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Well get back to you only if we require additional details or have more information to share. Note that email addresses and full names are not considered private information. Please mention this; Therefore, avoid filling in personal details. The manual is 1,76 mb in size. If you have not received an email, then probably have entered the wrong email address or your mailbox is too full. In addition, it may be that your ISP may have a maximum size for emails to receive. Check your email Please enter your email address. In plants, this cation also plays a key role in the control of stomatal movement. To gain further insight into the regulation of these channels, we performed a splitubiquitin proteinprotein interaction screen searching for KAT1 interactors in Arabidopsis Arabidopsis thaliana . We characterized one of these candidates, BCL2ASSOCIATED ATHANOGENE4 BAG4, in detail using biochemical and genetic approaches to confirm this interaction and its effect on KAT1 activity. Importantly, lines lacking or overexpressing the BAG4 gene show altered KAT1 plasma membrane accumulation and alterations in stomatal movement. Our data allowed us to identify a KAT1 regulator and define a potential target for the plant BAG family. Ion homeostasis is a dynamic process essential for the normal functioning of any organism. Some minerals are required for biological processes, but their excess or deficiency is deleterious. In addition, cells must discriminate between the physiologically relevant ions and the toxic ions that may be chemically similar. For this reason, all living organisms have developed efficient systems to capture and store ions and complex mechanisms to maintain homeostatic concentrations. In plants, ion homeostasis must provide the environment required to maintain all internal processes, prevent toxicity, and

enable the response to environmental changes using the minerals present in the soil.http://www.polimak.pl/userfiles/bosch-rtt-100-user-manual.xml

Potassium is a key monovalent cation necessary for many aspects of growth and survival, among them, compensation of the negative charges generated in processes such as glycolysis, the maintenance of electroneutrality, turgor pressure and cell volume, phloem loading, enzymatic activity, protein synthesis, and the establishment of proper membrane potential and an adequate intracellular pH RodriguezNavarro, 2000 . Potassium homeostasis is essential for optimal water use efficiency, as potassium currents participate in stomatal movement. Stomatal opening depends on potassium and anion uptake coupled to increased proton efflux, while stomatal closing depends on potassium and anion efflux Lawson and Blatt, 2014 . Understanding the molecular mechanisms underlying potassium regulation in guard cells can provide valuable information with applications to the development of new varieties of droughtresistant crops. In response to elevated CO 2, drought may be among the main threats to world food production because of its dramatic impact on agricultural productivity. The third family, Shaker channels, is present in animals, plants, yeast, and bacteria. The genome of Arabidopsis contains nine members that are classified into five different groups depending on their phylogeny and functional aspects Pilot et al., 2003 . Groups 1 and 2 contain four inwardrectifying channels AKT1, AKT6, KAT1, and KAT2, while group 3 contains a weak inward rectifier AKT2. Group 4 contains a “Silent” channel KC1 and group 5 consists of two outwardrectifying channels GORK and SKOR. KAT1 is considered the prototype of inwardrectifying potassium channels and plays an important role in potassium fluxes in the guard cell, as mentioned above Anderson et al., 1992; Schachtman et al., 1992; Nakamura et al., 1995 . Several proteins have been implicated in KAT1 regulation. In our study, we used a splitubiquitin approach to identify proteins interacting with KAT1.

We found that the BCL2associated athanogene BAG 4 protein interacts with KAT1. BAG4 is a member of an evolutionarily conserved family defined by the presence of the BAG domain. BAG family proteins have been extensively studied in mammalian systems, where they have been shown to regulate several processes, in many cases by recruiting cochaperones and different chaperone systems, including the Heat shock protein 70 Hsp70, which binds to helices 2 and 3 of the BAG domain Takayama and Reed, 2001; Kabbage and Dickman, 2008 . In plants, BAG proteins have been related to processes such as the unfolded protein response, pathogen resistance, and abiotic stress and have been shown to conserve the ability to bind to Hsp70 Doukhanina et al., 2006; Williams et al., 2010; Kabbage et al., 2016 , although the molecular mechanisms underlying their function are largely undefined. More specifically, overexpression of BAG4 is able to increase salinity tolerance in Arabidopsis and rice Doukhanina et al., 2006; Hoang et al., 2015 , and BAG1 and BAG6 have been implicated in the proteasomal degradation of plastid proteins and fungal resistance, respectively Kabbage et al., 2016; Lee et al., 2016 . In this report, we show that BAG4 expression increases KAT1 activity in both yeast and Xenopus oocytes. Moreover, we have confirmed the KAT1BAG4 interaction in plants and provide evidence that BAG4 plays a role in the arrival of KAT1 at the plasma membrane in both gain and lossoffunction experiments. In addition, mutants lacking or overexpressing the BAG4 gene present alterations in stomatal opening dynamics, consistent with a physiological role in modulating potassium fluxes. Taken together, our data suggest that in plants, BAG4 acts as a KAT1 regulator. Our work uncovers an important potential client for the plant BAG protein family.

RESULTS In order to gain further insight into the posttranslational regulation of the KAT1 inwardrectifying potassium channel, we carried out a highthroughput screening for physical interactors using the splitubiquitin yeast twohybrid assay with an Arabidopsis complementary DNA cDNA library, as described in “Materials and Methods.” Previous reports have shown that KAT1 interactions can be detected using this method Obrdlik et al., 2004 . Using this approach, we

identified BAG4 as a KAT1 interacting protein. As a first step in the characterization of this interaction, we carried out a functional complementation assay in yeast for selected candidates. We cotransformed KAT1 with BAG4 and two other candidate proteins into a yeast strain lacking the endogenous highaffinity potassium transporters Trk1 and Trk2. This strain grows very poorly in media with limiting amounts of potassium 12.In order to determine whether BAG4 could functionally regulate KAT1, we performed growth assays in liquid media under three conditions 1 low KAT1 expression Met supplementation and low potassium no KCl supplementation; 2 low KAT1 expression and high potassium 50 m m KCl; and 3 high KAT1 expression and low potassium. Correct expression of the proteins was confirmed by immunodetection Fig. 1 . As observed, both BAG4 and PPI1 accumulated to similar levels, whereas RPT2 accumulated to lower levels in yeast. This result is consistent with BAG4 improving KAT1 activity in this heterologous system. Based on this phenotype, BAG4 was selected for further analysis. We next wanted to confirm that the increase in growth in this assay was not due to increased expression of the KAT1 protein upon BAG4 overexpression. For this, we determined the levels of KAT1 in six control strains and seven strains coexpressing BAG4.

As shown in Figure 1, we observed no change in KAT1 protein levels, suggesting that the effect of BAG4 is not due to increased accumulation of KAT1, and so mechanisms based on transcriptional regulation and protein turnover in this model system can be discarded. Effect of the coexpression of interacting proteins on functional complementation by KAT1 in yeast. The graph shows the average value of the optical density at 72 h for triplicate determinations, and the experiment was done with at least three independent transformants for each plasmid combination. B, Immunoblot analysis of protein extracts from the indicated strains, showing the correct expression of each of the fusion proteins. Results for a representative clone are shown. The long exposure is included to visualize the expression of the RPT2 prey protein, which accumulates less than the other two prey proteins. A, The indicated plasmids were cotransformed in the trk1 trk2 mutant strain PLY240 and the growth of the strains was assayed as described in “Materials and Methods” using the Translucent media which contains 12.The graph shows the average value of the optical density at 72 h for triplicate determinations, and the experiment was done with at least three independent transformants for each plasmid combination. The KAT1 bait vector protein is detected with the antiLexA antibody LexA and the prey proteins with the antiHA antibody HA. Results for a representative clone are shown. BAG4 belongs to a sevenmember family of proteins, all containing a BAG domain Doukhanina et al., 2006 . BAG1 and BAG7 have domain structures similar to that of BAG4 and so were chosen for further analysis. Using the yeast assays described above, we compared both the interaction and the functional complementation between BAG family members. Since the original BAG4 clone recovered from the screening had a 13amino acid Nterminal truncation, we cloned the fulllength BAG4 gene and included it in these assays.

A moderate interaction was observed for BAG1, whereas the interaction between KAT1 and BAG7 was very weak. The data presented in Figure 2 confirm the proper expression of each of the proteins. The combinations between KAT1 and the two versions of BAG4 show the highest growth in lowpotassium medium when KAT1 is limiting black bars. Some growth is detected under these conditions upon coexpression of BAG1, but in the presence of BAG7 the level of growth is the same as for the control. Thus, we provide evidence for some level of specificity between KAT1 and BAG family members, lending further support to the possible physiological relevance of the KAT1BAG4 interaction. Study of the specificity of the interaction between KAT1 and other BAG family members. A, The indicated plasmids were transformed into the THY.AP4 strain and grown to saturation in selective media. Serial dilutions were spotted onto media with the indicated compositions to test for the proteinprotein interaction between KAT1 and the indicated BAG family proteins. Identical results were observed for four independent clones. L, leucine; W, tryptophan; H, histidine; A, adenine; Xgal, 5bromo4chloro3indolylbdgalactopyranoside acid. B, Immunoblot analysis of protein extracts from the indicated strains showing the correct expression of each of the fusion proteins. The KAT1 bait

protein is detected with the antiLexA antibody and the prey proteins with the antiHA antibody. C, The indicated plasmids were cotransformed in the trk1 trk2 mutant strain PLY240 and the growth of the strains was assayed as described in Figure 1A. The average value of triplicate determinations of the optical density of the growth normalized to the potassiumsupplemented media is shown for each strain. As shown in Figure 3, coexpression of BAG4 increased both the total amount and the initial rate of potassium uptake from the media. Potassium uptake and external acidification.

The change in the external pH was determined during the first 15 min after Glc addition and was normalized to the wet weight of the cells. Xenopus oocytes have been extensively used to characterize potassium channels from many organisms. We studied the effect of BAG4 coexpression on KAT1mediated currents in this model system. BAG4 coexpression increases the KAT1 current in Xenopus oocytes. A, Voltageclamp protocol and representative current traces recorded by twoelectrode voltage clamp in the presence of 100 mm KCl on oocytes coexpressing KAT1 or KAT1 and BAG4. B, KAT1 current Ivoltage Vm relationships of oocytes coexpressing KAT1 and BAG4 white circles or KAT1 alone black circles. Mean currents are from B. D, Voltage dependence of KAT1current activation in the presence of BAG4 white circles or expressed alone black circles. A, Voltageclamp protocol and representative current traces recorded by twoelectrode voltage clamp in the presence of 100 m m KCl on oocytes coexpressing KAT1 or KAT1 and BAG4. C, Increase of mean KAT1 current upon BAG4 coexpression, at 110 mV black and 155 mV gray. Mean currents are from B. We next wanted to confirm that the interaction between BAG4 and KAT1 also takes place in plants. To this end, we performed both bimolecular fluorescence complementation BiFC and coimmunoprecipitation assays in Nicotiana benthamiana infiltrated with Agrobacterium tumefaciens containing the appropriate plasmids. As a positive control, we used the KAT1KAT1 interaction Fig. 5 , observing a uniform fluorescent signal at the plasma membrane. By contrast, we observed a punctate signal corresponding to the KAT1BAG4 interaction but observed no signal for the corresponding control experiments Fig. 5 . In addition, to add experimental support for this interaction in plants, we performed coimmunoprecipitation experiments upon transient expression in N. benthamiana.

We were able to efficiently recover BAG4 upon KAT1 immunoprecipitation performed in protein extracts obtained from N. benthamiana leaves transiently expressing the two proteins Fig. 5 . Confirmation of the interaction between KAT1 and BAG4 in N. benthamiana. Agrobacterium strains harboring the indicated plasmids were used to infiltrate N. benthamiana leaves, and images were obtained using fluorescence confocal microscopy 72 h postinfiltration. A, Representative BiFC images for the KAT1KAT1 interaction and control plasmids. The overlay of the grayscale and BiFC fluorescence is shown. Leaf epithelial cells and stomata are visible. B, Representative BiFC images for the KAT1BAG4 interaction. Representative images of the experiments performed with the control plasmids are shown below. The red signal corresponds to chloroplast autofluorescence. For A and B, similar results were observed in at least four independent experiments performed on different days. The amount of BAG4 recovered in the KAT1 purification is shown in the first lane on the left. Similar results were observed in two independent experiments performed on different days. We next performed colocalization experiments to determine the subcellular localization of the KAT1BAG4 complex. A, A plasmid containing the KAT1BAG4 BiFC interaction and the ER marker ChFPKDEL was infiltrated as described. The BiFC signal right, ChFP signal center, and overlay image of the grayscale, BiFC fluorescence, and ChFP signals left are shown. B and C, The same colocalization analysis of the KAT1BAG4 complex was performed with the ERES marker Sec24 fused to RFP Sec24RFP; B and the STtmdChFP Golgi marker C. The yellow arrows A indicate the points of colocalization with the ER marker. Chloroplast autofluorescence is shown in blue B. Interestingly, KAT1 was previously shown to interact with Sec24 through its diacidic ER export signal motif Sieben et al., 2008 .

Thus, our data confirm the interaction between BAG4 and KAT1 in a plant model system and show that the KAT1BAG4 interaction likely takes place at the ERES, possibly facilitating its incorporation in coat protein complex II COPII vesicles. This is not unexpected, as KAT1, like essentially all multispan plasma membrane proteins, before arriving to the cell surface transits through the ER, where the protein is thought to be assembled into tetramers to form a functional channel that will be inserted into the plasma membrane via the secretory pathway. Our data suggest that BAG4 interacts with KAT1 as it transits through this organelle on its way to the plasma membrane. This model is consistent with that proposed for mammalian BAG proteins that are involved in the regulation of potassium and chloride channels that also act at the ER in cooperation with Hsp70 Knapp et al., 2014; Hantouche et al., 2017 . Our results indicate that BAG4 favors KAT1 activity in yeast and oocytes and that the interaction appears to take place at the ERESs. We hypothesized that BAG4 acts to facilitate KAT1 transit out of the ER and thus would promote the arrival of active KAT1 channels at the plasma membrane. In order to test this model, we examined whether BAG4 influences the arrival of this channel at the plasma membrane. Since both the yeast and oocyte experiments suggest that BAG4 does not affect overall KAT1 protein accumulation, we tested whether this was also the case in this plant model system. Plants were agroinfiltrated with strains containing KAT1YFPdsREDHA alone or KAT1YFPdsREDHABAG4myc. We analyzed the amount of KAT1YFP and the internal control dsREDHA in the infiltrated areas using the same time course. As shown in Figure 7, BAG4 coexpression does not increase the steadystate amount of KAT1 protein. So, taken together, the data presented in Figure 7 clearly suggest that expression of BAG4 promotes KAT1YFP arrival at the plasma membrane.

BAG4 expression effects the subcellular localization of KAT1. A, Plasmids containing KAT1YFP or both KAT1YFP and BAG4 were transiently expressed in N. benthamiana using agroinfiltration. The fluorescence signal was analyzed by confocal microscopy at 1, 2, and 3 d postinfiltration. Representative images are shown. Similar results were observed in three independent experiments performed on different days. C, Experiments similar to the one described A were performed, but using GoldenBraid plasmids containing KAT1YFPdsREDHA or KAT1YFPmycBAG4dsREDHA. Wholecell extracts were prepared from infiltrated areas previously confirmed to express KAT1YFP and proteins were processed for immunodetection. The dsREDHA protein serves as an internal control for the efficiency of transient expression. DAY PI, Days postinfiltration. The fluorescence signal was analyzed by confocal microscopy 2 d after infiltration. Representative images are shown, and similar results were observed in three independent experiments. In order to corroborate these observations, we carried out the opposite approach. We investigated the localization of KAT1 in Col0 wildtype plants and bag4 mutant lines using transient expression in Arabidopsis Fig. 7 . Employing the AGROBEST transient transformation protocol Wu et al., 2014 , we observed KAT1 accumulation at the plasma membrane in wildtype control plants. However, under the same conditions, in bag4 mutants, the KAT1 signal observed at the cell surface was markedly decreased and an accumulation of punctate staining was observed Fig. 7 . We could complement this defect of KAT1 plasma membrane targeting observed in the bag4 mutant by employing vectors coexpressing BAG4 with KAT1. We observed a much lower percentage of KAT1YFP at the plasma membrane in bag4 mutants, as compared to the Col0 control. Moreover, KAT1YFP plasma membrane localization is recovered when we functionally complement the bag4 mutant.

In order to provide additional evidence showing that BAG4 is a physiologically relevant KAT1 regulator, we analyzed phenotypes related to KAT1 activity in Arabidopsis lines lacking or overexpressing the BAG4 gene. Two independent bag4 mutant lines and two Col0 lines and one kat1 line overexpressing BAG4 were tested for stomatal opening dynamics. The kat1 and kat2 single mutants and the kat1 kat2 double mutant were included for comparison. As shown in Figure 8, two mutant lines lacking the BAG4 gene show a delay in stomatal opening under all conditions tested. We also observed an initial delay in stomatal opening in the kat1 and kat2 mutant lines in response

to light treatment, but not potassiumcontaining opening buffer. Therefore, at high potassium concentrations, the single mutants are able to open their stomata, likely due to the redundancy of inwardrectifying potassium channels. This idea is supported by the phenotype observed for the kat1 kat2 double mutant, which shows a marked delay in both light and opening buffer. On the other hand, we observed that the overexpression of BAG4 in Col0 leads to an increase in stomatal aperture and this response is attenuated in the kat1 mutant overexpressing BAG4 Fig. 8 . The levels of expression of the BAG4 protein are shown in Supplemental Figure S2. Effect of BAG4 loss and gain of function on stomatal aperture. Similar results were observed in three independent experiments. As a complementary approach, we measured the temperature of the different mutants and BAG4 gain and lossoffunction lines using infrared thermography Fig. 9 . Several studies have shown that this technique can be used for analyzing mutants with altered stomatal function because a relationship exists between the temperature of the leaves and variations in stomatal conductance Jones, 1999; Merlot et al., 2002; Wang et al., 2004 .

We observed the expected increase in temperature in the lines that showed delayed stomatal aperture dynamics and a decrease in temperature in the Col0 lines overexpressing BAG4 Fig. 9 . When these results are considered together, they strongly suggest that BAG4 plays a physiologically relevant role in regulating potassium fluxes in stomata and possibly other cells. Importantly, the BAG4 gene has been reported to be expressed in guard cells, which is a prerequisite for a physiologically relevant KAT1 regulator Yang et al., 2008 . Effect of BAG4 loss and gain of function on leaf temperature. The same lines described in Figure 8 were analyzed for leaf temperature using infrared thermography, as described in “Materials and Methods,” for mutant lines A and 35S BAG4 lines B. Each symbol represents an individual measurement and the horizontal bar represents the average value for 10 measurements of six different plants for each genotype. The error bars represent the sd. For both experiments, black asterisks indicate statistical significance as compared to the Col0 control. As discussed above, in the stomatal response assay, we observed additional phenotypes in the bag4 mutant lines, as compared to the kat1 or kat2 single mutants. These data suggest that BAG4 may regulate proteins in addition to KAT1, including other potassium channels, like KAT2. Therefore, we studied whether BAG4 could interact with KAT2 in a BiFC assay in N. benthamiana. As shown in Figure 10, we observed a pattern of fluorescence very similar to that observed for the KAT1BAG4 interaction, but observed no signal in the control combinations. We used the KAT2KAT1 interaction as a positive control for these assays, showing a uniform interaction at the plasma membrane, similar to what we observed with the KAT1KAT1 interaction Fig. 5 , confirming the functionality of the KAT2 BiFC fusion.

Although further studies are required to characterize the molecular details of these interactions and ascertain whether there are additional targets, our data suggest that BAG4 may act as a regulator of at least these two potassium channels and provide a plausible explanation for the results obtained in the stomatal response assays described. BAG4 interacts with KAT2 in BiFC assays in N. benthamiana. Interaction assays were carried out and analyzed as described in Figure 5. Leaf epithelial cells and stomata are visible. As shown, a similar pattern of interaction is observed for KAT2 when tested with BAG4 compare with Fig. 5B. The BiFC signals corresponding to the KAT2KAT1 and KAT2BAG4 interactions are shown in green and the chloroplast autofluorescence is shown in red. YFC, Cterminal part of YFP; YFN, Nterminal part of YFP. BAG4 interacts with KAT2 in BiFC assays in N. benthamiana. Interaction assays were carried out and analyzed as described in Figure 5. As shown, a similar pattern of interaction is observed for KAT2 when tested with BAG4 compare with Fig. 5B . The BiFC signals corresponding to the KAT2KAT1 and KAT2BAG4 interactions are shown in green and the chloroplast autofluorescence is shown in red. As such, these channels are predicted to be highly regulated, and as expected, several proteins have been identified as regulators of the KAT1 channel Sottocornola et al., 2006, 2008; Sato et al., 2009; Eisenach et al., 2012; Ronzier et al., 2014; Zhang et al., 2015; Saponaro et al., 2017 . In this report, we describe the

identification and initial characterization of a KAT1 regulator that we recovered in a splitubiquitin screening in yeast. The BAG4 protein was found to physically interact with KAT1 and also to increase potassium uptake in yeast. In oocytes, a similar phenomenon was observed, as increased KAT1 currents were observed 1 d after injection.

Thus, our data clearly indicate that in two heterologous systems, BAG4 coexpression increases KAT1 transport activity, likely by increasing the number of active channels at the membrane. It is very unlikely that this regulation is at the transcriptional level in these model organisms, since we could show that the total amount of KAT1 does not change upon BAG4 coexpression in yeast, and in the oocyte experiments, the same amount of KAT1 cRNA is injected in both cases. We provide experimental evidence for the physical interaction between KAT1 and BAG4 in plants using two complementary approaches, BiFC and coimmunoprecipitation. The signal corresponding to the KAT1BAG4 complex colocalizes with a general ER marker and with an ERES marker, which supports the notion that BAG4 could be involved in KAT1 assembly at this organelle. BAG4 is a member of a highly conserved family of proteins that all contain a characteristic BAG domain. We provide experimental evidence supporting this idea using both gain and lossoffunction experiments, where we observe an improvement in KAT1 arrival at the plasma membrane upon BAG4 expression and a delay in its accumulation at the plasma membrane in lines lacking the BAG4 gene. Importantly, we show that the total amount of KAT1 is not affected by BAG4 coexpression, but the percentage of KAT1 that arrives at the plasma membrane is increased. Several studies have addressed KAT1 trafficking and its regulation. For example, efficient transport of KAT1 to the plasma membrane is mediated by a diacidic ER export signal in the C terminus of the protein, which binds to the Sec24 component of coat protein complex II COPII; Hurst et al., 2004; Meckel et al., 2004; Sieben et al., 2008 . Here, we observed the colocalization of the KAT1BAG4 complex with Sec24, which has been described as a marker of ER exit sites for review, see Matheson et al., 2006; Langhans et al., 2012 .