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Research Article

Spatiotemporal formation of the large vacuole regulated by the BIN2-VLG module is required for female gametophyte development in Arabidopsis

Li-Qin Hu,[1,2,3,†] Shi-Xia Yu,[1,2,3,†] Wan-Yue Xu,[4] Song-Hao Zu,[1] Yu-Tong Jiang,[1] Hao-Tian Shi,[2,3] Yan-Jie Zhang,[1] Hong-Wei Xue,[2,3] Ying-Xiang Wang[4] and Wen-Hui Lin[1,2,*]

1 [illegible] 200240, C[illegible]

2 [illegible] 200240, C[illegible]

3 [illegible] 200240, C[illegible]

4 [illegible] 200240, C[illegible]

*A[illegible] (W.-H.L.)

† [illegible]

[illegible]

Abstract

[illegible] (FG) [illegible] FG; [illegible] FG [illegible] AC LELE GAME H E (LG) [illegible] FG, [illegible] VLG [illegible] BRASSINOSTEROID INSENSITIVE2 (BIN2) (2-1) [illegible] LG [illegible] FG1, [illegible] FG. [illegible] BIN2 [illegible] (2-3 1 2) [illegible] LG [illegible] /VLG [illegible] VLG 2-1 [illegible] FG1, [illegible] FG1- [illegible] VLG [illegible] 2-1 [illegible] VLG [illegible] 2-3 1 2 [illegible] VLG [illegible] BIN2. [illegible] LG [illegible] BI 2 [illegible] LG [illegible] LG [illegible] 2-1. [illegible] BI 2 [illegible] LG FG [illegible] BI 2- LG [illegible] FG [illegible]

[illegible] 24, 2022. [illegible] 12, 2022. [illegible] 17, 2023

Open Access

Introduction

I A , m I m (FG) fw
I I I , fw
II I m I . I I m -
m II (fwfwC) I m I
I m , fw I . -
I m (FfwN) I I
, I m I ,
II fw I m , II I , I -
, II m FG, fw I I
II, I II, I fw I II (W
I G , 1990; fwN I I ., 1994; I I .,
1995; C I ., 1997). , I I
FfwN (. . fi I I I FG
FG1) I I FG I m .
I , I fi I m m -
I I I m I
I I FG I m . fwN
I I fi I I
A I , I I I A ABI GALAC A
EI 18 (AG 18) (A -G I II -C I I ,
2004), I B DDI G I HIBI ED
BE IfwNIDA LE (B B3.1) (L m I ., 2008),
I KI E I -1 m m A I (A KI -1)
(W H I ., 2014), I I 88- m I
fwN DIFIE C1,7 (fwN 7) (I ., 2014), HI E
ACE L A FE A E 1 (HA 1) I HA 2 (L
I ., 2008), CH fwNA I - EfwN DELI G 11 (CH 11)
(H -fwN m I ., 2005), I fwNAD - \

AGAfwN -LIKE 23 (AGL23) (C I. m I ., 2008),
II I FG I I m I - I
. I I , GA- I I I I
GA-LIKE1 (GL1) I m I FfwN
(G m I ., 2020). I m I , m II A -
I fw m I A G A E5 (AG 5)
I I fi I I (I .,
2012). KA HE I E ABLI G A
C LA fwNIC H L1 (KE CH1) fw m I
L27 I m m I -
I , I m I I
I fi I I (\ I ., 2020).

Results

Increased BIN2 activity leads to abnormal formation of large vacuoles at stage FG1

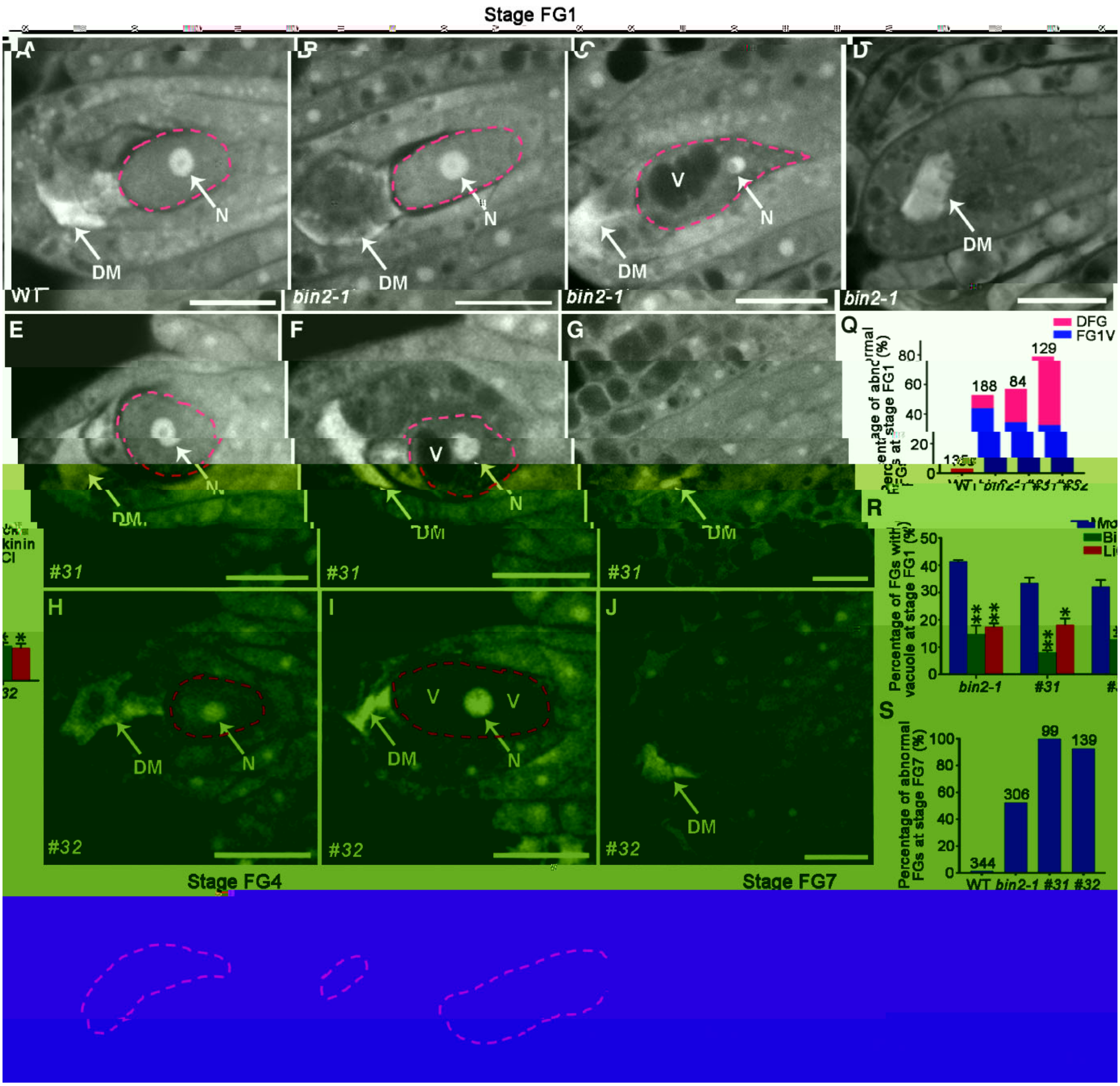

Figure 1 BIN2 ... FG1. (A–J) C... FG ... FG1 ... (A), bin2-1 (B–D), P STK:BIN2*-GFP ... #31 (E–G) #32 (H–J). ... FG ... (A), (B), (E), (H). A ... FG ... (C), (F), (I). A ... FG ... (D), (G), (J). (K) ... FG ... FG4 ... (L) A ... FG ... FG4 ... bin2-1. (M) ... FG ... FG7 ... (–) A ... FG ... bin2-1 ( ), #31 ( ), #32 ( ) ... FG7. ( ) ... FG ... FG1 ... bin2-1, #31 #32 ( ) ... FG ... FG1 ... bin2-1, #31 #32 ... 10 ... 10 ... L C ... FG ... ( ) ... FG ... FG7. ... FG ... ( ). FG ... (A–C, E–F, H–I, K–M). ... (A–C, E–F, H–I, K–L). DM ... (A–J). AFG ... FG (–). CC , EC ... C ... (M). FG, ... DFG, ... FG1 , ... FG1. E ... ± D. ... A A (**$P < 0.01$, ... D 2). B = 10 m.

... FG ... (C , 2006; ..., 2009). ... 2-3 1 2 ... -D A ... 2-3 1 2 FG ... FG1 ... 2-3 ...

(F 2, A B). A FG7, 97.7%
FG , 2.3%
(=348, F 2, C, D, I). B ,
85.6% 2-3 1 2 FG ( ),
3.1%
FG1, 1.3% FG2 ,
10.5% (=229, F 2, E–I).
BIN2 FG , BIN2
FG .

BIN2 is expressed in the female gametophyte

B (BIN2) BIN2
FG , BIN2 FG.
G BIN2 (L , 2002). G
P BIN2:GUS FG
FG1 FG7 (F 2A).
BI 2 FG, -BI 2
. -BI 2 ,
BI 2 (≈43 D) -BI 2
(F 2B).
BI 2 (K , 2009; L ,
2020). F , BI 2
2-3 1 2 (F 2C).
I , BI 2-GF
P BIN2:BIN2-GFP
-GF -BI 2 (F 2C).
-BI 2 . ,
FG BI 2 2-3 1
2 (F 2, D E),
BI 2 FG. G
BIN2 FG BI 2
(F 2, D E),
BI 2 ,
B C , (C , 2016, 2020). F
BI 2 GF - AN 711,
(E , 2011; F , 2017) (F 2, J K, F 3),
BI 2 GF - AN 711.
, BI 2
B / C FG FG .

The large vacuoles are formed early in 2-1 female gametophyte development

2-1 FG
C (P KNU:KNU-VENUS)
(, 2004; , 2018) (P FM1:GUS)
(H -M , 2005). E KNU FM1
2-1 FG FG0 FG1
(F 4A, –D),
2-1 FG .H
FM1:G 2-1 FG
FG1, FM FG
(F 4, E, –H).
FG1, FG ,
FG FG1,
. P UBQ10:
GFP-VAMP711 2-1 .
B
FG1 (. , FG1).
FG1 (F 3, A D),
FG1
(F 3, B E),
FG1 (F 3, C F). I FG , GF - AN 711
FG1,
FG1 (F 3, A–C),
(C , 1997). B ,
2-1 FG , GF - AN 711 FG1,
FG1, (F 3, D–F).
2-1 FG FG1.

The large vacuoles that form early block nuclear division at stage FG1

FG
2-1 FG .
A FG4, FG
(F 1K). B ,
2-1 FG
FG (F 1L). A FG7, FG
(F 1N), 52.6% (=306)
2-1 FG (F 1,),
FG FG1 (43.6%
9%) (F 1).

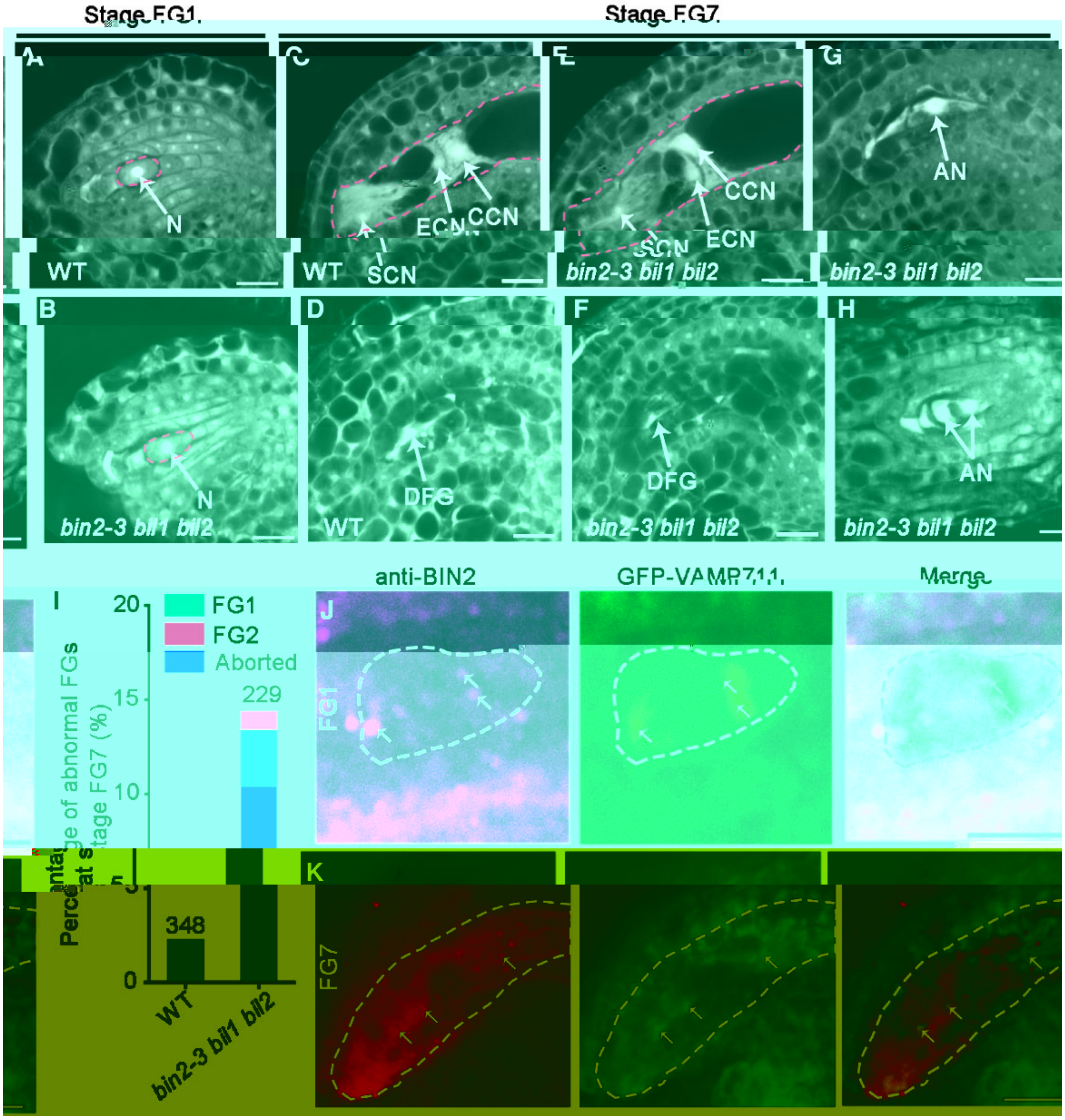

Figure 2 BI 2 . . . m m . (A–I) . . FG . m 2-3 . 1 . 2 m . (A) FG FG1 (. 2-3 . 1 . 2). (B) 2-3 . 1 . 2 FG FG1. (C–D) (C) . (D) FG FG7 . (E–H) Im 2-3 . 1 . 2 m FG7 m FG (E), FG (F), FG FG1 (G), FG FG2 (H). (I) m FG FG7 2-3 . 1 . 2 . m m FG . D . FG (A–C, E). FG (A–B). CC , EC C (C, E). DFG FG fl (D, F). A FG1 (G) FG2 (H). (J–K) BI 2 FG FG1 (J) FG7 (K) mm GF - A 711. FG . BI 2 GF - A 711. B = 10 m.

#31 #32, m P FM1:GUS FG (F 1,), m - , FG1 (m F 1B). (m F 4, C G), m FG1 2-1 (m F 4, D H). m FG m . I , L C m fi FG1 fi m 2-1 FG FG7 FG 2-1. (m F 5), m

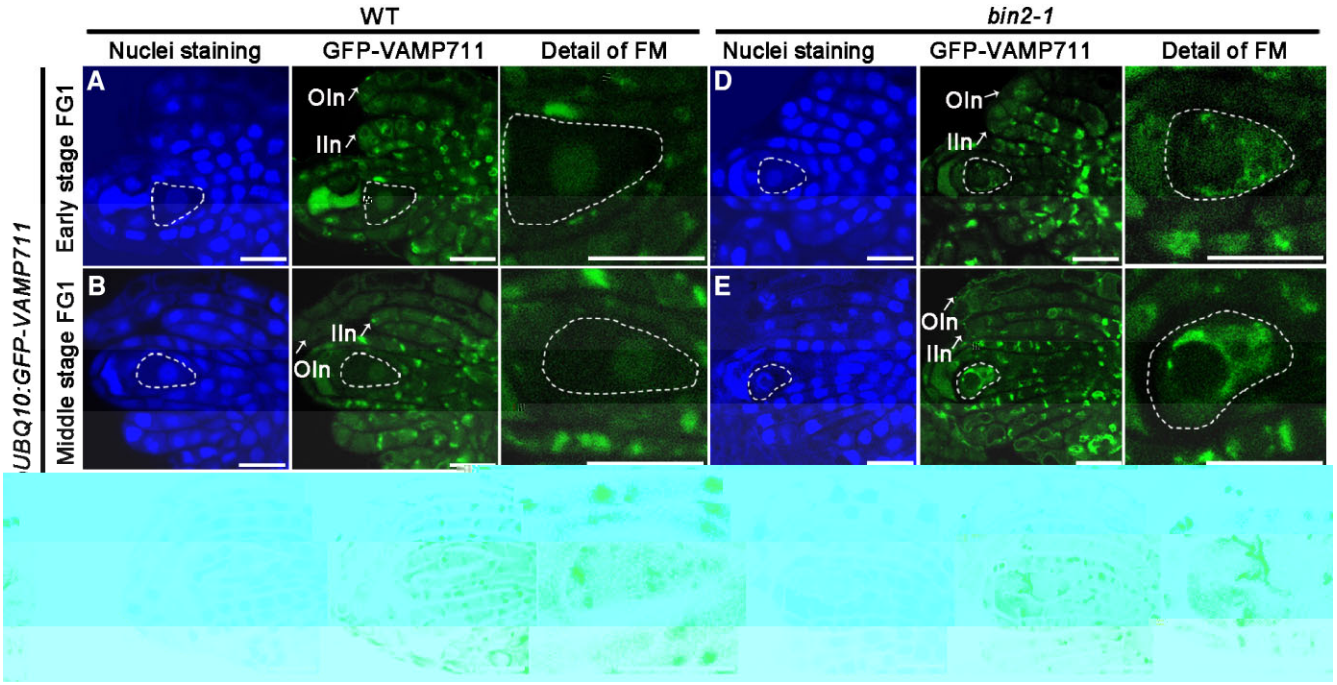

Figure 3 E l m l l m m l m P UBQ10:GFP-VAMP711 (A–C) 2-1 (D–F) FG H33258. I II m . (A–F) E l m l (A, D), m (B, E), (C, F) FG1. l FG . B =10 m.

FG1 (F 1). , fi FG fi . A , m - m 2-1 (l m l F 6A, –H), Bl 2 m FG m fi FG1.

BIN2 participates in female gametophyte development mainly by regulating vacuole formation

Bl 2 FG m , fi P DD45:GFP (V l., 2012) 2-1 m . E P DD45:GFP m 2-1 FG FG7, (l m l F 4, I J). B 2-1 m (l m l F 1, B C), l II, II l II m l. Bl 2 l FG m m l l m .

BIN2 interacts with VLG both in vitro and in vivo

Bl 2 l l m - FG m , m - C m m l l

FG m , A KIN-1 (V H l., 2014), B 3.1 (L m l., 2008), AGP18 (A -G II -C l , 2004), ABORTED GAMETOPH TE 1 (AOG1) (C l., 2015), MOS7 (l., 2014), AGL23 (C l. m l., 2008), l - l C CA1;1, C CB2;3, C CD2;1/3;1 (M l., 2006; D l., 2007; H l., 2010; E l., 2011). m fi l l l 2-1 (l m l F 7), l FG l m 2-1 l l l . B VLG m l m l FG (D'I l l., 2017), l m l 2-1 FG FG1. B LG l M B / C m - l m l l FG (D'I l l., 2017), l Bl 2 m l m - LG. - (2H), fi (F 4A). B m l l fl m l m (B FC) II - Bl 2 LG l m (F 4B). I II- , m m l (M B)- LG l - (G)-Bl 2, G (F 4C). m l l , - mm (C -I) - l l Bl 2 LG A - P 35S:BIN2-M C P 35S: VLG-GFP (F 4D). I , Bl 2 LG -l l

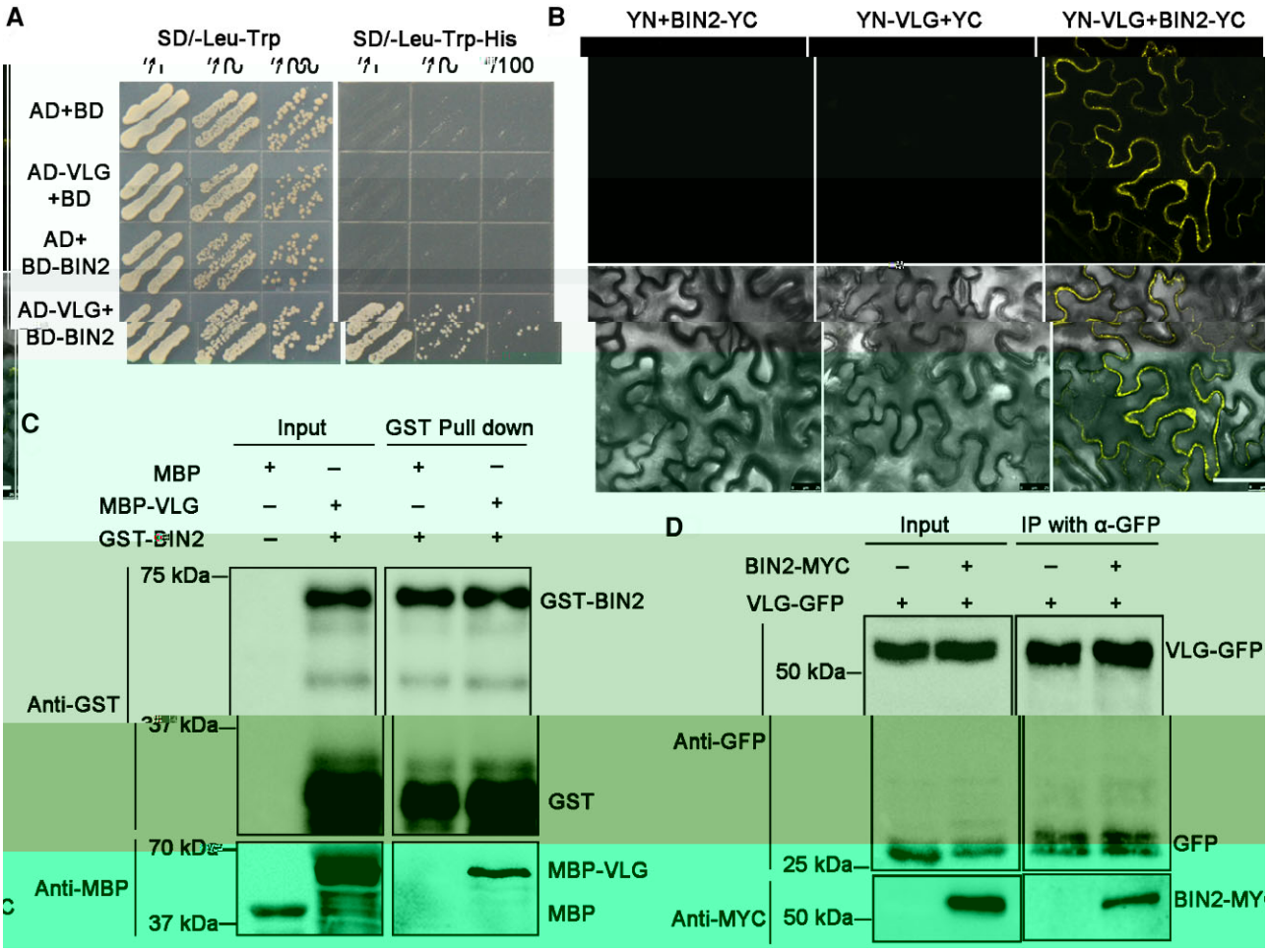

Figure 4 BI 2 LG . (A) - BI 2 LG.

N (F 8). BI 2 LG FG (F 2J–K, F 2 3; D'I ., 2017), , . , BI 2 LG FG .

BIN2 positively regulates VLG abundance and influences large vacuole formation

BI 2 (K 2015). BI 2 LG , *P 35S:VLG-GFP* 2-1 2-3 1 2 . C LG-GF fi 2-1 -

. I , fi 2-3 1 2 (F 5, A B), BI 2 - LG . LG 2-1 FG FG1, A (A) *FM1* fi *VLG* (K ., 2004; H -M ., 2005). P *FM1:VLG-RNA* 2-1 (#1 #2) fi LG (F 9A), FG FG1 fi (F 5C). fi *VLG* FG1. M , fi *P FM1:VLG-GFP* LG-GF FG1 (F 5D; F 9B). I , FG FG7 fi

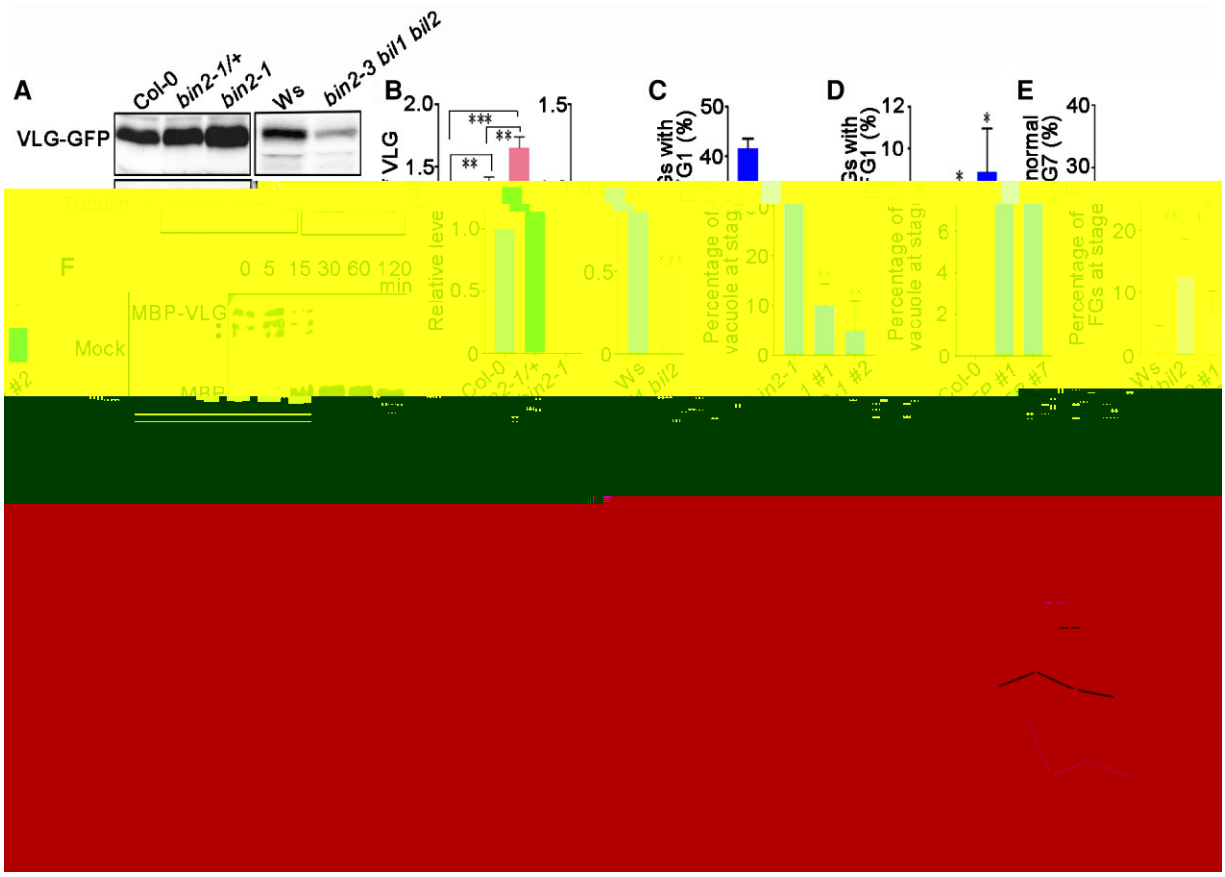

Figure 5 BI 2 LG . (A–B) LG m 2-1 -GF 2-3 1 2. mm m (A), LG-GF (B). -GF (C -0), 2-1 2-3 1 2 P 35S:VLG-GFP, . LG -GF , (I D) LG fi Im L (B -). LG I D LG/I D . D m ± D m . (C) fi FG FG1 P FM1:VLG-RNA 2-1 . FG m . (D) fi FG FG1 P FM1:VLG-GFP . FG m . (E) m FG FG7. #1 #2 P VLG: VLG-GFP 2-3 1 2 m . FG m 10 . (F) G132 LG -. A m B - LG -GF m (D) 100 G132 m , -B . (G) LG 2-1 -. B - LG m -B . D B - LG (F–G). (H–I) LG m 2-1 -GF 100 CH m . mm m (H) (I). LG-GF (A–B) m I D LG/I D 0 . D m ± D -. A fi (*P < 0.05, **P < 0.01, ***P < 0.001, A A, m D 2).

2-3 1 2 m P VLG:VLG-GFP (F 5E), LG 2-3 1 2 . LG fi m .

BIN2 enhances VLG stability via phosphorylation

LG , -. fi m B - LG , m -GF , G132, 26 m . LG G132- m (F 5F), LG 26 m . m , LG -GF 2-1 (F 5G), BI 2 LG . LG - (CH), LG-GF fi- , fi 2-1 m (F 5, H I), LG m 2-1 -GF .

BI 2 LG 26 B BI 2 LG, / - / G K3 (V 2002; 2007, 2010) (F 6, A B), LG BI 2 B - LG B -BI 2 LG BI 2 (F 6C). (LC-) LG B - LG B -BI 2 BI 2 99, 103, 115, 119, 204, 208 G K3 LG (F 10). LG BI 2, 99, 103, 115, 119, 204, 208 A LG (LG / -A) A LG (LG / -D). LG / -A BI 2 LG (F 6C). BI 2 LG (CI) G K3β LG CI G K3β (F 6D), BI 2 LG . I , LG / -A LG, LG / -D (F 6E), LG / -A LG / -D BI 2- LG .

BIN2 might participate in large vacuole formation and female gametophyte development by phosphorylating VLG

LG BI 2 fl LG FG P *FM1:VLG*$^{S/T-A}$*-GFP* P *FM1:VLG*$^{S/T-D}$*-GFP* FG FG1 1 . I P *FM1:VLG*$^{S/T-D}$*-GFP* 10% (#24) 4.1% (#30) FG 4.8% (#24) 3.3% (#30) , 2-1 (F 7, A–E). I P *FM1:VLG*$^{S/T-A}$*-GFP* 8.1% (#7) 6.8% (#11) FG (F 11, A– 1D), 2-3 1 2, /*VLG* (D'I 2017). I BI 2 FG LG.

, LG FG (F 8A). I BI 2 - 2-1 LG 26 , FG1 (F 8B). B , *BIN2* 2-3 1 2 LG , (F 8C). B FG (F 8, B C). C , BI 2- LG FG .

Discussion

FG FG2 (C 1997). FG (2002; 2015; D'I 2017). , LG /*VLG* FG , FG1 FG2, FG5, FG7 (D'I 2017). /*VLG* ( ) FG2. H , FG1 FG , BI 2 G K3- (/ - /) (2002; 2007, 2010), (2019; L 2020; 2021; 2021). I , BI 2 FG fl FG . I BI 2 FG1 (F 1, C, F, I,), BI 2 (F 1). L *BIN2* 2-3 1 2 FG (F 2H), *BIN2* FG. , BI 2 LG, LG (F 6, C E), fl FG . I , BI 2 LG FG, LG LG FG.

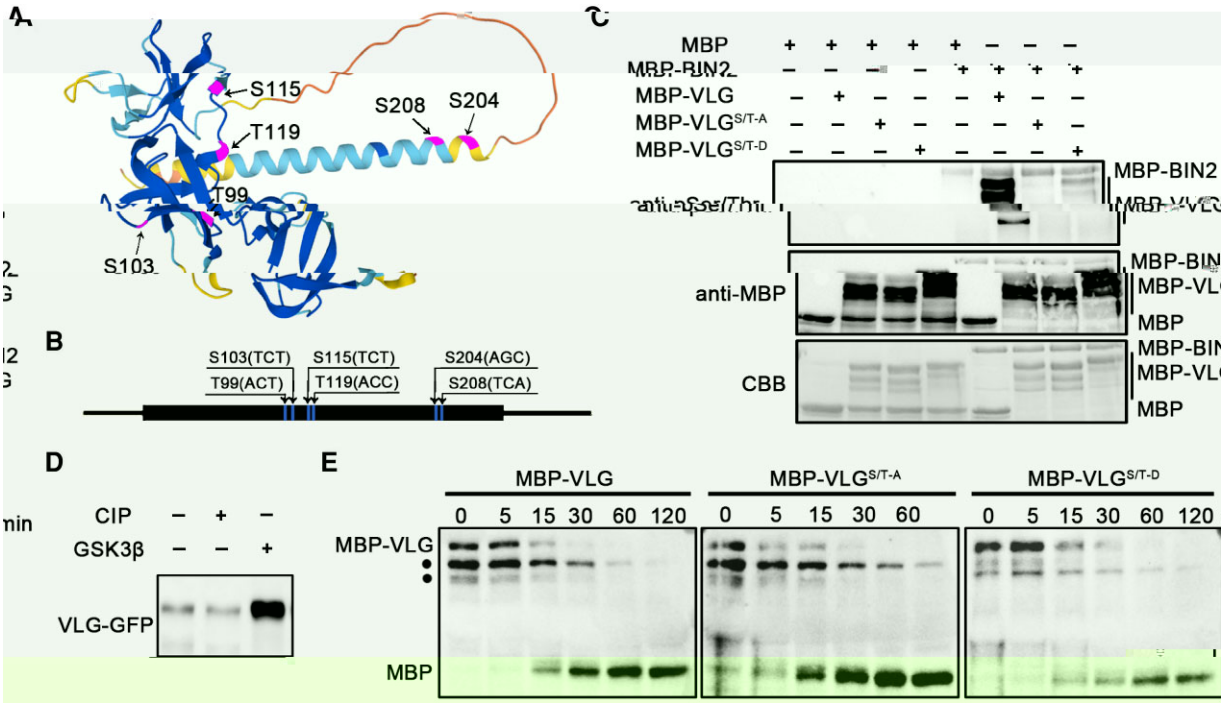

Figure 6 BI 2 LG . (A) LG A 2 (://ww . K). (B) LG. ; . A C, BI 2 LG. B - LG / -A BI 2 fi B - LG / -D . B , B -BI 2, B - LG, B - LG 30 C. (D) LG-GF CI , G K3β - . I -GF - P 35S:VLG-GFP , CI G K3β. (E) B - LG / -A , B - LG / -D B - LG. B - LG, B - LG / -A , B - LG / -D -B . D B - LG.

LG FG . fi VLG 2-1 FG FG1 - fi FG , VLG FG FG1 (F 5, C D). C , fi LG FG1 (F 7), fi LG FG (F 11). LG / -A LG, LG. LG LG BI 2 FG H , LG 2-3 1 2, (F 5, A B), BI 2 LG. P G K3- K4 K6 FG (D -F 1., 1995). G K3- FG A (J H , 2002). I , LG- FG - LG (F 10). C F 2-1, fi BI 2 fi (F 4, A, –H). 2-1 FG FG ( ) FG (F 4, I 4). B ,

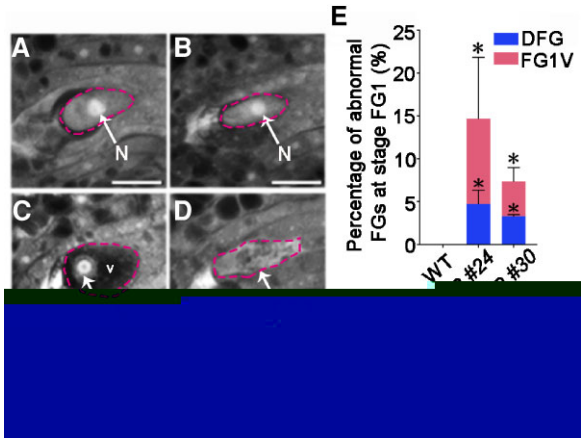

Figure 7 -m LG . (A) - FG FG1. B–D, m (B), m (C), (D) FG FG1 *P* *FM1:VLG*$^{S/T\text{-}D}$*-GFP* m . (E) FG1. FG m . D FG . . DFG FG . FG1 , FG FG1. B = 10 m. E m ± D. fi m A A (*$P < 0.05$, m D 2).

BI 2 FG . GF - AM 711 - *2-1* , FG *2-1* (F 3A–F), m FG *2-1*. A -m LG BI 2 (m F 12), , fl LG . LG B / C , -G (G) . B / C B / C (C ., 2016, 2020). I LG m B / C , BI 2- LG m FG1, BI 2- LG m FG2. B m FG - m , BI 2- LG m fl . m , *P* *FM1:GUS* , fi FG1 fi m FG (F 1, 3, 5). , FG m - F m . m m *2-1*

(m F 6), *2-1* (m F 7), FG m FG1; , . A m (., 2021), FG BI 2- LG FG BI 2- LG FG .

Materials and methods

Plant materials and growth conditions

, m, (C B , 1998; ., 2019). - A C -0, -2, L . m C -0 , *2-1* (L ., 2001), *P* *DD45:GFP* (., 2012), *P* *FM1:GUS* (H - m ., 2005; ., 2020), *P* *STK:BIN2*-GFP* (., 2019), *P* *35S:BIN2-M C* (., 2019). *2-3* 1 2 m (., 2009) -2 , *P* *KNU:KNU-VENUS* L (., 2004; ., 2018). A A 22 C -(16 /8) fl - 90 µm m^{-2} $^{-1}$ (F L LED 8-16-65/ A22B/24).

DNA manipulation

P *UBQ10:GFP-VAMP711* G (I). E m E /D/ (I) L- - (L) *P* *UBQ10:GFP-GW* *P* *UBQ10:GFP-VAMP711*. A C K (m). *P* *35S:VLG-GFP* , 747- m *VLG* (CD) m fi *CAMBIA1302* (., 2022) *B* II S I . *BIN2* m

N N (B) F 3
C A . *ACTIN7* (A 5G09810)
(., 2019; J ., 2020). A
m m
. m
D 1.

Confocal laser scanning microscopy

(C ., 1997; ., 2005). D
fi 30 m 4%
12.5 m (H 6.9).
fi . .
10%, 20%, 40%, 60%, 80%, 90% (10 m). A
90% ,
10 m 100%
2:1 (/)

II II B1 50 m -HC , H 8.0, 500 m , 1 m C 2, 10 m ED A, 5 m D , 2 m F, 1× ( ), 30 m . 18,514 10 m 4 C, II fi (C m) m 10 µL -GF (C m) 3 4 C. A B1 , 100 C 10 m . A 30-µL m -/ C (A ; . . AB0001; 1:3000) -GF (A ; . . AB0005; 1:3000).

Cell-free degradation assay

F II- , 0.1 7- - mm m (-/). II II (25 m -HC , H 7.5, 10 m C , 10 m C 2, 5 m D , 0.4 m F, 10 m A) 30 m . , 1 µ /B - LG m 22 C fi m . m 100 C 10 m II D - AGE. -/B (A ; . . AB0029; 1:3000) .

CIP and GSK treatment assays

F CI m , LG-GF mm . GF - B1 CI (m) 2 µL CI (E B) 500 µL CI - (50 m -HC , H 7.5, 5 m C 2, 1 m D , 1 m F, 0.1% -40) 60 m 37 C. CI . F G K3β m , LG-GF mm . GF - B1 - 2 µL G K3β 300 µL G K3β - 60 m 37 C mm (C m). B1 m 100 C 10 m . A 20-µL m -GF (A ; . . AB0005; 1:3000).

kinase treatment assay

/B - LG /B -BI 2 mm fi /B - . 5 µ /B /B -BI 2 20 µ fi /B /B - LG 30 C 1 . fi (25 m -HC H 7.4, 12 m C 2, 1 m D 1 m A) (., 2019). m 100 C 10 m . A 15-µL m -/B (A ; . . AB0029; 1:3000), -(/) (A m; . . AB17464; 1:4,000).

Immunoblot assay

F 7- 2× D . m 30 m , 18,514 10 m 4 C. 10 m . 10 µL 10% D - AGE II m m (m). m -BI 2 (A ; . . A 163203; 1:5,000) m F 2B, -GF (A ; . . AB0005; 1:5,000) (A m , . . 20045; 1:5,000) F 5, A H 4 C G - G (H + L) H (B ; B-AB0102; 1:5,000) G - G (H + L) H (B ; B-AB0101; 1:5,000). A 5% m (B 1% -20). m BI - AD C m D Im m. (I D) LG F 5, A H fi Im L (B -) (., 2019).

Root mitosis analysis

1/2× m m 7–10 . fi C ' fi (100% : = 3:1) (., 2014) m 1 m m . fi m H 2 20 m 37 C. fi . A H 2 , . 45 C 30 , 20 µL 60% . m m m 20-µL - II (−20 C) C ' fi m . 5–10 m . A 7–10 µ DA I, m , A A2 m (., 2014).

Accession numbers

m *ACTIN7* (A 5G09810), *AGP18* (A 4G37450), *AGL23* (A 1G65360), *AOG1* (A 5G57790), *ATKIN-1* (A 3G63480), *BIN2* (A 4G18710), *BIL1* (A 2G30980), *BIL2* (A 1G06390), *BUB3.1* (A 3G19590), *C CA1;1* (A 1G44110), *C CB2;3*

(A 1G20610), C *CD2;1* (A 2G22490), C *CD3;1* (A 4G34160). *DD45* (A 2G21740), *D AD* (A 5G51330), *FM1* (A 4G12250), *KNU* (A 5G14010), *MOS7* (A 5G05680), *PRL* (A 4G02060), *SNAIL1* (A 5G61770), *SWA1* (A 2G47990), *SWA2* (A 1G 72440), *VLG* (A 2G17740).

Supplemental data

Supplemental Figure S1.

Supplemental Figure S2. *BIN2*

Supplemental Figure S3.

Supplemental Figure S4.

Supplemental Figure S5.

Supplemental Figure S6. A

Supplemental Figure S7.

Supplemental Figure S8.

Supplemental Figure S9.

Supplemental Figure S10.

Supplemental Figure S11.

Supplemental Figure S12.

Supplemental Data Set S1.

Supplemental Data Set S2.

Acknowledgments

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