Biomechanics of rapid movements in plants:
poroelastic measurements at the cell scale

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1. Introduction

From a biomechanical perspective, plants offer a fascinating example of living systems capable of producing non-muscular movements (Skotheim and Mahadevan 2005; Dumais and Forterre, to be published). Although most of these movements are slow, some compete in speed with those observed in the animal kingdom and are involved in essential functions such as seed/pollen dispersal, defence and nutrition. Of these spectacular examples that have long fascinated scientists, the Venus flytrap (Figure 1(a)), for which the leaves snap together in a fraction of second to capture insects, has long been a paradigm for study. Recently, we have shown that this motion involves a snap-buckling instability due to the shell-like geometry of the leaves of the trap (Forterre et al. 2005). However, the origin of the active movement used by the plant to cross the instability threshold remains unknown. More generally, the physical mechanisms involved in rapid plant movements remain poorly understood, especially at the cell and tissue scale. Two main assumptions are found in the literature: (i) a rapid flow between the cells due to changes in osmotic pressure (Hill and Findlay 1981), (ii) a rapid cell expansion due to mechanical modifications (softening) in the cell wall (Williams and Bennett 1982). In both cases, the high-water pressure inside the plant cells (typically several bars), a water/oil meniscus rushes out in the tip as soon as the cell is perforated. The volume in the cell can be regulated by means of a movable rod inside the pressure chamber. The meniscus at the tip is visualised under a stereo-microscope and used as a point of reference. When the meniscus is fixed, the system is in equilibrium. The (measured) pressure in the chamber is then equal to the pressure inside which is inserted inside a single cell using a mechanical micromanipulator (Figure 1(b),(c)). The capillary is connected to a microfluidic chamber and both are filled with silicon oil of low viscosity. Owing to the high-water pressure inside the plant cells (typically several bars), a water/oil meniscus rushes out in the tip as soon as the cell is perforated. The volume in the cell can be regulated by means of a movable rod inside the pressure chamber. The meniscus at the tip is visualised under a stereo-microscope and used as a point of reference. When the meniscus is fixed, the system is in equilibrium. The (measured) pressure in the chamber is then equal to the pressure inside

2. Methods

2.1 The microfluidic pressure probe

The cell pressure probe technique consists of a microcapillary having a tip of diameter of about 4 μm,
Figure 2. Typical pressure relaxation experiment and corresponding position of the meniscus.

the cell (Laplace capillary pressure drop at the meniscus is negligible compared with the absolute pressure in the cell). The main difficulties with this technique are leaking at the tip/cell wall interface and clogging of the tip due to the cell organelles (plastids). To prevent these problems, we sharpened the capillary tip using a microbeveller and placed the whole set-up under an isolating table.

2.2 Plant cells and immobilisation technique

To measure the evolution of cell properties in real time during the triggering of the trap, we must immobilise the plant and prevent any motion of the leaves. This is achieved using a dental silicon paste, as shown in Figure 1(c).

The investigated cells are the large parenchyma cells in between the epidermis (cylindrical shape, typically 50 \( \mu \)m diameter and 200 \( \mu \)m length, mean volume \( V \sim 10^{-12} \) m\(^3\)). We ensured that the insertion of the tip inside the cell does not induce the triggering of the trap. Using our device, pressure measurements were possible and stable for a few minutes before destroying the cell or clogging the tip. Pressure inside the cells is highly variable depending on the chosen cell or plant (Table 1). This points to the need to measure the mechanical properties of a single cell during closure.

3. Results

To measure the elasticity and water transport properties of the cell, we carried out pressure relaxation experiment (Figure 2). The principle is to increase/decrease the cell pressure suddenly by injecting/removing a known volume of liquid, and then measuring the pressure relaxation to equilibrium. The relation between the pressure increment \( \Delta P \) and the volume increment \( \Delta V \) gives the elastic bulk modulus of the cell \( \varepsilon = (1/V)(\Delta P/\Delta V) \), which is related to the cell wall Young modulus \( E \) by the dimensional

\[
E \sim \varepsilon (R/h),
\]

where \( h \) is the cell wall thickness and \( R \) is the cell size. The characteristic time scale of the pressure decay \( T_{cell} \), which gives the time scale of water transport across the cell, yields the membrane permeability through the relation: \( T_{cell} = V\ln 2/(SL_p\varepsilon) \), where \( S \) is the mean cell area (Steudle 1993). Note that the cell volume \( V \) can be obtained directly from the small final pressure difference \( \delta P \) after a relaxation process (Figure 2). Table 1 gives the range of values for the bulk elasticity, membrane permeability and time scale of water transport measured in different cells \( (n = 10) \). The measurements were always carried out in the reference (open) state of the plant before any triggering. Values are within the range of those typically found in the literature for plants (Steudle 1993).

4. Discussion and conclusion

This study constitutes the first in vivo measurements of the pressure and other poroelastic quantities at the cell scale in a plant that exhibits rapid movements. The next step will be to monitor the time evolution of these quantities during trap closure by simultaneously monitoring the triggering signal (action potential). However, our results already questioned the most frequent assumption for fast movement in plants based on an active (osmotically driven) water transport between the cells. The time scale for water diffusion across a leaf of thickness \( H \) is given by [poroelastic time (Philip 1958; Skotheim and Mahadevan 2005)] \( \tau \sim T_{cell} (H/R)^2 \), where \( R \) is the typical cell size. This relation is obtained from the fact that water transport through cell aggregates may be described as a diffusive process, thus proportional to the square of the size of the leaf (Philip 1958; Skotheim and Mahadevan 2005). For the Venus flytrap, \( H/R \sim 5 \) and \( T_{cell} = 1 - 6 \) s, which gives a poroelastic time of about 20–150 s. This time seems much too large to account for the rapid closure of the trap (few 0.1 s), even when taking into account a buckling instability (Forterre et al. 2005). Further investigation is needed to understand the origin of this cryptic non-muscular engine.

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**Table 1. Cell poroelastic quantities for the parenchyma cells of a Venus flytrap leaf.**

<table>
<thead>
<tr>
<th>( V ) (10(^6) ( \mu )m(^3))</th>
<th>( P ) (MPa)</th>
<th>( \varepsilon ) (MPa)</th>
<th>( T_{cell} ) (s)</th>
<th>( L_p ) (m/s MPa)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.2–4</td>
<td>0.1–0.7</td>
<td>0.7–5</td>
<td>1–5.9</td>
<td>0.5–8 ( \times 10^5 )</td>
</tr>
</tbody>
</table>

\( E \) gives the elastic bulk modulus of the cell (1/V)(\Delta P/\Delta V), which is related to the cell wall Young modulus \( E \) by the dimensional relation: \( E \sim \varepsilon (R/h) \), where \( h \) is the cell wall thickness and \( R \) is the cell size.
References


