1* silencing or ectopic expression of *PpeTAC1*. A recent long-term study on *LAZY1*-silenced plums showed seasonal reductions in chlorophyll content (Kohler et al. 2024). Chlorophyll content was assessed using a SPAD chlorophyll meter. We found no significant differences between the *TAC1* genotypes and standard trees at either timepoint (Fig. 1C and 1D), suggesting that association between PpeTAC1 protein and the LHCB1 homolog Prupe.3G004100 may not be important for chlorophyll accumulation.

Additionally, given associations between *TAC1*, photosynthesis, and light, we mined published transcriptome data from standard and *tac1* mutant peach trees (Hollender et al. 2018) to reassess differential expression of photosynthesis- and plastid-related genes. 28 genes described as chloroplast- or light-related were identified, 19 of which had a positive or negative fold change of two or greater (Fig. 1E). These included downregulation of three homologs of *EARLY LIGHT INDUCIBLE PROTEIN 1 (ELIP1)*: *Prupe.1G021600* (-35X), *Prupe.1G021800* (-2.5X), and *Prupe.1G021400* (-2.4x). ELIP1 proteins co-isolate with arabidopsis LCHB proteins in the PSII antenna under high light, and *ELIP1* expression increases as photosystem damage increases (Heddad et al. 2006). Interestingly, *Prupe.1G021800* was identified as a candidate interactor of PpeDRO1 protein (Waite et al. 2024b). Other notable downregulated differentially expressed genes (DEGs) include two homologs of *PHYB ACTIVATION TAGGED SUPPRESSOR 1 (BAS1)*, a cytochrome p450 family member that mediates signaling between photoreceptors and brassinosteroid (BR) signal transduction (Neff et al. 1999); a homolog of *BLUE-LIGHT INHIBITOR OF CRYPTOCHROMES 1 (BIC1)*, a cryptochrome inhibitor involved in blocking cryptochrome dimerization in response to blue light (Wang et al. 2017); a Rubisco small subunit gene; and a homolog of *PGLP1*, a 2-phosphoglycolate phosphatase required for photoprotection through conversion of phosphoglycolate, a toxin produced by photorespiration (Schwarte et al. 2007). Notable upregulated DEGs include: a homolog of *AtMYC2*, which is involved in signal integration between photoreceptors and multiple hormone pathways, including regulation of light-inducible genes (Song et al. 2022, Yadav et al. 2005); a homolog of *GALACTINOL SYNTHASE 2 (AtGolS2)*, a gene associated with increased tolerance to light, heat, and drought stresses (Benedito dos Santos et al. 2020); and a homolog of *CPFTSY*, which is involved in integrating proteins into Light Harvesting Complexes (Yuan et al. 2002). We also addressed whether any of the candidate interactors of PpeTAC1 were differentially expressed in this dataset, and the genes for these interactors did not appear in the DEG list. The altered expression in these genes might suggest that *TAC1* acts upstream of chloroplast and photosynthesis genes. However, the upright branch growth phenotype of these plants could play a more indirect role in these changes, which we are unable to distinguish at this time.

Together, the PpeTAC1 Y2H interaction with a LHCB protein and the altered expression of multiple chloroplast- and photosynthesis-related proteins in a *PpeTAC1*-silenced background further supports a role for *TAC1* in integrating light and gravity cues for branch orientation control. Paired with the finding that *TAC1* expression in arabidopsis is highly regulated by photosynthetic pathways, *TAC1* may be involved in feedback loops regarding light-regulation of branch angle, however further experimentation is required. Arabidopsis DRO1 and DRO3 putative interactions with LCHB4 and PSI proteins suggest a common connection between IGT/LAZY proteins and photosynthetic pathways (Furutani et al. 2020).

## Methods

### Y2H library construction

Peach RNA was extracted from mature trees of the cultivar “Encore”, using Trizol reagent (ThermoFisher Scientific). An Oligotex kit (Qiagen) was used to enrich mRNA in a 2mg sample of total RNA, finally yielding 20ug of mRNA. To make the Y2H cDNA library, 8ug of mRNA was input into a HybriZAP®-2.1 two-hybrid cDNA gigapack cloning kit and HybriZAP®-2.1 two-hybrid cDNA synthesis kit (Agilent Technologies) including modifications: (1) Invitrogen Superscript III Reverse Transcriptase (ThermoFisher Scientific) was used as the enzyme; (2) cDNA purification was performed using Amersham GFX columns; (3) cDNA size selection was performed to remove cDNAs <600bp. 150ng of size selected cDNA

was ligated and 1 $\mu$ L of cDNA was used for phage packing five times to build the library. The library was then amplified, stored at -80C, and phagemid was excised. To screen the library, amplified phagemid was purified using the Qiagen Maxi prep kit (Qiagen) and co-transformed with linearized pGADT7 vector (the Y2H prey vector with activation domain) into the yeast strain Y187 via the Yeast transformation kit, Frozen-EZ yeast transformation II (Zymo Research).

### Yeast-two-hybrid Bait construct cloning

Y2H Binding Domain (BD/bait) vectors were constructed using the pXDGATcy86 backbone (Ding et al. 2007). The full length peach *TAC1* CDS sequence was amplified by RT-PCR from peach RNA using the following primers: PpeTAC1-CDS-EcoRI-F (5' GAA TTC ATG AAG ATC TTC AAC TGG GTT CAT A) and PpeTAC1-CDS-BamHI-R (GGA TCC TCA GTG CAC ACA AGG GG). The amplicon was sub-cloned into Invitrogen pENTR/D-TOPO (ThermoFisher Scientific, Waltham MA), sequenced, and then cloned into the pXDGATcy86 backbone vector using LR clonase, resulting in PpeTAC1-BD. The PpeTAC1-BD vector was then transformed into the yeast strain AH109.

### Yeast-two-hybrid mating and selection

Yeast containing the PpeTAC1-BD vector (AH109) and prey library vectors (Y187) were mated and plated according to the Clontech Yeast Protocols Handbook PT3024-1 (Clontech, now Takara Bio USA) and as previously described in Waite et al. 2024b. Briefly, AH109 bait cultures were grown overnight, centrifuged, and resuspended in YPD media to a concentration of  $\sim 2 \times 10^8$  cells. Library/prey aliquots containing  $\sim 1 \times 10^8$  cells were added to the bait cultures, then incubated at 30C for 3-4 hours with shaking. Liquid was removed, leaving yeast on a filter membrane, which was placed yeast-side-up on YPD media plates (pH 4.5), then incubated overnight at 30°C. Membranes were washed and yeast was collected and plated on selection plates (SD -His, -Leu, -Trp +3AT), reserving some yeast for serial dilutions and calculation of library size. Growing colonies were picked and re-streaked on SD -Trp and SD -His, -Leu, -Trp plates. DNA was then extracted from these yeast strains and sequenced. Sequences were used for a BLAST search on the Genome Database for Rosaceae (<https://www.rosaceae.org>) against the peach genome (v2.0) to determine interactor identity (Verde et al. 2017, Jung et al. 2019).

### Plant materials

Peach trees used for expression analyses were derived from a self-pollinated tree heterozygous for the pillar trait (KV991636) in 2002. For *TAC1* RNAi silenced plums and *PpeTAC1* OE plums, trees were generated as described in Hollender et al. 2018. Briefly, RNAi silencing vectors were developed by amplifying a 380bp fragment from peach cDNA, and cloning it into the pHellsgate 8 vector (Commonwealth Scientific and Industrial Research Organisation (CSIRO), Australia), using gateway cloning technology. OE vectors were developed by cloning the *PpeTAC1* coding sequence into a modified pBIN-ARS vector (called pBIN-AFRS) containing the 35S Cauliflower Mosaic Virus promoter, using restriction cloning methods. Vectors were transformed into plum hypocotyl slices using *Agrobacterium* strain GV3101, as described in Petri et al. 2012. Seedlings derived from open-pollinated “Bluebyrd” and “President” trees were used as a source of hypocotyl material and as standard controls.

### Chlorophyll measurements

Chlorophyll was measured at two time points during the summer of 2018, August 16<sup>th</sup> and September 14<sup>th</sup>. Three independent lines from plum transformation were used for each of *PpeTAC1* OE and *TAC1* RNAi silenced plums. Measurements were taken from 3 different locations in the canopy, using 3 trees from each line with a SPAD 502 Chlorophyll Meter (Konica Minolta, Inc., Tokyo, Japan). Measurements from each tree were averaged, then the 3 trees from each line were averaged and reported, with statistical tests.

### Tissue-specific gene expression

Generally, tissue was collected in liquid nitrogen from greenhouse or field grown trees. Tissues were dissected by hand and ground to powder in liquid nitrogen, or lyophilized and ground using a homogenizer. RNA was extracted using either a Norgen Plant/Fungi Total RNA Purification Kit (Norgen Biotek, Thorold, ON, Canada) or an Omega SQ Total RNA kit with 2% polyvinylpyrrolidone added to the red cell lysis buffer (Omega Bio-tek, Norcross, GA). RNA sequenced using Illumina Hi-Seq. Sequence analysis and heatmap generation methods were described previously (Waite et al. 2024b). Briefly, multiple RNA sequence datasets were analyzed to cover multiple tissue types. Differential gene expression from these datasets has been published previously: data from shoot tips were included in (Hollender et al. 2018); hypanthium and ovary wall in (Li et al. 2022); flower, petal, carpel, and stamen in (Zhu et al. 2020); lateral meristem, apical meristem, and pedicel in (Waite et al. 2024b). Raw RNA reads were re-mapped to the *Prunus persica* v2.0 genome (Verde et al. 2017) using STAR v2.7.10a transcript alignment software with default parameters (Dobin et al. 2013). The featureCounts v2.0.3 tool from the Subread software package was used for transcript counts (Liao et al. 2014). Counts were normalized using TMM (Trimmed Mean of M-values) to calculate effective library size using the R (v4.1.0, <https://www.r-project.org>) package edgeR's (v3.34.1)

calcNormFactors function (Robinson et al., 2010). Mean log counts per million (CPM) was calculated for each tissue type for each gene of interest, and R package heatmaply, v1.4.2 was used to generate the heatmap, using mean values as input.

### Comparative transcriptome analysis between *tac1* mutant and standard peaches

Transcriptome experimental procedures, dataset, and DEG analysis have been published and described previously (Hollender 2018). Here, the descriptions of all DEGs found in the dataset between *tac1* and standard peach trees were subjected to searches for “chloroplast”, “light”, “photosynthesis”, and “plastid”. These were then filtered for fold change above 2 and below -2. Processes that these gene are involved were identified from the literature. In cases where there was no literature, descriptions found from The Arabidopsis Information Resource (TAIR) were used (Berardini et al. 2015).

**Acknowledgements:** We would like to acknowledge Emma Acly and Courtney Knill for assistance with the yeast-two-hybrid screen, and Doug Raines for help with chlorophyll measurements.

### References

- dos Santos TB, Vieira LGE. 2020. Involvement of the galactinol synthase gene in abiotic and biotic stress responses: A review on current knowledge. *Plant Gene* 24: 100258. DOI: [10.1016/j.plgene.2020.100258](https://doi.org/10.1016/j.plgene.2020.100258)
- Berardini TZ, Reiser L, Li D, Mezheritsky Y, Muller R, Strait E, Huala E. 2015. The arabidopsis information resource: Making and mining the “gold standard” annotated reference plant genome. *genus* 53: 474-485. DOI: [10.1002/dvg.22877](https://doi.org/10.1002/dvg.22877)
- Chen J, Yu R, Li N, Deng Z, Zhang X, Zhao Y, et al., Chen. 2023. Amyloplast sedimentation repolarizes LAZYs to achieve gravity sensing in plants. *Cell* 186: 4788-4802.e15. DOI: [10.1016/j.cell.2023.09.014](https://doi.org/10.1016/j.cell.2023.09.014)
- Dall'Osto L, Bressan M, Bassi R. 2015. Biogenesis of light harvesting proteins. *Biochimica et Biophysica Acta (BBA) - Bioenergetics* 1847: 861-871. DOI: [10.1016/j.bbabi.2015.02.009](https://doi.org/10.1016/j.bbabi.2015.02.009)
- Dardick C, Callahan A, Horn R, Ruiz KB, Zhebentyayeva T, Hollender C, et al., Scorza. 2013. PpeTAC1 promotes the horizontal growth of branches in peach trees and is a member of a functionally conserved gene family found in diverse plants species. *The Plant Journal* 75: 618-630. DOI: [10.1111/tpj.12234](https://doi.org/10.1111/tpj.12234)
- Ding X, Zhang Y, Song WY. Undefined. Use of Rolling-Circle Amplification for Large-Scale Yeast Two-Hybrid Analyses. *Plant-Pathogen Interactions* : 85-98 DOI: [10.1385/1-59259-966-4:85](https://doi.org/10.1385/1-59259-966-4:85)
- Dobin A, Davis CA, Schlesinger F, Drenkow J, Zaleski C, Jha S, et al., Gingeras. 2012. STAR: ultrafast universal RNA-seq aligner. *Bioinformatics* 29: 15-21. DOI: [10.1093/bioinformatics/bts635](https://doi.org/10.1093/bioinformatics/bts635)
- Furutani M, Hirano Y, Nishimura T, Nakamura M, Taniguchi M, Suzuki K, et al., Morita. 2020. Polar recruitment of RLD by LAZY1-like protein during gravity signaling in root branch angle control. *Nature Communications* 11: 10.1038/s41467-019-13729-7. DOI: [10.1038/s41467-019-13729-7](https://doi.org/10.1038/s41467-019-13729-7)
- Heddad M, Norén H, Reiser V, Dunaeva M, Andersson B, Adamska I. 2006. Differential Expression and Localization of Early Light-Induced Proteins in Arabidopsis. *Plant Physiology* 142: 75-87. DOI: [10.1104/pp.106.081489](https://doi.org/10.1104/pp.106.081489)
- Hollender CA, Waite JM, Tabb A, Raines D, Chinnithambi S, Dardick C. 2018. Alteration of TAC1 expression in *Prunus* species leads to pleiotropic shoot phenotypes. *Horticulture Research* 5: 10.1038/s41438-018-0034-1. DOI: [10.1038/s41438-018-0034-1](https://doi.org/10.1038/s41438-018-0034-1)
- Hollender CA, Hill JL, Waite J, Dardick C. 2020. Opposing influences of TAC1 and LAZY1 on Lateral Shoot Orientation in Arabidopsis. *Scientific Reports* 10: 10.1038/s41598-020-62962-4. DOI: [10.1038/s41598-020-62962-4](https://doi.org/10.1038/s41598-020-62962-4)
- Jung S, Lee T, Cheng CH, Buble K, Zheng P, Yu J, et al., Main. 2018. 15 years of GDR: New data and functionality in the Genome Database for Rosaceae. *Nucleic Acids Research* 47: D1137-D1145. DOI: [10.1093/nar/gky1000](https://doi.org/10.1093/nar/gky1000)
- Kawamoto N, Morita MT. 2022. Gravity sensing and responses in the coordination of the shoot gravitropic setpoint angle. *New Phytologist* 236: 1637-1654. DOI: [10.1111/nph.18474](https://doi.org/10.1111/nph.18474)
- Kohler AR, Hollender CA, Raines D, Demuth M, Dardick C. 2024. Working smarter, not harder: silencing *LAZY1* in *Prunus domestica* causes outward, wandering branch orientations with commercial and ornamental applications.. : 10.1101/2024.07.03.601917. DOI: [10.1101/2024.07.03.601917](https://doi.org/10.1101/2024.07.03.601917)
- Kulich I, Schmid J, Teplova A, Qi L, Friml J. 2024. Rapid translocation of NGR proteins driving polarization of PIN-activating D6 protein kinase during root gravitropism. *eLife* 12: 10.7554/eLife.91523. DOI: [10.7554/eLife.91523](https://doi.org/10.7554/eLife.91523)
- Li Y, Tan X, Guo J, Hu E, Pan Q, Zhao Y, Chu Y, Zhu Y. 2022. Functional Characterization of MdTAC1a Gene Related to Branch Angle in Apple (*Malus x domestica* Borkh.). *International Journal of Molecular Sciences* 23: 1870. DOI:

[10.3390/ijms23031870](https://doi.org/10.3390/ijms23031870)

Li M, Galimba K, Xiao Y, Dardick C, Mount SM, Callahan A, Liu Z. 2021. Comparative transcriptomic analysis of apple and peach fruits: insights into fruit type specification. *The Plant Journal* 109: 1614-1629. DOI: [10.1111/tpj.15633](https://doi.org/10.1111/tpj.15633)

Liao Y, Smyth GK, Shi W. 2013. featureCounts: an efficient general purpose program for assigning sequence reads to genomic features. *Bioinformatics* 30: 923-930. DOI: [10.1093/bioinformatics/btt656](https://doi.org/10.1093/bioinformatics/btt656)

Neff MM, Nguyen SM, Malancharuvil EJ, Fujioka S, Noguchi T, Seto H, et al., Chory. 1999. *BAS1* : A gene regulating brassinosteroid levels and light responsiveness in *Arabidopsis*. *Proceedings of the National Academy of Sciences* 96: 15316-15323. DOI: [10.1073/pnas.96.26.15316](https://doi.org/10.1073/pnas.96.26.15316)

Nishimura T, Mori S, Shikata H, Nakamura M, Hashiguchi Y, Abe Y, et al., Morita. 2023. Cell polarity linked to gravity sensing is generated by LZY translocation from statoliths to the plasma membrane. *Science* 381: 1006-1010. DOI: [10.1126/science.adh9978](https://doi.org/10.1126/science.adh9978)

Pietrzykowska M, Suorsa M, Semchonok DA, Tikkanen M, Boekema EJ, Aro EM, Jansson S. 2014. The Light-Harvesting Chlorophyll a/b Binding Proteins Lhcb1 and Lhcb2 Play Complementary Roles during State Transitions in *Arabidopsis*. *The Plant Cell* 26: 3646-3660. DOI: [10.1105/tpc.114.127373](https://doi.org/10.1105/tpc.114.127373)

Robinson MD, McCarthy DJ, Smyth GK. 2009. edgeR: a Bioconductor package for differential expression analysis of digital gene expression data. *Bioinformatics* 26: 139-140. DOI: [10.1093/bioinformatics/btp616](https://doi.org/10.1093/bioinformatics/btp616)

Scarpin MR, Busche M, Martinez RE, Harper LC, Reiser L, Szakonyi Dr, et al., Brunkard. 2022. An updated nomenclature for plant ribosomal protein genes. *The Plant Cell* 35: 640-643. DOI: [10.1093/plcell/koac333](https://doi.org/10.1093/plcell/koac333)

Schwarte S, Bauwe H. 2007. Identification of the Photorespiratory 2-Phosphoglycolate Phosphatase, PGLP1, in *Arabidopsis*. *Plant Physiology* 144: 1580-1586. DOI: [10.1104/pp.107.099192](https://doi.org/10.1104/pp.107.099192)

Song C, Cao Y, Dai J, Li G, Manzoor MA, Chen C, Deng H. 2022. The Multifaceted Roles of MYC2 in Plants: Toward Transcriptional Reprogramming and Stress Tolerance by Jasmonate Signaling. *Frontiers in Plant Science* 13: 10.3389/fpls.2022.868874. DOI: [10.3389/fpls.2022.868874](https://doi.org/10.3389/fpls.2022.868874)

Takenaka M, Zehrmann A, Verbitskiy D, Kugelmann M, Härtel B, Brennicke A. 2012. Multiple organellar RNA editing factor (MORF) family proteins are required for RNA editing in mitochondria and plastids of plants. *Proceedings of the National Academy of Sciences* 109: 5104-5109. DOI: [10.1073/pnas.1202452109](https://doi.org/10.1073/pnas.1202452109)

Verde I, Jenkins J, Dondini L, Micali S, Pagliarani G, Vendramin E, et al., Schmutz. 2017. The Peach v2.0 release: high-resolution linkage mapping and deep resequencing improve chromosome-scale assembly and contiguity. *BMC Genomics* 18: 10.1186/s12864-017-3606-9. DOI: [10.1186/s12864-017-3606-9](https://doi.org/10.1186/s12864-017-3606-9)

Waite JM, Dardick C. 2018. TILLER ANGLE CONTROL 1 modulates plant architecture in response to photosynthetic signals. *Journal of Experimental Botany* 69: 4935-4944. DOI: [10.1093/jxb/ery253](https://doi.org/10.1093/jxb/ery253)

Waite JM, Dardick C. 2021. The roles of the IGT gene family in plant architecture: past, present, and future. *Current Opinion in Plant Biology* 59: 101983. DOI: [10.1016/j.pbi.2020.101983](https://doi.org/10.1016/j.pbi.2020.101983)

Waite JM, Dardick C. 2024. IGT/LAZY genes are differentially influenced by light and required for light-induced change to organ angle. *BMC Biology* 22: 10.1186/s12915-024-01813-4. DOI: [10.1186/s12915-024-01813-4](https://doi.org/10.1186/s12915-024-01813-4)

Waite JM, Hollender CA, Eilers JR, Burchard E, Dardick C. 2024. Peach LAZY1 and DRO1 protein-protein interactions and co-expression with PRAF/RLD family support conserved gravity-related protein interactions across plants. *MicroPubl Biol* 2024. PubMed ID: [38287925](https://pubmed.ncbi.nlm.nih.gov/38287925/)

Wang X, Wang Q, Han YJ, Liu Q, Gu L, Yang Z, et al., Lin. 2017. A CRY–BIC negative-feedback circuitry regulating blue light sensitivity of *Arabidopsis*. *The Plant Journal* 92: 426-436. DOI: [10.1111/tpj.13664](https://doi.org/10.1111/tpj.13664)

Wang H, Tu R, Ruan Z, Chen C, Peng Z, Zhou X, et al., Cheng. 2023. Photoperiod and gravistimulation-associated Tiller Angle Control 1 modulates dynamic changes in rice plant architecture. *Theoretical and Applied Genetics* 136: 10.1007/s00122-023-04404-z. DOI: [10.1007/s00122-023-04404-z](https://doi.org/10.1007/s00122-023-04404-z)

Xu D, Qi X, Li J, Han X, Wang J, Jiang Y, Tian Y, Wang Y. 2017. PzTAC and PzLAZY from a narrow-crown poplar contribute to regulation of branch angles. *Plant Physiology and Biochemistry* 118: 571-578. DOI: [10.1016/j.plaphy.2017.07.011](https://doi.org/10.1016/j.plaphy.2017.07.011)

Yadav V, Mallappa C, Gangappa SN, Bhatia S, Chattopadhyay S. 2005. A Basic Helix-Loop-Helix Transcription Factor in *Arabidopsis*, MYC2, Acts as a Repressor of Blue Light–Mediated Photomorphogenic Growth. *The Plant Cell* 17: 1953-1966.

DOI: [10.1105/tpc.105.032060](https://doi.org/10.1105/tpc.105.032060)

Yang P, Wen Q, Yu R, Han X, Deng XW, Chen H. 2020. Light modulates the gravitropic responses through organ-specific PIFs and HY5 regulation of *LAZY4* expression in *Arabidopsis*. *Proceedings of the National Academy of Sciences* 117: 18840-18848. DOI: [10.1073/pnas.2005871117](https://doi.org/10.1073/pnas.2005871117)

Yoshihara T, Spalding EP. 2017. *LAZY* Genes Mediate the Effects of Gravity on Auxin Gradients and Plant Architecture. *Plant Physiology* 175: 959-969. DOI: [10.1104/pp.17.00942](https://doi.org/10.1104/pp.17.00942)

Yoshihara T, Spalding EP. 2019. Switching the Direction of Stem Gravitropism by Altering Two Amino Acids in AtLAZY1. *Plant Physiology* 182: 1039-1051. DOI: [10.1104/pp.19.01144](https://doi.org/10.1104/pp.19.01144)

Yuan J, Kight A, Goforth RL, Moore M, Peterson EC, Sakon J, Henry R. 2002. ATP Stimulates Signal Recognition Particle (SRP)/FtsY-supported Protein Integration in Chloroplasts. *Journal of Biological Chemistry* 277: 32400-32404. DOI: [10.1074/jbc.M206192200](https://doi.org/10.1074/jbc.M206192200)

Zhu H, Chen PY, Zhong S, Dardick C, Callahan A, An YQ, et al., Liu. 2020. Thermal-responsive genetic and epigenetic regulation of DAM cluster controlling dormancy and chilling requirement in peach floral buds. *Horticulture Research* 7: 10.1038/s41438-020-0336-y. DOI: [10.1038/s41438-020-0336-y](https://doi.org/10.1038/s41438-020-0336-y)

**Funding:** The work at AFRS was supported by Agriculture and Food Research Initiative Competitive grants 2017-67012-26099 and 10891264 from the USDA National Institute of Food and Agriculture and by the National Science Foundation grant number 1339211. CAH is funded by Department of Agriculture National Institute of Food and Agriculture HATCH project 1013242.

**Author Contributions:** Jessica M. Waite: conceptualization, formal analysis, investigation, writing - original draft, methodology, writing - review editing, visualization. Erik Burchard: visualization, methodology, formal analysis, investigation. Chris Dardick: conceptualization, funding acquisition, resources, writing - review editing, project administration. Courtney A. Hollender: conceptualization, investigation, methodology, writing - original draft, writing - review editing, visualization, funding acquisition, formal analysis.

**Reviewed By:** Anonymous

**History:** Received September 29, 2024 **Revision Received** February 17, 2025 **Accepted** February 14, 2025 **Published Online** February 19, 2025 **Indexed** March 5, 2025

**Copyright:** © 2025 by the authors. This is an open-access article distributed under the terms of the Creative Commons Attribution 4.0 International (CC BY 4.0) License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

**Citation:** Waite JM, Burchard E, Dardick C, Hollender CA. 2025. Peach (*Prunus persica*) TAC1 protein interaction with a LIGHT HARVESTING CHLOROPHYLL A/B BINDING (LHCB) homolog and transcriptomic analyses reveal connections to photosynthesis. *microPublication Biology*. [10.17912/micropub.biology.001371](https://doi.org/10.17912/micropub.biology.001371)