The Role of Grass MUTE Orthologues During Stomatal Development

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Gas exchange between the plant and the atmosphere takes place through stomatal pores formed by paired guard cells. Grasses develop a unique stomatal structure that consists of two dumbbell-shaped guard cells flanked by lateral subsidiary cells. These structures confer a very efficient gas exchange capacity, which may have contributed to the evolutionary success of grasses. Recent works have identified orthologues of Arabidopsis MUTE in three grass species: BdMUTE in Brachypodium distachyon, BZU2/ZmMUTE in maize, and OsMUTE in rice. These genes induce the recruitment of subsidiary cells, and it appears to rely upon the ability of intercellular movement, from the guard mother cell to subsidiary mother cells, of the proteins encoded by them. Unexpectedly, this function of these grass MUTE genes contrasts with that of Arabidopsis MUTE, which promotes guard mother cell identity. These MUTE orthologues also appear to control guard mother cell fate progression, with the action of BdMUTE being less severe than those of BZU2/ZmMUTE and OsMUTE. The emerging picture unravels that grass MUTE genes have not only diverged, due to neo-functionalization, from Arabidopsis MUTE, but also among them.

Keywords: grasses, MUTE, orthologues, polarization, stomata, subsidiary cells

INTRODUCTION

Plants colonized land more than 400 million years ago (Edwards et al., 1998; Berry et al., 2010). One of the key innovations that enabled this to be possible was the development of a waxy cuticle to prevent water loss from the plant surface (Berry et al., 2010). The appearance of this impermeable layer coincides with the presence of stomatal pores, thus allowing the uptake of carbon dioxide to perform photosynthesis with a minimal loss of water vapor (Edwards et al., 1998; Berry et al., 2010). These microscopic innovations, bordered by a pair of kidney-shaped guard cells (GCs), are conserved across all land plants except liverworts and some mosses and hornworts (Chater et al., 2017; Renzaglia et al., 2017). Although to date no other structures has replaced the stoma, its shape, and its relationship with other epidermal cells have changed over time. Grasses, which develop a unique stomatal structure consisting of two dumbbell-shaped GCs flanked by two lateral subsidiary cells (SCs) (Stebbins and Shah, 1960; Rudall et al., 2017; Hepworth et al., 2018; Nunes et al., 2019), are a beautiful example of these changes. In addition, several works comparing stomatal responses between grasses and species with different stomatal morphology suggest that the stomatal complexes of grasses increase stomatal responsiveness with large and rapid GC movements.
Moreover, it has even been proposed that this developmental innovation has contributed, at least in part, to the extraordinary evolutionary success of this plant group (Kellogg, 2001; Hetherington and Woodward, 2003; Chen et al., 2017).

In the leaves of grasses, stomatal development occurs only in some epidermal cell files and it proceeds acropetally, with early stages of this process taking place in the basal regions of the leaf and stomata developing later in the distal ones (Stebbins and Shah, 1960). The development of four-celled stomatal complexes takes place through a simple and invariant pattern of cell divisions (Stebbins and Shah, 1960; Serna, 2011; Hepworth et al., 2018; Nunes et al., 2019; Figure 1A). They initiate with an asymmetric cell division from a protodermal cells leading to a smaller guard mother cell (GMC) and a larger sister cell. Before GMC division, cells from files in either side of newly formed GMC acquire subsidiary mother cell (SMC) identity and divide asymmetrically. The smaller cells resulting from these divisions, which are always placed next to the GMC, differentiate as SCs. Following SCs recruitment, the GMC divides symmetrically, with the cell division plane being parallel to the main axis of leaf growth, and it yields the paired GCs. This cell division pattern differs from that taking place in Arabidopsis (Serna and Fenoll, 2000; Bergmann and Sack, 2007; Figure 1A). First, in Arabidopsis, stomatal precursors, named meristemoids, are self-renewing cells. They can undergo several rounds of cell division in an inward spiral, regenerating themselves in each division, before assuming GMC identity. In contrast, in grasses, an asymmetric division directly gives rise to the stomatal precursor. Thus, meristemoids appear to be absent in this plant group. Second, the GMC of Arabidopsis does not recruit SCs. In addition, while grasses form dumbbell-shaped GCs, eudicots and most monocots develop kidney-shaped GCs pairs (Stebbins and Shah, 1960).

The recruitment of SCs in grasses is preceded by a process of polarization of the SMC that is very well known in maize (Serna, 2015; Apostolakos et al., 2018; Figure 2). This begins with the accumulation of the SCAR/WAVE regulatory complex (WRC) at the cell surface of the SMC, specifically at the site of GMC.
contact (Facette et al., 2015). Unknown signals emanating from GMC activate PANs receptors, which also, in a WRC-dependent manner (Facette et al., 2015), accumulate at the SMC/GMC contact site (Cartwright et al., 2009; Zhang et al., 2012). Then PANs recruit and activate ROPs (Humphries et al., 2011), which activate the WRC complex (Facette et al., 2015). Finally, activated WRC activates the ARP2/3 complex giving rise to a dense F-actin and inducing the migration of the nucleus toward the GMC (Deeks and Hussey, 2005).

Over the last twenty-five years, the isolation and characterization of numerous genes have illuminated our understanding of stomatal development in Arabidopsis. In this model plant, three basic helix-loop-helix (bHLH) transcription factors, SPEECHLESS (SPCH), MUTE, and FAMA sequentially specify stomatal lineage identity, regulate the transition from meristemoids to GMCs, and promote GCs differentiation, respectively (Ohashi-Ito and Bergmann, 2006; MacAlister et al., 2007; Pillitteri et al., 2007). The function of these transcriptional factors requires heterodimerization with the functionally redundant bHLH proteins ICE1 or SCREAM2 (Kanaoka et al., 2008). With origins which predate the divergence of the mosses and hornworts, these bHLH genes diverged prior to the monocot-dicot split (Chater et al., 2017; Hepworth et al., 2018, and references therein). This divergence enabled the emergence of new protein functions, which are essential for the unique stomatal development of grasses (Raissig et al., 2017; Wang et al., 2019; Wu et al., 2019).

Recent works have uncovered the role of three orthologues of Arabidopsis MUTE during stomatal development in three grass species (Raissig et al., 2017; Wang et al., 2019; Wu et al., 2019): BdMUTE of Brachypodium distachyon, BZU2/ZmMUTE of Zea mays (maize) and OsMUTE of Oryza sativa (rice). The role of these genes, regulating the formation of SCs (Raissig et al., 2017; Wang et al., 2019; Wu et al., 2019), differs from that of AtMUTE. These orthologues of MUTE also seem to regulate the identity of the GMC, with the action of BdMUTE in this process being less severe. Taken together, these recent discoveries suggest not only that MUTE orthologues of grasses have diverged from AtMUTE, but also that MUTE genes of domesticated grasses studied thus far have diverged comparatively to BdMUTE.

**MUTE ORTHOLOGUES OF GRASSES RECRUIT SCs**

In Brachypodium, maize and rice, like in other grass species, stomatal complexes comprise a pair of dumbbell-shaped GCs associated with two SCs (Campbell, 1881; Stebbins and Shah, 1960; Shoemaker and Srivastava, 1973; Kamiya et al., 2003; Raissig et al., 2017). Interestingly, the mutants subsidiary cell identity defective (sid) of B. distachyon, bizui2 (bzu2) of maize and c-osmute of rice, in addition to having impaired other steps of the stomatal developmental, fail to recruit SCs (Raissig et al., 2017; Wang et al., 2019; Wu et al., 2019). These mutants have alterations in their orthologues of Arabidopsis MUTE (Raissig et al., 2017; Wang et al., 2019; Wu et al., 2019): sid in BdMUTE, bzu2-1 in BZU2/ZmMUTE and c-osmute in OsMUTE. The function of these MUTE orthologues contrasts with that of AtMUTE, which triggers GMC formation only in Arabidopsis (MacAlister et al., 2007; Pillitteri et al., 2007; Table 1).

How do these grass orthologues of Arabidopsis MUTE recruit SCs? The expression of the yellow fluorescent protein (YFP) under the control of the BdMUTE promoter showed that its
induction is restricted to GMCs and GCs (Raissig et al., 2017). However, analysis of transgenic plants expressing the protein encoded by YFP-BdMUTE construct driven by the BdSPCH2 promoter showed that BdMUTE locates not only in GMCs but also in SMCs (Raissig et al., 2017). Considering that the BdSPCH2 promoter is active only in the stomatal lineage cells (Raissig et al., 2016), Raissig et al. (2017) inferred that BdMUTE protein moves from the GMC to epidermal cells of neighboring files. In consonance, successful complementation experiments of sid mutants with a fusion of the BdMUTE promoter to the YFP-BdMUTE construct lights up not only GMCs and young GCs, but also SMCs and young SCs (Raissig et al., 2017). In rice, YFP-OsMUTE expression driven by the OsMUTE promoter, whose induction in the developing four-celled complex is restricted to GMCs (Liu et al., 2009; Wang et al., 2019), lights up also GMCs and SMCs (Wang et al., 2019). This indicates that OsMUTE, like BdMUTE, also moves from the GMC to epidermal cells of neighboring files (Wang et al., 2019). Maize expressing YFP-ZmMUTE driven by the ZmMUTE promoter illuminates also GMCs, young GCs and SMCs (Wang et al., 2019). Assuming that the cellular localization of the ZmMUTE promoter induction is restricted to GMCs and young GCs, ZmMUTE would also move from the GMC to epidermal cells of neighboring files. Indeed, ZmMUTE protein is also able to move from the GMCs to SMCs in rice, and to epidermal cells adjacent to the stoma in Arabidopsis (Wang et al., 2019). These experiments strongly suggest that the recruitment of SCs in grasses depends on the intercellular movement of the grass MUTE proteins. Interestingly, the overexpression of BdMUTE driven by the Ubi constitutive promoter produces not only lateral, but also polar SCs (Raissig et al., 2017). This emphasizes the relationship between SCs recruitment and intercellular movement of MUTE orthologues in grasses. However, direct proof conclusively validating that the SCs formation relies upon the grass MUTE intercellular movement is lacking.

Multiple studies have shown that transcriptional factors move among cells via plasmodesmata (Han et al., 2014). GMCs of Brachypodium are symplastically connected with surrounding epidermal cells (Raissig et al., 2017). Therefore, BdMUTE may also move from the GMC to cells of neighboring files through plasmodesmata. But, what allows this protein to move laterally but not radially? Plasmodesmata continuously adjust their permeability in response to multiple cues (Sager and Lee, 2018). In addition, it is known that the control of this permeability is essential to the proper segregations of cell fate determinants during stomatal development in Arabidopsis (Guseman et al., 2010; Kong et al., 2012). Therefore, the lateral mobility of BdMUTE, and the unique design of the grass stomatal complexes, could depend on the restriction of the permeability of the plasmodesmata that symplastically connect cells of the same row. Future research should include delving in this direction.

### ZmMUTE REGULATES EARLY EVENTS IN SMC POLARIZATION

MUTE orthologues of grasses move from the GMC to the cells of neighboring files and this is linked with the formation of SCs. But, what do they do there? Wang and co-workers (2019) examined the role of ZmMUTE, specifically with regard to the regulation of SMC polarization. They found that cells adjacent to stomata, placed in neighboring epidermal files, of the bzu2-1 mutant, in contrast to the wild type, do not show enrichment of F-actin patches at the GMC contact sites or polarization of their nuclei (Wang et al., 2019). This indicates that SMC polarization is not cell-autonomous, and that ZmMUTE regulates this process (Table 1). The bzu2-1 mutation downregulates the transcription of both PAN1 and PAN2, indicating that ZmMUTE transcriptional factor positively regulates PAN1 and PAN2 expression (Wang et al., 2019). Because PAN1, whose polarization at the SMC/GMC interface requires PAN2 (Cartwright et al., 2009; Zhang et al., 2012), recruits and activates ROPs (Humphries et al., 2011), ZmMUTE must induce PANs expression before ROPs polarization (Figure 2). Interestingly, while the bzu2-1 mutant is almost devoid of SCs (Wang et al., 2019), most of the SCs of pan1 and pan2 mutants show no defects and most probably they derive from normal asymmetric cell divisions (Gallagher and Smith, 2000; Cartwright et al., 2009; Zhang et al., 2012; Facette et al., 2015). Therefore, ZmMUTE, or its downstream transcriptional factors, controls the expression not only of PANs, but also of other unknown genes to induce the recruitment of SCs. Among these genes could be those that encode for the hypothetical ligands of PANs, and his discovery would reveal one of the best-kept secrets of SMC polarization. If this is so, and assuming that these ligands emanate from the GMC, ZmMUTE may have both cell-autonomous and non-cell-autonomous functions (Figure 2).

Yeast one-hybrid and EMSA experiments showed that ZmMUTE binds to the E-box P1 and P2 motifs of the PAN1 and PAN2 promoters respectively (Wang et al., 2019). This suggests that the action of ZmMUTE on the expression of these genes may be direct. This does not rule out that ZmMUTE could also indirectly affect the activity of PAN1 and PAN2 promoters through upregulation of positive regulators.

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**Table 1** | Functions of AtMUTE and MUTE orthologues of grasses.

| Gene name | Species | Gene function | References |
|-----------|---------|---------------|------------|
| AtMUTE    | Arabidopsis thaliana (Eudicot) | Transition from M to GMC | MacAlister et al., 2007; Pillitteri et al., 2007 |
| BdMUTE    | Brachypodium distachyon (Monocot, Poaceae) | Recruitment of SCs. Less severely, GMC and GCs identities | Raissig et al., 2017 |
| BZU2/     | Zea mays (Monocot, Poaceae) | Recruitment of SCs and GMC identity. Early events in SMC polarization | Wang et al., 2019 |
| ZmMUTE    | Oryza sativa (Monocot, Poaceae) | Recruitment of SCs and GMC identity | Wu et al., 2019 |

GMCs, guard cells; GMC, guard mother cell; M, meristemoid; SMC, subsidiary mother cell; SCs, subsidiary cells.
and/or downregulation of repressors of PANs expression. For example, the transcriptional factor Glis3, directly and indirectly, regulates the expression of the insulin gene (Yang et al., 2009). The ZmMUTE protein does not bind the E-box P3 motif of the PAN2 promoter in vitro, but ChlP-qPCR data indicate that it binds this motif in vivo (Wang et al., 2019). This suggests that the ZmMUTE protein physically interacts with other proteins to activate the E-box P3 of the PAN2 promoter (Wang, et al., 2019). Interestingly, yeast two-hybrid and bimolecular fluorescence complementation assays have just showed that its orthologue of rice, OsMUTE, interacts with OsICE1 and OsICE2 (Wu et al., 2019). Therefore, ZmMUTE may interact with their homologs to regulate the E-box P3 of the PAN2 promoter.

**AtMUTE AND GRASS MUTE ORTHOLOGUES FUNCTIONS HAVE DIVERGED**

BdMUTE, ZmMUTE and OsMUTE conserve the motifs that could promote their intercellular movement or lack those that could prevent such movement (Raisig et al., 2017; Xu et al., 2018; Figure 1B). These proteins move from the GMC to epidermal cells of neighboring files, where they may specify SMC identity to recruit SCs (Raisig et al., 2017; Wang et al., 2019; Wu et al., 2019). In contrast, the Arabidopsis MUTE protein, whose gene is expressed in GMCs (MacAlister et al., 2007; Pillitteri et al., 2007), does not move among cells (Wang et al., 2019). As expected, AtMUTE does not have the conserved mobility motifs of grass MUTE proteins, but those conserved in eudicots (Raisig et al., 2017; Figure 1B). In accordance, the recruitment of SCs does not take place in Arabidopsis. The role of AtMUTE is restricted to control the meristemoid to GMC transition (MacAlister et al., 2007; Pillitteri et al., 2007).

The fact that the YFP-BdMUTE construct, driven by the GMC-specific AtMUTE promoter (MacAlister et al., 2007; Pillitteri et al., 2007), illuminates not only stomatal precursors but also adjacent epidermal cells in Arabidopsis (Raisig et al., 2017; Wang et al., 2019), underlines the very likely importance of the mobility motifs in the protein movement. Interestingly, this construct does not induce the recruitment of SCs in Arabidopsis (Raisig et al., 2017; Wang et al., 2019), highlighting that AtMUTE and BdMUTE have diverged. AtMUTEp: YFP-ZmMUTE in Arabidopsis also lights up GMCs and neighboring epidermal cells (Wang et al., 2019). Given that OsMUTE conserve the motifs that could promote its movement or lack those that could prevent it (Raisig et al., 2017), it is expected that this protein also moves from stomatal precursors to neighboring epidermal cells in Arabidopsis. OsMUTE and ZmMUTE expressed under the control of the AtMUTE promoter partially complement the defects of Arabidopsis mute-1 by inducing the formation of stomata from some stomatal precursors (Liu et al., 2009), but, like BdMUTE, they do not induce the recruitment of SCs (Figure 4 in Liu et al., 2009). Although OsMUTE and ZmMUTE, and perhaps BdMUTE, retain the function of inducing stomata formation, they are unable to induce the recruitment of SCs in Arabidopsis. This underlies that these proteins have diverged from the AtMUTE protein acquiring of a new function: the recruitment of SCs.

**ZmMUTE AND OsMUTE FUNCTION DIFFERS FROM THAT OF BdMUTE**

Although the three orthologues of MUTE regulate the formation of SCs, their function during stomatal development is not identical (Table 1). The bzu2-1 mutant forms GMCs but displays defects in their divisions, undergoing excessive, randomly oriented and/or asymmetric divisions (Wang et al., 2019). This gives rise to short columns of elongated cells instead of stomata, which results in a slower transpiration rate and in a decreased photosynthetic activity (Wang et al., 2019). c-osmute exhibits also columns of undifferentiated cells, produced by misoriented and/or asymmetric cell divisions (Wu et al., 2019). Morphologically, the phenotype of the c-osmute mutant is reminiscent of the bzu2-1 one, and the physiology of c-osmute mutants must also be dramatically affected. Certainly, both mutants exhibit a lethal phenotype at the seedling stage (Wang et al., 2019; Wu et al., 2019).

The sid mutant is fully viable and fertile, although its stomatal physiology is also affected (Raisig et al., 2017). Like the bzu2-1 and c-osmute mutants, the sid mutant also undergoes misoriented GMC divisions (Raisig et al., 2017). However, in contrast to these mutants, about 70% of the GMCs of this mutant develop dicot-like two celled stomata (Raisig et al., 2017). Therefore, while bzu2-1 and c-osmute mutants exhibit a fully penetrant phenotype affecting the division of the GMC (Wang et al., 2019; Wu et al., 2019), many of GMC divisions of the sid mutant are normal (Raisig et al., 2017). The molecular nature triggering the lack of a fully penetrant phenotype in sid is unknown, and to delve into this question is one of the most exciting future directions. OsFAMA also controls GC morphogenesis, with c-osmute exhibiting stomata with swollen GCs (Wu et al., 2019). This mutant also exhibits a fraction of swollen SCs, suggesting that, in addition to OsFAMA, other genes regulate SC differentiation (Wu et al., 2019). Among these unknown genes could be OsMUTE.

The defects induced by mutations in the grass MUTE orthologues in the maintenance of the GMC identity could reflect a mechanism of cellular signaling from the SMC towards the GMC to induce stomatal formation. It has been proposed that, prior SC formation, high levels of a grass peptide similar to AtEPF1/2 may cause GMC arrest (Hughes et al., 2017; Hepworth et al., 2018), perhaps through the suppression of grass MUTE orthologues activity specifically in GMCs. Grass MUTE activity in SMC would allow SC formation. Then, signals from SCs may activate grass MUTE orthologues in GMCs, perhaps by reducing grass EPF1/2 production, to promote stomatal formation. Agree with this, 1) GMCs do not progress to become stomata until SC formation, and 2) barley overexpressing HvEPF1 exhibits arrested GMCs (Hughes et al., 2017). It is then
likely that grass MUTE genes, in addition to having a non-cell-autonomous role specifying the SMC fate, have a cell-autonomous one triggering the progression of the GMC fate. The complementation of the Arabidopsis mute-1 mutant phenotype, inducing stomatal development from some stomatal precursors, with at least the OsMUTE and ZmMUTE genes (Liu et al., 2009), also supports the cell-autonomous role of MUTE orthologues regulating GMC fate.

GRASS STOMATAL COMPLEXES IMPROVE STOMATAL FUNCTION

Several works comparing physiological stomatal behaviors among species with different stomatal complexes suggest that those of grasses are more efficient (Grantz and Zeiger, 1986; Franks and Farquhar, 2007; Vico et al., 2011; Merilo et al., 2014; McAusland et al., 2016; Haworth et al., 2018). The isolation of the sid mutant, the first grass mutant to date that disrupts the two main attributes of the grass stomatal complexes, the presence of dumbbell-shaped GCs and the recruitment of SCs (Raissig et al., 2017), underscores the important role of this innovative morphology in the stomatal function (Nunes et al., 2019). The maximum area of the open pore in the sid mutant, and its gas exchange capacity, were noticeably smaller than those in the wild type, even when stomatal opening was induced by the toxin fusicoxin (Raissig et al., 2017). The sid mutant also exhibited slower stomatal movements to fluctuating light conditions, and its stomata could not open as wide compared with the wild type (Raissig et al., 2017). Consequently, sid mutants produced less biomass than the wild types (Raissig et al., 2017). These results link the morphology of the stomatal complexes with its impact on gas exchange and biomass production in the wild grass Brachypodium, and strongly they suggest that this relationship may extend to the remaining grass species.

The improvement of stomatal function in grasses could have contributed to their expansion and diversification, 30 to 45 million years ago, when a progressive and global aridification took place (Kellogg, 2001; Hetherington and Woodward, 2003; Chen et al., 2017). The inability of the sid mutant to open widely its pores indicates that grass stomatal complexes are associated with greater stomatal openings and conductance. Interestingly, species with greater maximum stomatal conductance exhibit higher sensitivity to closure during drought (Henry et al., 2019). Under a global drought, a more sensitive stomatal closure could have allowed to capture carbon dioxide without losing too much water, thus favoring the successful diversification of this plant group. Certainly, Poaceae, with around 12,000 species, includes almost a quarter of all monocots of the planet, and it is one of the largest families of flowering plants. Curiously, the enrichment of species in genera of monocotyleons is associated with geographical variables, like larger ranges and lower elevations, rather than with biological attributes (Tang et al., 2016). It is likely that the success of the grasses lies partly in their morphology, including their unique stomatal complexes, and partly in the places they have occupied.

CONCLUDING REMARKS

The development of the unique grass stomatal complex is a great advantage, which may have contributed to the expansion of this plant group. Undoubtedly, MUTE orthologues of grasses provide a starting point to unravel not only the mechanism underlying stomatal complexes formation, but also the evolution of this essential trait. MUTE orthologues of grasses have not only functionally diverged, due to neo-functionalization, from AtMUTE, but also among them, with BdMUTE exhibiting divergence from ZmMUTE and OsMUTE. Certainly, protein phylogenetic analysis of bHLH regulators of stomatal development supports this view (Wu et al., 2019). The comparison of the grass MUTE function between domesticated plants and their wild relatives, will allow us to know if the agricultural practices have driven the divergence of these genes. Because grass stomatal complexes have largely contributed to the adaptive success in hotter and drier environment, delving into the function of these genes will also provide useful genetic tools for producing plants with better tolerance to drought caused by climate change.

AUTHOR CONTRIBUTIONS

LS wrote the article and designed the figures.

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