### **REVIEW PAPER**

## Biomechanics in plant resistance to drought

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#### Abstract

During drought, plant functions at multi-levels (i.e., tissue, cellular and molecular) are adjustable with the change of water condition, which is known as drought resistance. Various biological, chemical and physical mechanisms have been found in plant drought resistance, among which the role of physical cues (especially mechanics) has attracted significantly increasing attention. Recent studies have shown that mechanics is one of the fundamental factors that control the responses and self-adaptation from tissue to molecular levels in plant when the external conditions changes. In the review, we examine how the factor of mechanics acts on the multi-level plant functions under drought stress, including water transport, tissue deformation, cell growth, cell movements, molecules interaction and signal pathway.

Keywords Water transport  $\cdot$  Deformation  $\cdot$  Molecule interaction  $\cdot$  Multi-level  $\cdot$  Self-adaptation

Botanical vocabular	'y	Conduits	Cells that can conduct water in
Stamens	The pollen-producing repro-		trees
	ductive organ of a flower	Sapwood	The newest part of xylem, and
Xylem	One transport tissue in vas-		contains living ray cells
	cular plants that can transport	Xylem sap	Water flowing in xylem
	the roots to logues	Dhloom	Conduits
Vessels	A system in xylem that can	rmoem	plants that consists of sieve
V035015	conduct water and consists of		tubes, parenchyma cells and
	a column of cells		so on, and can also transport
Tracheid	Elongated cells in the xylem		sugars from the leaves to other
	that can transport water and		parts, like roots
	mineral salts	Cavitation	Bubbles are formed in liquid
			phase under relatively low
			pressure and break the water
🖂 Tian Jian Lu		<b>—</b>	transporting in trees
tjlu@nuaa.edu.cn		Transpiration	water evaporation through a
Feng Xu			as stems leaves and flowers
fengxu@mail.xjtu.edu.cn		Transpiration pull	The force driving water
<sup>1</sup> State Key Laboratory of Mechanics and Control of Mechanical Structures, Nanjing University of Aeronautics and Astronautics, Nanjing 210016, China		Transpiration part	upward from the root to leaves especially from the stomata
<sup>2</sup> Nanjing Center for Multifunctional Lightweight Materials and Structures, Nanjing University of Aeronautics and Astronautics, Nanjing 210016, China		Trichome	Epidermal outgrowths pro- duced into an elongate hair- like structure
<sup>3</sup> MOE Key Laboratory of Biomedical Information Engineering, School of Life Science and Technology, Xi'an Jiaotong University, Xi'an 710049, China		Pollen grains	Male microgametophytes of seed plants
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Pollen tube	Germinate from pollen grains
	to acts as a conduit to trans-
	port the male
Cytoplasmic streaming	Directed flow of cytosol and
	organelles in fungal and plant
	cells
Stomata	A pore surrounded by a pair of
	guard cells is used to control
	gas exchange and water budget
Guard cells	Specialized cells in the epider-
	mis of leaves, stems and other
	organs form the stomata
Cytoskeleton	Epidermal outgrowths pro-
	duced into an elongate hair-
	like structure
Arabinogalactan-proteins	A class of glycoproteins in
	periphery of plant cells
Extracellular matrix	Extracellular substance
	secreted by cells that provides
	structural, biophysical and
	biochemical support to the
	surrounding cells
Actin filament bundles	Filamentous structures in
	the cytoplasm of eukaryotic
	cells and form part of the
	cytoskeleton

## 1 Introduction

With the global population rising and climate becoming hotter or more parched, drought result in crop production losing, which is becoming a significant problem in agriculture worldwide [1]. Besides, deteriorating extreme environments are also threating the survival of plant species on the earth [2]. For instance, drought-induced hydraulic failure results in largely mortality of forest plants (e.g., ponderosa pine), which may change the ecosystem structure [3]. To survive under such extreme conditions, plants have evolved with the ability of stress-adaptive responses to mitigate the negative effects, which is known as the plant resistance [4, 5]. In drought resistance, plants will regulate their functions of water transport in xylem, oscillating tip—growth, folding pollen grains, stomata opening and protein aggregating.

Various biological, chemical and physical mechanisms have been found in plant drought resistance [6–8], among which the role of physical cues (especially mechanics) has attracted significantly increasing attention. Biomechanics at tissue, cellular and molecular levels involves fluid and solid mechanics, continuum and statistic mechanics, thermodynamics and network dynamics (Fig. 1). For example, in drought and dry environment, pollen grains possess a structure-foldable adaptations [8], stomata adjust the aperture and movement by tuning the turgor pressure of guard cells [14, 15] and Arabinogalactan-proteins (AGPs) rearrange their patterns [16].

Although there are some review papers on the plant resistance from the biochemical aspects [17–19], the mechanical mechanisms of plant adaptive responses to drought at different levels remain rudimentary and fragmentary. Recently, we witnessed large numbers of reports on the mechanical factors in plant drought resistance, which calls for an urgent need to summarize the biomechanics at multi-level of plant. Thus we here present a state-of-the-art review on biomechanics in plant resistance, with focus on the mechanical behavior at multi-levels in plant resistance to drought (Fig. 1). We also highlight the challenges and future perspectives in the field of biomechanics in plant drought resistance.

## 2 Biomechanics in plant resistance to drought at tissue level

The water transport in plant tissue and compliant deformation of plant tissue in response to the change of water condition are in favor of the survival and functions, such as, elongation of long leaf, flower bloom and seeds dispersion.

#### 2.1 Water uptake and collection

In drought, plants uptake water from soil or collect water from atmosphere to maintain the normal metabolism and growth [20-22].

#### 2.1.1 Water uptake from soil

Water uptake from relatively dry soils is originally driven by the transpiration pull (Fig. 2a) [24]. As described in Ref. [25], "soil is a porous media made of small aggregates and particles." According to the Laplace law, the negative hydrostatic pressure of soil  $P_{\text{soil}}$  is given by Eq. (1a). Water flow rate through the xylem J (kg s<sup>-1</sup>) depends on the water potential difference of soil and leaf, hydraulic conductivity  $k_{\text{xylem}}$  (kg m Pa<sup>-1</sup> s<sup>-1</sup>) and transport distance  $x_{\text{xylem}}$  (m), as described by Eq. (1b) [26, 27]:

$$P_{\rm soil} = -\frac{2\gamma_{\rm soil}}{r_{\rm cm}},\tag{1a}$$

$$J = \frac{k_{\text{xylem}}}{x_{\text{xylem}}} (P_{\text{leaf}} - P_{\text{soil}}), \tag{1b}$$



**Fig. 1** Biomechanics in plant drought resistance at different scales. Biomechanics at tissue [9], cellular [8, 10, 11] and molecular levels [7, 12, 13] for plant resistance involves fluid and solid mechanics, continuous and statistic mechanics, equilibrium and non-equilibrium state. Tissue level involves water transportation (i.e., cavitation and embolism refilling), peasecod explosion and surface wrinkling of pea during drought or dehydration. Cellular level involves fast tip-growth of pollen tube, stoma control and foldable structure of pollen grains in drought. Molecular level involves lateral diffusion of plasma-membrane proteins and regulation network in drought. Of cause, the process of cases above may not involve in only one level but trans-scale problems, such as, cavitation and embolism refilling, stomatal movement control and cytoplasmic streaming



Fig. 2 Biomechanics of plant water uptake from soil and collection from fog [23]. (a) Water uptake from soil; (b) conical-shaped surface of conical spines with aligned grooves; (c) drop movement to the larger end of needle-like trichome of cactus

where  $\gamma_{soil}$  (N/m) is water–air surface tension and  $r_{cm}$  (m) is the radius of curves meniscus.  $P_{leaf}$  (Pa) is leaf water pressure.  $P_{soil}$  (Pa) is the negative soil water pressure. The model reveals the original driving force for water transport in plant and describes the relationship of water flow rate and the potential difference between soil and leaf (Fig. 2a). When the soil dehydrates during drought, the large pores empty first, water then retracts into pores of smaller dimension. According to the theories above,  $P_{soil}$  should be increased with the decrease of the radius of curves meniscus (related to the dimension of soil particles) and therefore the water flow rate (J) will decrease. To keep the relatively constant but not too low water flow rate, the size of soil particles should be distributed with appropriate proportion.

#### 2.1.2 Water collection from fog

Some plants (e.g., Cactaceae species) live in arid environments but are with extremely resistance to drought. Taking an example of the cactus (e.g., Opuntia microdasys), water collection from fog in desert area, which is one of its survival strategies [21]. There are three integrated parts and mechanisms for water collection on the needle-like trichome [23]. Firstly, a drop on a conical trichome (Fig. 2b) will flow to the end with larger radius, which is driven by the gradient Laplace pressure. The gradient Laplace pressure  $(\Delta P_{car})$  is given by Eq. (2a) due to the spine radius difference on the two sides of a drop. Secondly, the microgrooves are sparser near the base than those near the tip of the spine (Fig. 2b). The gradient of roughness generates a gradient of wettability and thus a gradient of surfacefree energy, which produces a driving force F, driving the water drops collection on the tip towards the base, as described as Eq. (2b).

$$\Delta P_{\rm carv} = -\int_{R_1}^{R_2} \frac{2\gamma_{\rm drop}}{(R+R_0)} \sin \alpha dz, \qquad (2a)$$

$$\mathbf{F} = -\int_{l_{\rm tip}}^{l_{\rm base}} \gamma(\cos\theta_{\rm A} - \cos\theta_{\rm R}) \mathrm{d}l_{\rm needle}.$$
 (2b)

Herein, *R* is the radius of the needle-like trichome where the drop lies on ( $R_1$  and  $R_2$  are the local radii at the two sides of a drop),  $\gamma_{drop}$  is the surface tension of drop,  $R_0$  is the drop radius, and dz is the incremental radius of the spine cone.  $\theta_A$ and  $\theta_R$  are the forward and backward contact angles of water drops, resepctively, and  $d_{needle}$  is the incremental length of needle-like trichome. The drop moved from the tip end to the base end as driven by the gradient of Laplace pressure and surface-free energy, which contributes to the water collection from fog (Fig. 2c). Inspired by the cactus fog collection system, a three-dimensional (3D), omnidirectional fog collector was designed [23]. However, highly efficient cactus-inspired water connector (3D) should be designed and manufactured for the survival of plants, animals and human beings in water-deficit area and arid environment.

#### 2.2 Water transport in plant tissue

In normal condition, water transport in plant xylem is continuous as controlled by hydrodynamics [28]. However, during drought, discontinuous fluid flow (i.e., hydraulic failure) is probably the most important factor limiting plant survival [29]. Then, hydraulic failure repairing is a critical mechanism in plant drought resistance.

#### 2.2.1 Hydrodynamics

Plants (i.e., trees) are able to transfer water tens of meters above ground driven by the transpiration pull and evaporated



**Fig. 3** Biomechanics in plant drought resistance at tissue level: water transport and cavitation. (a) Water flows from the soil to leaf, and then transpires into the air. Cavitation may occur in xylem under the drought [27]. (b) A stem segment: sap flow, transpiration, and diameter shrinkage,  $Q_{in}$ ,  $Q_{out}$ , and *E* are the inward, outward and transpiration mass flow rate, respectively [31]. (c) Three possible causes of nucleation of cavitation in xylem [25]

through the leaves [30]. The transport system of a tree generates continuous water columns in the vessels and tracheid of xylem (transport water and some minerals from soil [31]), as shown in Fig. 3a. The movement of water columns in the vessels is due to the tension from the site of evaporation and the huge cohesive strength of the liquid (force that holds together the liquid molecules), which is known as the "cohesion-tension" (C-T) theory [25, 32]. Based on the theory, a dynamic model can be used for describing water flow in a tree. Due to the transpirational pull, the volume change of water in the stem segment includes transpiration, sap (water flowing in xylem conduits) flow, and diameter shrinkage [31] (Fig. 3b). In this model, because the sapwood (the newest part of xylem) is a permeable water-conducting material, so the water flow is driven by pressure gradient according to Darcy's law (Eq. (3a)) [31, 33]. Because the sapwood is also an elastic material so the radius changes with the pressure according to Hooke's law (Eq. (3b)) [34], and the mass of stem segment is balanced (Eq. (3c)).

$$Q = \frac{k_{\rm sap}}{\eta} \frac{dp_{\rm wood}}{dl_{\rm seg}} A\rho, \tag{3a}$$

$$\frac{\mathrm{d}r_{\mathrm{stem}}}{\mathrm{d}p_{\mathrm{wood}}} = \frac{r_{\mathrm{stem}} - r_{\mathrm{hw}}}{E_{\mathrm{r}}},\tag{3b}$$

$$\frac{\mathrm{d}m_{\mathrm{w},i}}{\mathrm{d}t} = Q_{\mathrm{in},i} - Q_{\mathrm{out},i} - E, \qquad (3c)$$

where Q (kg s<sup>-1</sup>) is sap flow;  $k_{sap}$  (m<sup>2</sup>) is permeability of sapwood;  $\eta$  (Pa s) is dynamic viscosity of water;  $p_{wood}$  (Pa)

Table 1 Different viewpoints for cavitation in plant during drought

is water pressure in wood; A (m<sup>2</sup>) is basal area of sapwood;  $\rho$  is water density;  $l_{sag}$  (m) is the length of stem segment;  $r_{stem}$  (m) is stem radius;  $r_{hw}$  (m) is radius of heartwood;  $m_{w,i}$ (kg) is the mass of water in an element i;  $Q_{in,i}$  (kg s<sup>-1</sup>) is the inward mass flow rate;  $Q_{out,i}$  (kg s<sup>-1</sup>) is the outward mass flow rate; E (kg s<sup>-1</sup>) is mass flow rate of transpiration. The theoretical model bridges the water transport and the microstructure of sapwood, which help to further understand the water transport and balance in plant under drought.

#### 2.2.2 Hydraulic failure during drought

During drought, cavitation (the formation of small liquidfree zones) is a common phenomenon of hydraulic failure in plant water transport system (Fig. 3a) [25]. Four possible mechanisms have been proposed to explain the induction of cavitation in plant water transport system [25], each of which has got different viewpoints (approval and opposition), as listed in Table 1. The first mechanism is the homogeneous cavitation (Fig. 3c) induced by the loss of cohesion between water molecules. However, the homogeneous cavitation of plants xylem cannot occur because that the rupture of cohesive forces of water molecules occurs at pressures below -20 MPa [35], much lower than the negative pressures in xylem sap (about -13 MPa). The second mechanism is the hypothesis of heterogeneous cavitation. The cavitation is induced by the loss of adhesion between conduit wall and water (Fig. 3c) [38]. The probability of cavitation has been calculated by the heterogeneous nucleation rate [41, 42]. The third mechanism is air-seeding hypothesis, which is currently widely accepted [43]. According to the hypothesis, water under tension tends

Cavitation mechanisms	Approval	Opposition
Homogeneous cavitation		The rupture pressure of cohesive force between water molecules [35] is far beyond the pressure in xylem conduits [36, 37]
Heterogeneous cavitation		Hölttä et al. [27] found that heterogeneous nucleation plays a rather minor role in cavita- tion, because it requires the existence of very hydrophobic surfaces at conduit walls, and Pickard [38] found that most of the conduit walls are highly wettable because the high content of cellulose and hemicellulose
Air-seeding cavitation	Cochard et al. [39] presented a strongest willow branch experiment to support air-seeding mecha- nism. They found that increasing the air pressure to +P and decreasing the xylem pressure to $-P$ have the same effect and the cavitation is caused by capillary rupture of an air/water meniscus located on a pore through the conduit wall	Hacke et al. [40] found that air-seeding is not fully understood in confiers because the pores in the cell wall are too large to account for the cavita- tion pressure
Cell wall crevices bubbles cavitation	Pickard [38] proposed this cavitation mechanism based on Laplace's law in theory	

to pull gas from the adjacent embolized conduits through pores in the cell wall. If the pressure difference at the air/ water interface becomes sufficiently large, the meniscus passes through the pore and the air is released into the conduit [44, 45]. The fourth mechanism is that the cavitation origins from the release of vapor bubbles in the cell wall crevices [31]. The bubbles are normally stabilized in cracks or crevices of cell wall due to the surface tension forces. But it can be released into the water when the pressure difference between the bubble and water reaches a larger value [31, 42]. Comparing with the four hypotheses above, it is more reasonable for the two hypotheses of air-seeding and cell wall crevices bubbles cavitation, because the reported willow branch experiment verifies these hypotheses.

#### 2.2.3 Hydraulic failure repairing

Lower water conduction induced by hydraulic failure leads to the reduction of photosynthesis efficiency and even plant mortality [27]. To maintain hydraulic capacity, plants must repair the embolized conduits by refilling the gas-filled space [31, 46], which is known as the embolism resistance [47, 48]. There are three main hypotheses that explain the mechanisms of embolism refilling (Table 2). The first one is that the driving force for embolism refilling is achieved by the thin sap layer with the increasing solute [46]. It can lower the osmotic potential of embolized vessel, and lead the water from the living cells to flow into the embolized vessel to refill it (Fig. 4a). The second one is reverse osmotic hypothesis that the living cells reduce their osmotic potential via the starch-to-sugar hydrolysis, which raise their turgor pressure (Fig. 4b). Then tissue pressure occurs and it would squeeze water from the other living cells to the embolized vessel and refill it [55]. The

Table 2	Different	viewpoints	for embolism	refilling
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Refilling mechanisms	Approval	Opposition
Osmotic hypothesis	Zwieniecki et al. [49] calculated that the amount of stored starch corresponded well to needed amount for refilling	Tyree et al. [50] and McCully et al. [51] objected this hypothesis because they failed to observe the high solute concentration enough to support the refilling process by X-ray microanalysis techniques
Reverse osmotic hypothesis	Canny [52] proposed the reverse osmotic hypothesis after confirming the compensating pressure theory by sun flower leaf experiment	Comstock [53] and Tyree [50] found that objected to this hypothesis. Because the surrounding parenchyma cells would absorb the flowing water to maintain cell turgor and then deliver water via mass flow to refill conduits
Phloem-driven refilling hypothesis	Salleo et al. [54] verified this hypothesis on laurel plants that embolized stems with phloem first inactivated and then subject to external radial pressure to simulate native and then recovered from embolism through applying the external radial pressure to simulate native environment	



**Fig. 4** Biomechanics in plant drought resistance at tissue level: embolism refilling. (a) Osmotic hypothesis for embolism refilling [46]. (b) Reverse osmotic hypothesis for embolism refilling [55]. (c) Phloem-driven refilling hypothesis for embolism refilling [56–59]

third hypothesis is the phloem-driven refilling hypothesis that auxin signal would increase the solutes of the phloem (transport sugars from leaves to other organs), then solutes would flow into the embolized vessel through the ray cells (Fig. 4c). The lower osmotic potential would drive more water transport to the embolized vessel and refill it [56–59]. There are a lot of models to describe the refilling process. Taking the phloem-driven refilling hypothesis as an example, the illustrated model consists of a refilling vessel, living cells and water-conducting vessels where the refilling vessel is partly filled by the gas (Fig. 4b). The surrounding living cells can release water and solute into the refilling vessel. The flow rate includes the water flow between two parts, solutes releasing from the ray cells, and the solute transport between segments [58, 60, 61]. There is lack of any experimental evidences to support the osmotic and reverse osmotic hypothesis. Thus, it is more reasonable for the phloem-driven refilling hypothesis as verified by the experiment of laurel plants.

## 2.3 Solid deformation of plant tissue under different water conditions

Plant tissue generates compliantly large deformation with different time scales (i.e., steady-state and transient-state deformation) when the water conditions changes with the degree of drought or mature [62].

## 2.3.1 Steady-state deformation of plant tissue under different water conditions

Plant tissue performs its functions by compliantly swelling and shrinking at different water conditions, such as blooming lily [63] (Fig. 5a), morphologies of drying leaf [64] (Fig. 5c), and surface wrinkling pea [9] (Fig. 5e). In these structures of plants, various morphological instabilities are triggered by nonuniform mechanical, physical and chemical properties, which is largely influenced by different water conditions. Based on Föppl–von Kármán plate theory, Liang et al. [63] developed the model of blooming lily by introducing the in-plane differential and transverse curvature growth tensor.



**Fig. 5** Biomechanics involved in water condition at tissue level: solid deformation. The left column shows the steady-state deformation of plant tissue: (a) mechanics of a blooming lily [63], (c) morphologies of drying leaf [64], (e) surface wrinkling pea [9]. The right column shows the transient-state deformation of plant tissue: (b) a drying cycle of *Erodium cicutarium* [9], (d) catapult of the fern sporangium [65, 66], (f) venus flytrap snaps [67]

Xiao et al. [64] established the phenomenological buckling models to explain the curled configuration of dried leaves. Li et al. [9] developed another plant tissue model of the surface wrinkling (3D) on a core–shell soft sphere (such as peas) under different water conditions. Interestingly, the pea goes through a complex deformation pathway: isotropic shrinking, buckyball-like buckling and then folding (Fig. 5e). The critical buckling condition depends not only on the structure factors (e.g., shell thickness) but also to mechanical properties related to water conditions. In drought, the strain energy in plant tissue due to the change of water condition release through the deformation, which reduces the damage of plant.

#### 2.3.2 Transient-state deformation of plant tissue in drought

Rapid movements are used in many essential plant functions, such as, climbing (*Erodium cicutarium* [9] (Fig. 5b)), defense (Mimosa), and seed dispersion (fern sporangium [65, 66] (Fig. 5d)), nutrition (Venus flytrap [67, 68] (Fig. 5f)). However, the typical scales in time  $(\tau)$ and length (L) vary over many orders of magnitude. Hura crepitans [69] disperse seeds at great speeds 70 m/s by using explosive fractures, the Venus flytrap [67] catch insects in 0.1 s by using an elastic buckling instability, and Dactylaria brochophaga [68] uses rapid swelling traps nematodes in less than 0.1 s. Theoretically, the rapid movement is dependent on elastic instabilities, explosive fracture or snap-buckling. But slow movement is limited by the swelling and water transport in plant tissue, which is governed by the porous elastic theories (i.e., Darcy's law and elastic deformation). The range of time scales  $(\tau)$ , length scale (L) and control factors for plant movements are listed in Table 3. Since the elastic modulus and mass density are affected by water conditions [70], the boundaries of fast (buckling/cracks), slow (swelling/ growth) and impossible movement in the phase diagram [65, 68] will be shifted with the changes of water condition during drought. For example, the pod will transform the swelling movement (slow) to explosive movement (fast) when dehydrating, which is in favor of the seed dispersing [71].

Besides the deformation, the original morphologies (e.g., shape and size) of plant tissue and their formation

process affect distinctly the resistance to drought. For example, plants limit the surface area and number of leaves in response to drought stress to reduce the water budget [72, 73]. Plant increase water uptake by growing thick and deep root systems [74].

## 3 Biomechanics in plant resistance to drought at cellular level

As is well known, the behavior of animal cells (both normal and cancer cells) is mainly controlled by the cytoskeleton and extracellular matrix [75]. Unlike animal cells, plant cells (i.e., pollen tubes, guard cells) perform their functions with their rigid cell wall made of cellulous microfibrils and pectin matrix, such as growth (materialincreasing) and non-growth (material-constant) deformation, against strong turgor pressure change in drought.

#### 3.1 Growth: materials-increasing deformation

Walled cell growth is typical mechanochemical processes of plastic deformation of cell wall coupling with chemical synthesis [76–78]. Irreversible expansion occurs when the turgor pressure exceeds a critical value (plastic yield stress) while wall deposition leading to a rapid wall thickening [78]. Plant cell (tip) may have steady, dynamic and oscillating growth at different turgor pressure and water conditions. Here, we introduce the mechanochemical behavior in tipgrowth of plant cell.

#### 3.1.1 Steady growth

From mechanical aspects, plant cell growth is ultimately driven and controlled by turgor pressure. The Lockhart equation [79] yields the time-dependent ratio of volume increasing

$$\mathrm{d}V/\mathrm{d}t = \boldsymbol{\Phi}(P - Y),\tag{4}$$

where  $V(m^3)$  is the volume of plant cell at zero turgor pressure, P - Y(P > Y) is the turgor pressure P (Pa) above the

Table 3 Physical principle of plant movements

Time and length scale	Control factor	Typical plants
$\tau > 1.6L^2$	Poroelastic: water transport	Lonicera, Arabidopsis thaliana, Zoophagus insidians
$10^{-5}L < \tau < 1.6L^2$	Elastic instabilities: snap-buckling and explo- sive fracture	Dionea muscipula, Utricularia, Ruellia brittoniana, Pilobolus kleinii
$\tau < 10^{-5}L$	Physically impossible	



**Fig. 6** Biomechanics of walled cell growth. (a) The mechanochemical coupling in walled cells growth [77]: the cell wall will grow when the activated wall materials and the existing network of cell wall with mechanical stress driven by the turgor pressure. But the mechanical energy will reduce after the new cell wall assembled. (b) Plastic deformation of plant cell wall due to the bending of walled cell [76]: the tensile stress increases speed of processive motion of synthesis machinery, while the compressive stress has the opposite effect

yield threshold Y (Pa), and  $\Phi$  (Pa<sup>-1</sup> h<sup>-1</sup>) is an extensibility coefficient.

From the energy aspects, the growth of walled cell is a dynamic balance between strain energy in cell wall pushed by turgor pressure and chemical energy for synthesis of cell wall [77]. The total energy of the walled cell includes the mechanical stretching energy, the bending energy, the pressure energy and the chemical energy. Jiang et al. [77] and Boudaoud [80] gave the detailed expressions of each energy. The shape and size limits of walled cell reaches the steady state where the increased strain energy balancing reduced chemical energy (Fig. 6a). When suffering from drought (e.g., reduction of pressure energy), the guard cells became more numerous and smaller [81].

Amir et al. [76] found that cell wall are remarkably plastic to adapt the external forces and constraints. They proposed a dislocation-mediated theory to quantify the relationship of growth and formation of the cell walls (Fig. 6b). In the theory, tensile (stretching) stress has two different effects, i.e., increasing the speed of dislocations (Fig. 6b, left) or reducing the activation energy for nucleation (Fig. 6b, right). But compressive stress has the opposite effect. This indicate that the plasticity of plant cell wall enhances the adaption to drought.

#### 3.1.2 Dynamic growth

Plant cells grow dynamically when suffering from extreme environments [82]. Cosgrove [83] analyzed the dynamic responses of growth rate and turgor pressure to instantaneous changes in one of parameters by using a differential equation

$$\frac{\mathrm{d}P}{\mathrm{d}t} = \alpha P^2 + \beta P + \rho, \tag{5}$$

where the combined parameters are  $\alpha = (-L-\phi)$ ,  $\beta = (L\sigma\Delta\pi + \phi Y - L\varepsilon - \phi\varepsilon)$ , and  $\rho = (L\varepsilon\sigma\Delta\pi + \phi\varepsilon Y)$ . *P* is cell turgor pressure; *L* is the hydraulic conductance of cell;  $\phi$  is wall extensibility;  $\sigma$  is the solute refection coefficient;  $\varepsilon$  is the volumetric elastic modulus of the cell;  $\Delta\pi$  is the difference in osmotic potentials between the inside of the cell and the external medium; *Y* is the yield threshold. The solution of the equation shows that the growth rate and turgor pressure will exponentially approach another steady state when a growing cell perturbed by external environment (Fig. 7a, b). When the plant cell suffering an instantaneous decrease in wall extensibility, the turgor pressure in plant cell increases and the water flux through the cell wall decreases slowly. But the growth rate (irreversible wall expansion) instantaneously decreases and slowly rises to another steady value.

#### 3.1.3 Oscillating growth

The tip of plant cells (i.e., pollen tubes) may grow fast in an oscillatory mode [86]. To investigate the oscillatory growth, Kroeger et al. [84, 87] coupled the Lockhart equation with the cell wall viscoelasticity, thickness variation, calcium dynamics and stretch-activated channels, which leads to a feedback loop of low amplitude oscillatory growth and chemical synthesis.

In the model, the elongation of wall material is modelled as the viscoelastic flow driven by the turgor pressure [84, 88]. The correlation between the velocity of the tip growth and the elastic constant is described by using the perturbation theory [84]. Simulated results show that the growth rate, thickness changing, and calcium concentration are phasing synchronous (Fig. 7c). The period of oscillation becomes larger with the increasing of calcium concentration in drought (Fig. 7d). In addition, the decreasing of turgor pressure induced by drought will increase the oscillation period but reduce the average growth rate obviously (Fig. 7e) [85]. Similar results have also been obtained through an energy method [89].

#### 3.2 Non-growth: material-constant deformation

In drought, plant cells also undergo movement with different time scales due to different water conditions. Statically, plant



**Fig. 7** Biomechanics in plant drought resistance at cellular level: Dynamic and oscillating growth. (a) Change in turgor pressure following an instantaneous decrease in wall extensibility [83]; (b) Change in growth rate and water flux following an instantaneous decrease in wall extensibility [83]. (c) Time course for normalized growth rate, apical cell wall thickness and cytosolic calcium concentration [84]. (d) Influence of external calcium concentration on oscillation period [84], and (e) influence of turgor pressure on oscillation period (blue) and average growth rate (green) [85]

cells (i.e., pollen grains) deform and change the shape to avoid the damage of plant cell structure. Dynamically, plant cells (i.e., guard cells) change the frequency of movement for water budget.

#### 3.2.1 Static deformation of plant cells in drought

Pollen grains will dehydrate at relatively dry environment when releasing from the anther of stamens. For survival in such a harmful environment, pollen grains fold the wall onto itself to prevent further desiccation (Fig. 8a, b). The significant phenomenon is known as harmomegathy [91], which meets the two conflicting demands (exchange and desiccation of cellular materials) on the pollen grain. Katifori et al. [8] demonstrate how wall structure of pollen grains guides itself toward distinct folding pathways through simple mechanical and geometrical principles. They modeled as a thin elastic shell and give the discretized stretching energy, bending energy and the energy related to volume changing. Simulated results show that the high compliance apertures



**Fig. 8** Biomechanics in plant drought resistance at cellular level: non-growth deformation [8]. (a) Pollen grains folds but not buckles in response to change in humidity; (b) cell wall structure of a typical tricolpate (tri-aperturate) pollen grain; (c) Opening and (d) closure stomata induced by drought [11]; (e) relative volume of guard cell changes with turgor pressure [90]; (f) the aperture of stomata changes with the turgor pressure of guard with different epidermal turgor [14]

of cell wall lead to a reversible and predictable folding pattern, which provided new insight into the significant plant cell functions in response to drought.

#### 3.2.2 Dynamic deformation of plant cells in drought

Stomata or guard cells respond rapidly to drought to maintain water transport and budget [92–94]. The movement of stomata is controlled by the turgor pressure in the two surrounding guard cells [95]. When the guard cells are fully turgid, the pore of stomata open and exchange gas (Fig. 8c), while the pore closes with the loss of turgor pressure under drought stress (Fig. 8d) [14, 96, 97].

A lot of studies focus on the mechanics of stomata regulation, Aylor and Krikorian [98] show that the radial distribution of guard cells microfibrils contribute to the opening of stomata by using an illustrative model of bloom with striping. Raschke et al. [99] found that the mechanical properties of cell wall are analogous to the polymers and described by the Flory theory [100]. Wu et al. [101] found the materials of guard cell wall is elastic anisotropic. Then a dynamic anisotropic factor (q) was postulated to describe the directional elongation [102, 103]. And the turgor pressure of guard cell (p) can be expressed as

$$p = \kappa \left[ (1+\nu)^{\frac{1-q}{1+2q}} - (1+\nu)^{-\frac{3(1+q)}{1+2q}} \right],\tag{6}$$

where  $\nu = V/V_0 - 1$ , defines as the relative volume change,  $\kappa = GV_W/[2\rho_0L_0(a_0-b_0)]$  represents the initial characteristics of guard cell [101].  $V_0$  is the lumen volume of the guard cell at transition;  $V_W$  is the wall volume of guard cell; *G* is the shear modulus of cell wall;  $\rho_0$  is the guard cell inner crosssectional radius at transition;  $L_0$  is the length of guard cell center line at transition;  $a_0$  is the semi-major axis of guard cell apparatus;  $b_0$  is the guard cell cross-sectional width at transition. The relation between the relative volume vs. turgor pressure (Fig. 8e) and stomatal aperture vs. turgor pressure (Fig. 8f) are sigmoidal, which agree with the experimental observations.

## 4 Biomechanics in plant resistance to drought at molecular level

However, more complex plant functions in drought are related to the molecular behaviors. The behavior of molecules (e.g., arabinogalactan-proteins) is mainly controlled by the thermodynamics of molecule interactions (molecule–molecule, molecule-wall and molecule-fluid interactions) and network dynamics of signal pathways under drought.

### 4.1 Thermodynamics of molecules

On one hand, Van der Waals force and static electrostatic force control the interactions between molecules. On the other hand, unlike animal cells, the behavior of molecules at the membrane-wall interface is constrained by the rigid wall and flexible membrane. In addition, the molecule-fluid interaction should be considered in the process of cytoplasmic streaming generation driven by protein motors.

#### 4.1.1 Molecule-molecule interaction

Basically, the two protein molecule chains can be simply considered as a pair of charged rod-like polyions oriented in parallel. The potential between the two protein molecule chains relates to charge density, ionic strength, counterion valence and dielectric constant. Recalling a theoretical model for a pair of polyion [104, 105], the reduced pair



**Fig. 9** Thermodynamics of molecules: molecule-molecule interaction. Wall-independent interaction between molecules [104]. (a) The reduced pair potential  $W_2(r)$  in different ionic strength. Red dot corresponds to  $10^{-2}$  M NaCl; black square corresponds to  $10^{-3}$  M NaCl; (b) the free energy for assemble a cluster of *N* polyions changes with the number *N*, expressed in units of  $Pk_BT$ . (c) The edge region of radius R(t) of the adhesion zone (upper), sketch of the radial distribution of binder density c(r, t) at a fixed time (lower). (d) Binder concentration with perturbed front

potential are dependent on ion concentration and the interaction energy will be influenced by the drought-induced concentration change (Fig. 9a).

For a cluster of N molecules of proteins, the work of assembly can be calculated in a hexagonal parallel array [104]. The free energy decreases as the cluster grows when the cluster is small but increases for the further growth. That is because, the attractions stabilize the cluster when it is small but the number of repulsive interactions increases as the cluster grows. There is then a maximum cluster (Fig. 9b). Since the free energy depend on the ionic strength, the formation of protein cluster is influenced by the drought-dependent ions concentration.

#### 4.1.2 Molecules-wall interaction

At the membrane–wall interface, lateral diffusion of plasmamembrane proteins is constrained in a focal adhesion complex where the mobile binders connect the membrane and cell wall [7] (Fig. 9c). In this system, the free energy generates from the elastically deformation of membrane and the resistance of glycocalyx separation from substrate. Shenoy &



**Fig. 10** Thermodynamics of molecules: molecules-fluid interaction. (a) 3D rotational steaming and section view [80]. (b) Side view and section view of fountain streaming in a pollen tube [107]. (c) Microscope mechanism of streaming formation in plant cells: cargo-carrying myosin motor binds and walks along the filament [108]

Freund [12] give the expression of free energy in system of plasma-membrane proteins diffusion. The simulated results show that the circular shape of adhesion front increases its radius under sinusoidal perturbations as the root of time (Fig. 9d). During drought, the circular shape of adhesion front will be changed due to the changed turgor pressure.

#### 4.1.3 Molecules-fluid interaction

Cytoplasmic streaming, with the functions of transport, mixing and position in plant cells, is sensitive to the change of external environment. For example, the velocity of cytoplasmic streaming is linearly related to the temperature and turgor pressure (as induced by drought) [106]. Cytoplasmic streaming in plant cells present strikingly organized flow patterns, such as rotational (Fig. 10a) and fountain streaming (Fig. 10b) [109]. The mechanism is that the motor proteins entrain cytoplasm streaming along the actin filament bundles at the periphery of plant cells (Fig. 10c). Woodhouse and



**Fig. 11** Network of Guard Cell ABA Signal pathway [114]. The color of the nodes represents their function: enzymes are shown in red, signal transduction proteins are green, membrane transport-related nodes are blue, and secondary messengers and small molecules are orange. Arrow heads represent activation, and short perpendicular bars indicate inhibition and light purpose lines denote interactions derived from species other than *Arabidopsis* 

Goldstein [108] proposed a critical theory for the hydrodynamics of the flow field generation in plant cells (i.e., *Chara corallina*) by introducing a filament-induced forcing into the incompressible Stokes equations. The model bridged the gap between cytoplasmic streaming and movement of motor proteins.

# 4.2 Dynamics of network of molecular signal pathway

Complexly, the behavior of plant cells in drought may be regulated by the signal pathway of various molecules in a network. In recent years, network dynamics has been successfully used to describe the process of signal transduction, metabolic pathways, and gene regulatory [110, 111]. During drought, abscisic acid (ABA) is rapidly produced, triggering a cascade of physiological responses, including stomatal closure for water budget. At the same time, dozens of cellular components participate in the function in ABA regulation [112, 113], as simplified in Fig. 11. The dynamics of state transition for each component are governed by logical (Boolean) rules [114]. The simple model provides an efficient tool to identify the regulating process of drought tolerance.

However, not all the processes in plant resistance occur at a single level of plant and some trans-scale problems and synergistic effect should be considered. For example, water transport involves many mechanisms at cellular level, while growth is coordinated at the tissue scale. In the process of cavitation refilling, the living cells reduce their osmotic potential through the starch-to-sugar hydrolysis (molecular level). Stomatal movement is controlled by a pair of guard cells and the surrounding epidemic cells (tissue level) and regulated by abscisic acid (molecular level) at the same time. Cytoplasmic streaming (cellular level) in plant cells is organized striking flow patterns through the motor proteins (molecular level) entraining along the actin filament bundles at the periphery.

 Table 4
 Future perspectives and challenges of biomechanics at multi-level in plant drought resistance

Multi-level in plant	Future perspectives and challenges
Tissue level	To develop the theoretical model of homogeneous cavitation To experimentally validate the hypothesis of cavitation in plant xylem for water transport during drought To further understand the mechanisms of embolism refilling (i.e., reverse osmotic hypothesis) in plant resistance to drought To design and manufacture the high efficient cactus—inspired water connector (3D) in arid environment
Cellular level	To developed the mechanochemical model for tip-growth of plant cell in resistance to drought To simulate the stomatal movement (including a pair of guard cells) during drought. To develop the stoma-inspired microfluidic pump/valve using for the application in agriculture and biomedical engineering
Molecular level	To develop the mechanoelectrical model for the drought-induced aggregation behavior of plasma membrane proteins (i.e., AGPs) at the membrane-wall interface. To propose the dynamics of the signal transduction network for stomatal regula- tion under drought

### 5 Conclusions and future perspectives

Plant biomechanics opens a window for us to flourishing interdisciplinary research [107, 115–120]. Advances in plant biomechanics provide the opportunities to bridge the multilevel structures (i.e., tissue, cellular and molecular) and the plant functions in resistance to drought. This review has examined interesting results, critical issues and representative examples, mechanical responses to drought (dehydration) in terms of water transport and collection, plant deformation and movements, plant cell growth, stomatal regulation, molecular aggregation and signal pathways. An important step in drought resistance involves the microfluidics, cell elasticity and thermodynamics of molecules. In spite of the rapid growth in the field of biomechanics, many challenges remain in understanding the plant drought resistance from biomechanics view: water budget (uptake, collection and transport), physical properties of cell membrane (i.e., stiffness, permeability and fluidity), and signal pathway of molecules. Some novel ideas have emerged for the solutions of drought [23, 121–123], but more bioinspired and biomechanical engineering methods should be paid much more attention to the field of drought resistance. Some more future perspectives are listed in Table 4.

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#### **Compliance with ethical standards**

**Conflict of interests** The authors declare that they have no conflicts of interest.

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