A Review: Role of Aquaporin in Plant Leaf Movement

A Research Project

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CERTIFICATE

This research project has been written under my supervision and has been submitted for the award of the BSc. degree in Biology with my approval as a supervisor.

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DEDICATION

I dedicate my work to my Parents whom always have encouraged me during all the steps of the study. Also, I dedicate it to my sisters and my brothers whom have been helped me in every way possible to finish the study. My love for you all can never be quantified.

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First of all, my thanks are addressed to God for inspiring me with patience and strength to fulfill the study.

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SUMMARY

Plant leaf movements can be mediated by specialized motor organs, the pulvini, or can be epinastic (i.e. based on different growth velocities of the adaxial and abaxial halves of the leaf). Both processes are associated with diurnally regulated increases in rates of membrane water transport, which in many cases has been shown to be facilitated by aquaporins. Rhythmic leaf movements are known from many plant species, but few papers deal with the involvement of aquaporins in such movements. Many details of the architecture and function of pulvini were worked out by Ruth Satter and co-workers using *Samanea saman* as a model organism. More recently a contribution of aquaporins to pulvinar movement in *Samanea* was demonstrated. Another model plant to study pulvinus-mediated leaf movements is *Mimosa pudica*. The contribution of both plasma membrane and tonoplast localized aquaporins to the seismonastic leaf movements in *Mimosa* was analysed. In tobacco, as an example of epinastic leaf movement, it was shown that a PIP1 aquaporin family member is an important component of the leaf movement mechanism.

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1-AQP1: Aquaporin-1 is a membrane channel that allows rapid water movement driven by a transmembrane osmotic gradient

2-GIPs: glycerol facilitator like proteins, a highly selective transmembrane channel that conducts glycerol and certain other small uncharged organic molecules,

3- NtAQP1: Nicotiana Tabacum Aquaporin1

4- MIP; major intrinsic protein are integral membrane proteins

5-NPA**:** asparagine-proline-alanine sequences (NPA motifs) cc are highly conserved in aquaporin water channel family. l

6- AQP1: Aquaporin-1 is a membrane channel that allows rapid water movement driven by a transmembrane osmotic gradient

7- PIP: Plant plasma membrane-type plasma membrane intrinsic protein (PIP) aquaporins are classified into two groups, PIP1s and PIP2s.

8- AtPIP: Arabidopsis thaliana plasma membrane intrinsic protein

9- OsPIP; oryza sativa plasma membrane intrinsic protein

10-VfPIP1: Vicia faba plasma membrane intrinsic protein

11-ROS; reactive oxygen species

12- BjPIP1 ;Brassica juncea plasma membrane intrinsic protein

13- TIP; tonoplast intrinsic protein

14- ER; endoplasmic reticulum

1. INTRODUCTION

Aquaporins are an old family of small (24–30 kDa) pore-forming integral membrane proteins. They belong to the class of major intrinsic proteins (MIPs) and numerous members have been found in all kingdoms from Archaea to animals. Aquaporins provide a proteinaceous pathway for water (Preston et al, 1992; (Quigley et al., 2001), some small uncharged solutes Biela et al. (1999); (Gerbeau et al., 1999) and even gases (Uehlein et al., 2003); (Jahn et al., 2004, Endeward et al., 2006) across biological membranes. Based on results from sequence analyses and functional characterization, the MIP family was divided into the aquaporins , which are strictly water-selective, and the aquaglyceroporins (glycerol facilitator-like proteins, GLPs), which are permeable to small molecules like glycerol and urea in addition to water(Heymann and Engel, 1999, Zardoya, 2005).

Aquaporins are channel proteins which facilitate the passive diffusion of water and small neutral molecules across biological membranes. Aquaporins can be found in the plasma membrane (PM) and in most intracellular compartments of plant cells. They are involved in the maintenance of the whole plant water status by mediating osmoregulation of every single cell and trans-cellular water transport in roots and leaves. In the past decade, numerous integrative studies have addressed the role and regulation of aquaporins during plant response to the environment (reviewed in (Chaumont and Tyerman, 2014, Li et al., 2014). Aquaporin homologues are particularly abundant in plants. They show greater functional diversity than the main metazoan paralogues, which has been attributed to a higher degree of compartmentation in plant cells and a greater necessity for finely tuned water control. Plant leaf movements can be mediated in two ways: reversible (swelling) or irreversible (growth) changes in cell volume. In contrast to typical growth movements, turgor-regulated movements are reversible. They have been observed in many plants, e.g., *Mimosa*, *Phaseolus*, *Albizzia*, *Desmodium* and *Samanea*, which possess specialized motor organs called pulvini. As

the direction of leaf movement is determined by the architecture of the pulvinar joint and not by the direction of the controlling stimulus, this type of movement is referred to as nyctinastic. In other plant species, e.g., tobacco, leaf movements (described as epinastic) occur without the presence of specialized motor organs. In those cases, the movements are the result of periodically different elongation growth velocities of the adaxial and abaxial sides of the leaf blades and petioles. Many data on pulvinus architecture and function were collected on the nyctinastic, leguminous tree *Samanea saman* as a model organism, (Satter et al., 1974) (Gorton, 1987). Aquaporins are therefore thought to contribute to the rapid movement in *M. pudica* (Fleurat-Lessard et al., 1997). *Mimosa pudica* L. is a creeping annual or perennial herb. It has been identified as lajjalu in Ayurveda and has been found to have antiasthmatic, aphrodisiac, analgesic, and antidepressant properties. The leaves of the sensitive plant *M. pudica* can adapt their closing response to electrical and mechanical stimulation so that they reopen to repeated stimulation. The more intense the stimuli and the longer the intertribal interval, the longer it takes to adapt. Leaves adapted to the effects of mechanical stimulation can still respond by closing to electrical stimulation and vice versa.

The aim of this review was to find the relationship between aquaporin and plant leaf movement.

2. LITERATURE REVIEW

2.1 Aquaporin Structure

Aquaporins have acharacteristic conserved structure with six tilted transmembrane helices linked by three extracellular and two intracellular loops. N- and C-terminal domains protrude into the cytosol and a highly conserved amino-acid motif (asparagine-proline-alanine; NPA) occurs twice in the pore region and is important for aquaporin function. Aquaporins are incorporated into the membranes in a tetrameric arrangement comprising four individual poresThe protein operates as a two-stage filter. One is built up by the conserved NPA motifs forming a selectivity-determining region and another is formed by an aromatic/arginine-region functioning asaproton exclusion filter. Hydrophobic regions near the NPA motifs are rate-limiting water barriers and reduce interactions between water molecules. It was shown for human AQP1 that water permeates in a single-file arrangement and that a finely tuned water dipole rotation during passage is essential for water selectivity(Murata et al., 2000, de Groot and Grubmuller, 2001)

2.2 Aquaporin Function in Plants

Many observations concerning the physiological role of aquaporins in plants result from analyses of transgenic plants with a modified expression of certain aquaporin genes or from analysis of aquaporin mutant plants. The

first evidence for a function in cellular water uptake and whole plant water transport came from PIP antisense plants. These developed a larger root system than the control plants (Kaldenhoff et al., 1998). In tobacco, the plasma membrane aquaporin NtAQP1 was shown to be important for root hydraulic conductivity and water stress resistance (Siefritz et al., 2002). Studies on plants with impaired production of PIP1 and PIP2 indicated that both of these aquaporins are required for an important role in the recovery from water deficiency (Martre et al., 2002). In addition to their ability to transport water, some aquaporins facilitate the passage of gases such as CO2 and ammonia across membranes(Niemietz and Tyerman, 2000);(Loqué et al., 2005) ; (Endeward et al., 2006). Production of the human AQP1 or the plant NtAQP1 in the heterologous Xenopus oocyte expression system increases the CO2 permeability of the oocyte membrane (Nakhoul et al., 1998) (Uehlein et al., 2003). The mechanism and the physiological significance of the CO2 transport facilitated by aquaporins is still a matter of debate (Cooper et al., 2002, Hub and de Groot, 2006). Recently a clear contribution of human AQP1 to CO2 transport across the erythrocyte membrane was shown (Endeward et al., 2006). Plants with impaired expression of NtAQP1 showed changes not only in water transport (Siefritz et al., 2002) but also in CO2-limited processes such as stomatal opening and closing, photosynthesis and leaf growth (Uehlein et al., 2003). In another study it was shown that NtAQP1 increases mesophyll conductance to CO2 in tobacco (Flexas et al., 2006). Overexpression of Arabidopsis PIP1b in tobacco resulted in increased growth rates under optimal irrigation (Aharon

et al., 2003), which could be interpreted as the sum of effects on water uptake and photosynthesis. In addition to their function in water management, plant aquaporins play a role during leaf movement, a process requiring high rates of cellular water transport.

2.3 Responses of Leaf Aqps to Enviromental Conditions

While many AQPs coexist in plants, most isoforms seem to have their own specific characteristics which allow the plant to develop and grow adequately in ever changing external conditions.

2.3.1 Water Stress

Water deficit, initially sensed by the roots, can affect the regulation of water movement in the shoots. A number of studies have shown that water stresses, including drought and salinity, can alter leaf AQP expression and activity. In the aerial part of Arabidopsis plants, drought stress induced with 250 mM mannitol significantly alters the expression of most PIP genes (Jang et al., 2004). For example, drought treatment rapidly decreases levels of PIP1;5, PIP2;2, PIP2;3, and PIP2;6 transcripts to one-tenth of the levels innormal condition. The expression of PIP1;1 initially increases, while that of PIP1;2, PIP2;7, and PIP2;8 remains constant during the first 12 h of mannitol treatment, then gradually decreases. Using a longer term (up to 12 d), but

gradual, drought stress, Alexandersson et al. showed that PIP transcripts in Arabidopsis leaves are generally down-regulated, except those for AtPIP1;4 and AtPIP2;5, which are up-regulated. The different responses of AQP expression (up/down-regulation or no change) to water stresses suggest that AQP isoforms can be divided into different groups which contribute differently to water transport and regulation, with some being stress-responsive (Hachez et al., 2006). Different responses of AQPs to water stress were found in upland (drought-resistant) and lowland (drought-sensitive) rice. PIP proteins increase markedly in the roots of both types, but only in upland rice leaves. OsPIP1;2, OsPIP1;3, OsPIP2;1, and OsPIP2;5 mRNA levels in roots and OsPIP1;2 and OsPIP1;3 mRNA levels in leaves are significantly up-regulated in upland rice, but their expression is unchanged or down-regulated in lowland rice(Lian et al., 2006) , indicating that AQPs present in the same species, but in different cultivars, can respond differently to water stress depending on their tolerance to water deficits. Expression of the V. faba VfPIP1 gene in Arabidopsis improves drought resistance in the mutant plants, probably by promoting stomatal closure under drought conditions, thus highlighting an important role of AQPs when plants are subject to water stress (Cui et al., 2008). Using double antisense Arabidopsis plants with reduced amounts of both PIP1 and PIP2 proteins, Martre et al. found that the leaf hydraulic conductance was similar in the mutants and control plants. However, upon water stress application, the mutant plants recovered their hydraulic conductance and transpiration rates less rapidly than the control plants and had a significantly lower leaf water potential after

rewatering. These data led the authors to conclude that PIPs play an important role in the recovery of Arabidopsis from water-deficient conditions. In the heavy-metal accumulator Brassica juncea, BjPIP1 expression is up-regulated in leaves subjected to drought, salt, or low temperature, or exposed to heavy metals (Zhang et al., 2008). When overexpressed in tobacco plants, BjPIP1 enhances drought and cadmium resistance by decreasing the transpiration rate and stomatal conductance, suggesting that it might increase abiotic stress resistance by maintaining a reasonable water status in tobacco leaves(Zhang et al., 2008) . However, overexpression of AQPs is not always beneficial to the plants. For instance, tobacco plants overexpressing AtPIP1;2 wilt more rapidly than control plants under drought stress(Aharon et al., 2003) .

2.3.2 Freezing and Cold Stress

Perennial plants are able to survive tough winters through a phenomenon called cold acclimation. Low non-freezing or subfreezing temperatures can increase the freezing tolerance of plants by 3–5 C. Northern blot analysis and comparison of expressed sequence tags from non-acclimated (NA) and cold-acclimated (CA) Rhododendron catawbiense leaf tissues showed a 10-fold down-regulation of RcPIP2;1 in CA tissues (Wei et al., 2006). Similarly, overexpression of RcPIP2s and Panax ginseng PIP1 in transgenic Arabidopsis plants compromised their freezing tolerance and cold acclimation ability, which is presumably due to their decreased capacity to

resist freeze desiccation (Peng et al., 2007, 2008). The authors further demonstrated that all 13 endogenous PIPs except PIP2;5 are down-regulated in wild-type Arabidopsis plants during cold acclimation, confirming previous data concerning the impact of different abiotic stresses on Arabidopsis PIP transcription in the aerial parts of 2-week-old seedlings (Jang et al., 2004). Similar down-regulation of most rice PIP genes was recorded when seedlings were chilled to 7 C, and their expression recovered on return to 28 C. During recovery, significantly higher expression of OsPIP1;1, OsPIP2;1, and OsPIP2;7 was seen in shoots of a chilling tolerant variety than in those from a chilling sensitive one (Yu et al., 2006). All these data suggest that down-regulation of PIP transcripts during cold acclimation helps to prevent freezeinduced cellular dehydration, leading to increased freezing tolerance. Moreover, rapid rehydration of the leaf after cold/freeze stress might be mediated by AQPs. However, these mechanisms might be species-dependent as, in wheat leaves, a large increase in PIP transcript levels was seen after cold acclimation (from 22 C to 4C) (Herman et al., 2006

2.3.3 Inhibition of AQPs by Reactive Oxygen Species

Among the many internal or external factors that can affect AQP activities, hydrogen peroxide (H2O2) has been shown to be an effective inhibitor of leaf AQPs. In *Tradescantia fluminesis*, H 2O2 perfusion via the leaf petiole results in a drop in the water permeability of epidermal cells measured with

a cell pressure probe (Ye et al., 2008). Similarly, H2O2 treatment following Fe2+ pretreatment decreases the water permeability of parenchyma cells in maize leaves by a factor of 30 (Kim and Steudle, 2008). The effect could be overcome using an antioxidant, suggesting that the inhibition of AQP activity is probably due to an oxidative gating by ROS, such as *OH radicals, which can be produced in the Fenton reaction (Ye and Steudle, 2006). However, on the basis of the lack of effect of H2O2 on the activity of individual AQPs expressed in Xenopus oocytes, Boursiac et al. (2008) proposed that ROS do not gate AQPs through a direct oxidative mechanism, but rather act through a cell signalling mechanism and showed that H2O2 induces internalization of plasma membrane AQPs in unidentified vesicles. This process could therefore decrease the cell membrane water permeability. In addition, recent studies showed that, instead of being inhibited by H2O2, several AQPs isoforms are able to facilitate H2O2 transport across the tonoplast and plasma membranes (Bienert et al., 2006, 2007; Dynowski et al., 2008). The exact means by which H2O2 regulates the cell membrane permeability is still under investigation, but could involve different mechanisms, including direct oxidative gating, signal transductionleading to the internalization of AQP proteins, or modification of their phosphorylation status, a post-translational modification thought to regulate their gating (Johansson et al., 1998; Tornroth-Horsefield et al., 2006; Van Wilder et al., 2008). It has to be noted that ROS like H2O2 and *OH are very aggressive and reactive chemicals. It is possible that the inhibition of cell water permeability was also due to indirect effects on AQPs such as lipid

peroxidation, which needs to be verified in future experiments. Nevertheless, responses of AQPs to ROS may represent an efficient way to adjust water relations and cope with different types of stresses from which plants may suffer.

4. Subcellular Location of Plant Aquaporins

4.1 MIPs Are Abundant Proteins

A typical feature of plant aquaporins is that their expression is highly regulated, in response to developmental, hormonal, and environmental stimuli. The 7. Aquaporins of Plants first plant MIP, Nod26, was identified as a protein specifically expressed during the establishment of the soybean-Rhizobium symbiosis (Fortin et al., 1987). The plasma membrane aquaporin gene RD28 and the tobacco TIP homolog TobRB7 were characterized as dehydration-induced or root-specific genes, respectively (Conkling et al., 1990);(Yamaguchi-Shinozaki et al., 1992). The identification of these genes, by means of screening procedures of moderate sensitivity, was also possible because these genes were expressed at high levels. MIPs generally represent major protein constituents of plant membranes and this has been a crucial feature for their identification by biochemical and immunological methods. Interestingly, these are the same charactersitics that led to identifying MIP and CHIP 28 in the membranes of lens fiber and erythrocytes, respectively(van Os et al., 1994). For instance, bean cx-TIP was chosen as a

model to study tonoplast protein biogenesis in seeds because it is the most abundant intrinsic polypeptide of the protein storage vacuoles (PSVs) (Johansson et al., 1998). Five Arabidopsis PIPs were identified by an immunoscreening procedure because antibodies directed against purified plasma membrane mostly recognized these proteins (Kammerloher et al., 1994). In spinach leaves, aquaporin PM28a can represent up to 15% of plasma membrane proteins (Johansson et al., 1996). Despite a molecular structure reminiscent of membrane channels, this abun- dance initially suggested a role for plant MIPs in membrane stabilization, in particular when plant cells undergo stringent dehydration or temperature cycles (Johnson et al., 1989). Although these ideas cannot be completely discarded, the finding that most MIPs function as water channel can now easily rationalize their abundance. To be significant in terms of volume exchange, the flows of water ob- served in plant cells must correspond to billions and billions of transported water molecules. Although the intrinsic water permeability of aquaporins i (Yang and Verkman, 1997), high expression levels of these proteins are needed to mediate such a flow. In these respects, water channels differ from ion channels, which can generate an electrical signal with a few thousandtransported ions

4. Plant Leaf Movment

When a leaf of M. pudica is mechanically stimulated (e.g., touched by hand), it drops and leafle are folded upward (Figure A)(Hagihara and Toyota, 2020)

. Such rapid movements are only possible due to the existence of thepulvini, found at the base of leaflet, rachilla, and petiole(Figure B)(Hagihara and Toyota, 2020) . Of the three types of pulvini found in M. pudica, the primary and tertiary pulvini are more sensitive to mechanical stimuli than the secondary pulvinus. Early literature reported that movement was still generated in M. pudica even when the upper half of the primary pulvinus (the flexor side) was removed , suggesting that the lower half (the extensor side) plays an essential role in the generation of rapid movements. Asprey and Palmer (Asprey and Palmer, 1955) also tested this hypothesis using a different experimental condition wherein they horizontally placed a leaf to disregard leaf weight on the primary pulvinus from which either the extensor or flexor half was removed and found that both the extensor and flexor halves of the primary pulvinus were necessary for movement. Subsequently, researchers observed a redistribution of water from the extensor to the flexor half in the primary pulvinus after movement (Tamiya et al., 1988). These findings led to the view that sudden turgor loss on the extensor side of the pulvinus caused by water redistribution was the driving force behind rapid movements in plants. Generally, turgor-driven movements (e.g., nyctinastic leaf movement) are triggered by the release of electrolytes such as K^+ and Cl^- from extensor motor cells(Cote, 1995) . Supporting this idea, Toriyama (Toriyama, 1955) reported that K^+ migrated from the intracellular to the extracellular space of the motor cells after movement, suggesting that water efflux osmotically driven by K^+ migration results in the turgor loss of the pulvinus of M. pudica. This phenomenon was confirmed by Allen (Allen,

1969) using radioactive 42K +. It was later demonstrated that extracellular (apoplastic) Cl− concentration also increases during movement (Samejima and Sibaoka, 1980). Extensor cells release more Cl− than the flexor cells and Cl− migration from the pulvinar cells is initiated immediately, before, or almost simultaneously with rapid pulvinar bending (Samejima and Sibaoka, 1980). Several reagents affecting K+ or Cl− flux across the plasma membrane inhibit movement, supporting the idea that the migration of these ions is a critical precursor event for turgor loss and movement in the pulvinus (Roblin and Fleurat-Lessard, 1987). Although ion channels on the motor cells' plasma membrane in M. pudica have not yet been identified, the outwardly rectified K+ current, which is activated by membrane depolarization, has been electrophysiologically described(Stoeckel and Takeda, 1993) . In addition to K+ and Cl−,it has also been reported that photoassimilates (such as sucrose) may be associated with rapid movement in M. pudica. Fromm and Eschrich (Fromm and Eschrich, 1988) observed that 14C-labeled photoassimilates, which were restricted to the phloem of the pulvini, were found in the apoplastic regions of other tissues after stimulation (e.g., in the extensor motor cells in the pulvini).

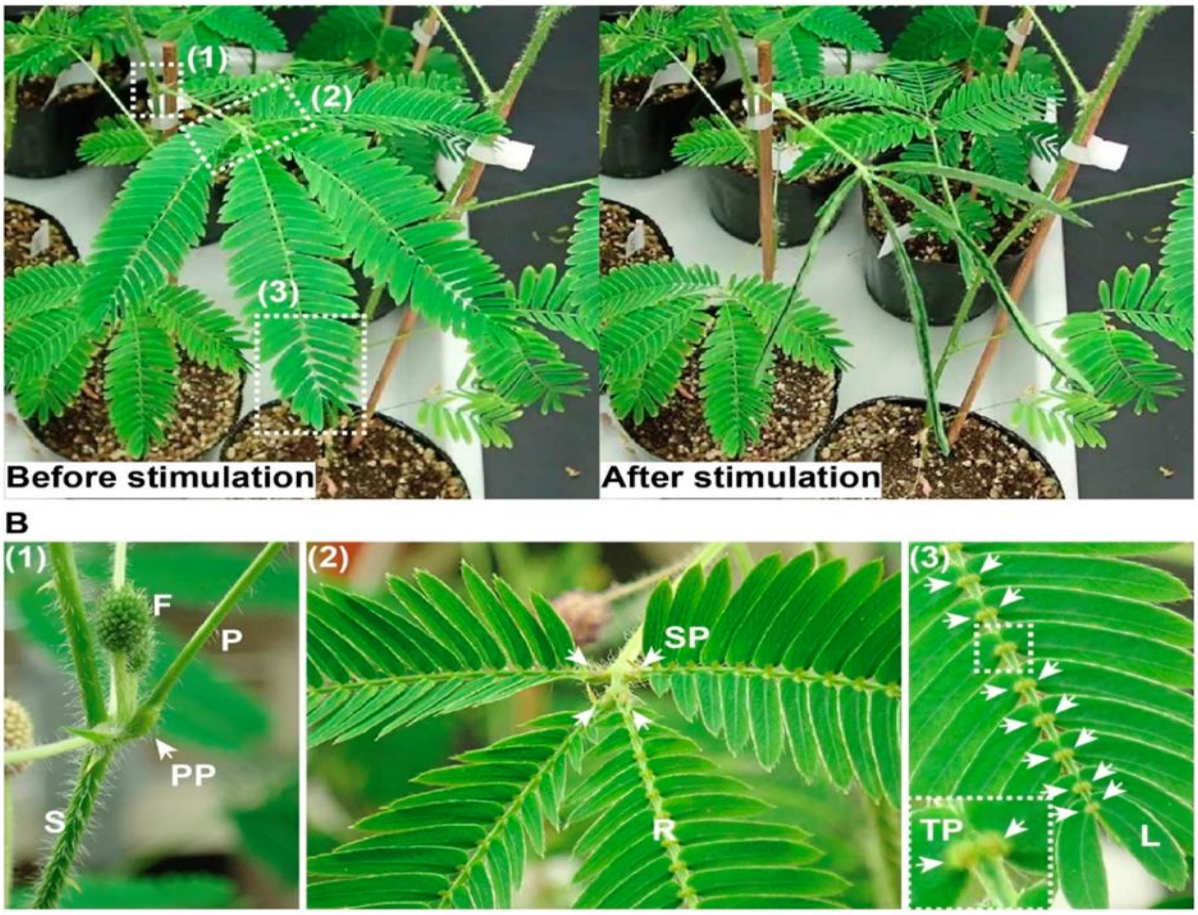

Figure 1. Rapid movement characteristics in *M. pudica*. (A) The leaf of M. pudica, shown expanded before mechanical stimulation (left panel) and folded after the stimulation (touched by hand, right panel). (B) The motor organs pulvini. (1) Primary pulvinus (PP, white arrow). S, stem; F, floral bud; P, petiole. (2) Secondary pulvini (SP, white arrows). R, rachilla (the central axis of the pinna). (3) Tertiary pulvini (TP, white arrows). The inset shows a magnified image of pairs of tertiary pulvini enclosed by the dashed line in (3). L, leaflet. The numbers in each panel correspond to those shown in .(Hagihara and Toyota, 2020)

5. Mechanical Stimulation of *M. Pudica*

Figure 3 shows different shapes and curvatures of pinnulesin open or closed states. , is shown in Fig. 2a. The shape of thistime dependence for the distance between the edges ofone pair of pinnules is very similar to the shape

of similardependencies for the Venus flytrap(Markin et al., 2008, Volkov et al., 2009). However, the speed ofclosing is about 10 times slower. Figure 3 shows the time) dependence for pinnules opening after being mechanicallystimulated to close. The process of pinnules closing takesplace in 4–5 s, whereas the opening of the pinnules occurs inabout 600 s.

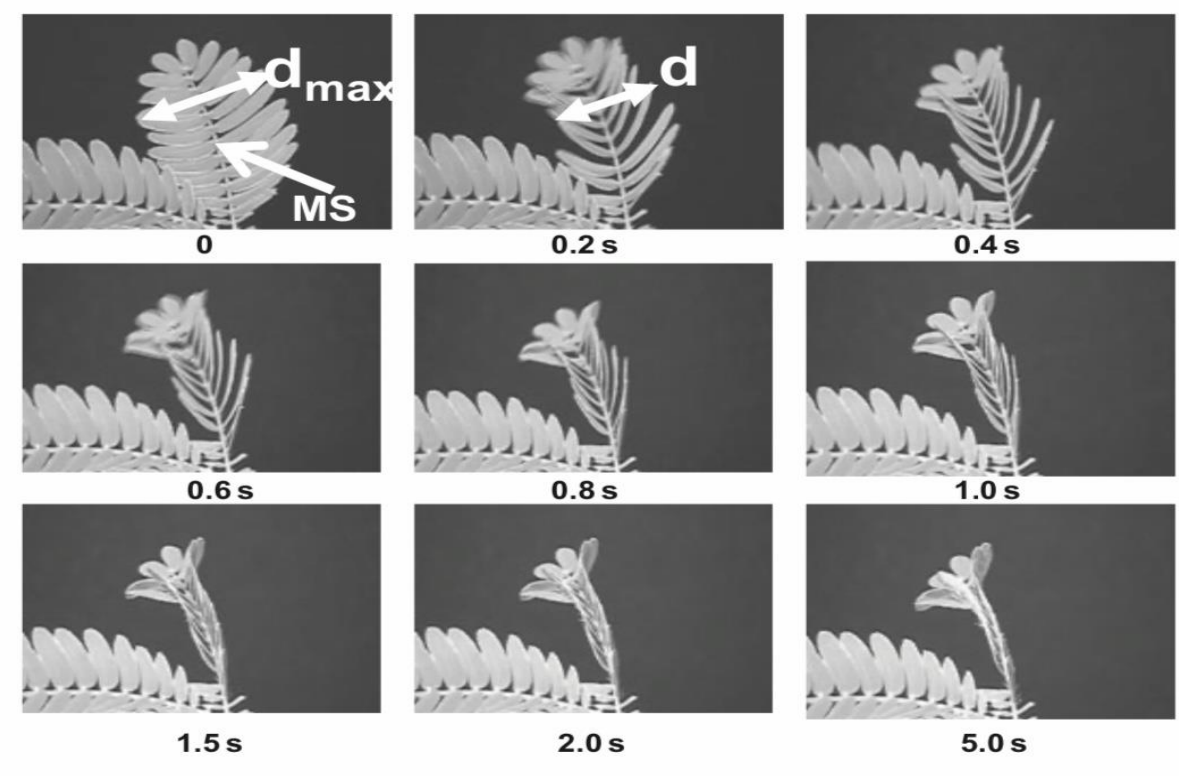

Figure 2. Kinetics of pinnules closing, mechanically stimulated (MS) by a touch of the midrib. Points are experimentaldata, solid line is the theoretical dependence estimated from Eqn 3.d, distance between rims of pinnules in the middle of pinna; dmax, maximaldistance between rims of pinnules in the Time middle of pinna.(Volkov et al., 2010)

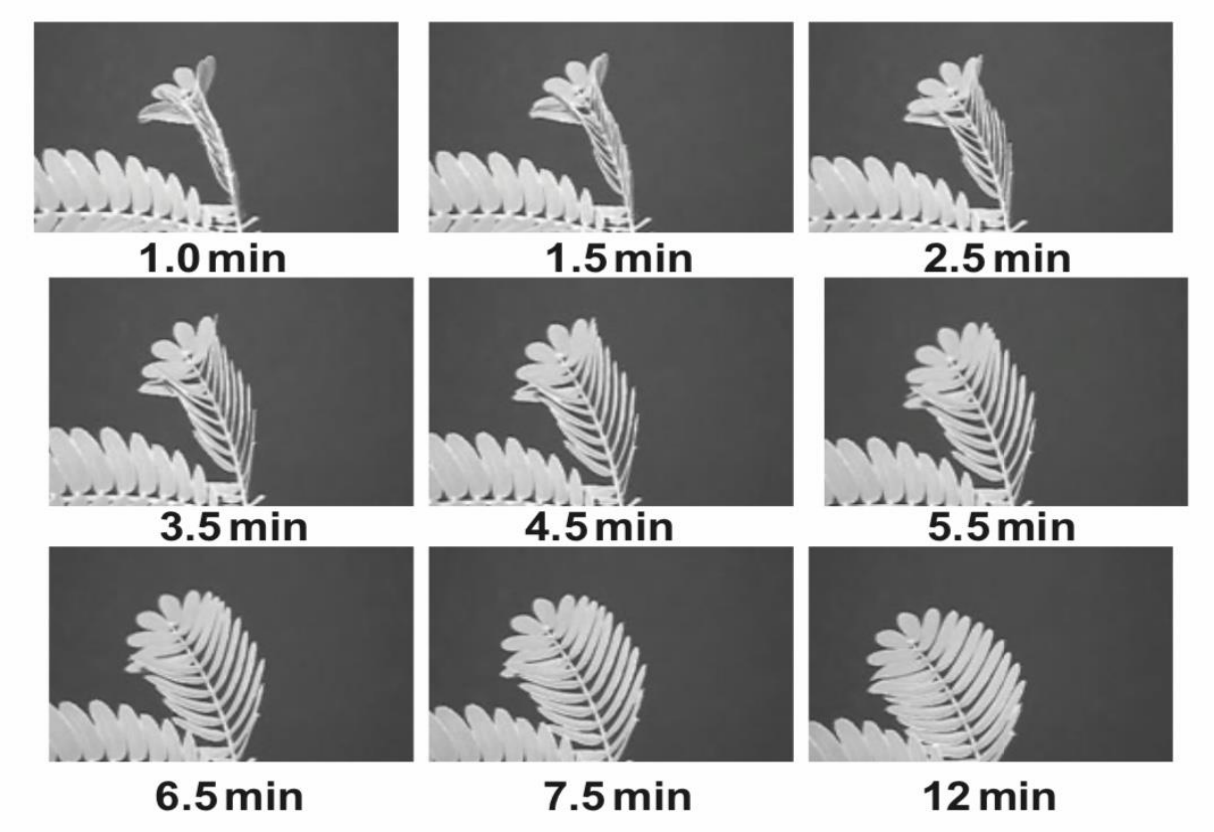

Figure 3. Kinetics of pinnules opening after closing by a touch of the midrib. d, distance between rims of pinnules in the middle of pinna; dmax, maximal distance between rims of pinnules in the middle of pinna. (Volkov et al., 2010)

3. CONCLUSION AND RECOMMENDATION

Current literature presents a few contributions dealing with the involvement of aquaporin expression and regulation to instantaneous or diurnally regulated plant leaf movements. The studies were performed on *Mimosa pudica* and *Samanea saman* regarding pulvinus-mediated leaf movements and on tobacco with regard to epinastic leaf movements. Swelling assays of protoplasts isolated from petiole tissues at different times of day connected the expression data with the proposed function at the cellular level. Furthermore, a direct contribution of specific aquaporins to properly regulated leaf movement has been analysed through a comparison of genetically modified tobacco plants with an impaired aquaporin expression and the controls. The slow epinastic leaf movement of the tobacco plants is highly affected by the genetic modification. For an analysis of the contribution of aquaporins to fast, pulvinus-mediated leaf movements it could be helpful to analyse genetically modified plants, for example in *Mimosa,* with an altered expression of the respective aquaporin regarding their ability to exhibit leaf movement. The involvement of aquaporins in growth movements suggests that aquaporins may also play an equally prominent role in overall growth regulation of leaves, stems and roots. Tobacco, and particularly *Arabidopsis*, where collections of T-DNA insertional mutants exist, could serve as model systems to study the importance of single aquaporins for regulation of plant organ growth. However, pleiotropic effects as well as functional compensation by closely

related homologues have to be considered during attempts to manipulate the expression of single aquaporin isoforms in plants.

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پوختە

جوولّەی گەڵای ڕووەک دەتوانێ لە لایەن ئەندامە تایبەتەکانی مۆتۆرەوە، پۆلقینی، یان دەکرێت ببێت بە ئیپیناستیک (بۆ نموونە لەسەر بنەمای جیاوازی گەشەی نیوەئاکسی و ئەبەکسیالەکانی گەڵا). هەردوو پرۆسەکە پەیوەندیان هەیە بە زیادبوونی ڕێکوپێککراو لە ڕێژەی گواستنەوەی ئاوی پەراسوو کە لە زۆر حاڵەتدا دەرکەوتووە کە لەلایەن ئاواپۆرینەکانەوە ئاسانکارییان بۆ کراوە جوولّەی گەڵای ڕیتمی لە زۆر جۆری ڕووەک ناسراون، بەڵام هەندێک لە کاغەزەکان مامەڵە لەگەڵ تێوەگلانی ئاواپۆرینەکان دەکەن لەو جۆرە جوولّانە. زۆرێک لە وردەکارییەکانی تەلارسازی و کارکردی پولقینی لەلایەن ڕوث ساتەر و هاوکارەکان کە سامانیان وەک زیندەوەرێکی مۆدێل بەکار هێنابوو، کاری بۆ کراوە. لەم دواییانەدا بەشداری لە ئاواپۆرینەکان بۆ جولّانەوەی پولقیناری لە سامانیا نیشان درا مۆدێلێکی تری ڕووەک بۆ خوێندن لە جوولّەی گەڵای بە نێوەندیی میمۆسا پودیکا هەروەها هەردوو گلّاسەکە و تۆنۆپلاست ئەکواپۆرینی خۆمالّی کرد بۆ جوولّەی گەڵای سیزمۆناستیک لە میمۆسا شیکرایەوە. لە تووتندا، وەک نمونەیەک لە جوولّەی گەڵای ئیپیناستیک،، ئەوە پیشان درا کە ئەندامی خێزانی ئەکواپورین PIP1 پێکهاتەیەکی گرنگە لە میکانیزمی جوولّەی گەڵا .

زانکۆی سەلاحەدین - هەولێر
Salahaddin University-Erbil

ڕۆژی ئەکواپورین لەبزوتنەوەی گەڵای ڕووەک

پرۆژەی دەرچوونە

پێشکەش بە بەشی بایۆلۆژی کراوە، وەک بەشێک لە پێداویستیەکانی بەدەستهێنانی بروانامەی بەکالۆریۆس لە زانستی بایۆلۆژی

ئامادەکراوە لەلایەن:

شیلان سلمان قادر

بە سەرپەرشتی:

م. هیوا حسین حسن

نیسانی-٢٠٢٢