Langevin and Navier–Stokes Simulations of 3D Protoplasmic Streaming and a Nontrivial Effect of Boundary Fluid Circulation

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Abstract

We report numerical results obtained by Langevin Navier–Stokes (LNS) simulations of the velocity distribution of three-dimensional (3D) protoplasmic streaming. Experimentally observed and reported peaks of velocity distribution in plant cells such as Nittela were recently reproduced by our group with LNS simulations. However, these simulations are limited to Couette flow, a simplified and two-dimensional (2D) phenomenon of protoplasmic streaming. Therefore, to reproduce the peaks in natural 3D flows, the simulation dimension should be extended to 3D. This paper performs LNS simulations on 3D cylinders discretized by regular cubes, where fluid particles are activated by a random Brownian force with strength $D$. We find that for finite $D$, the distribution of velocity $h(V), V = |\vec{V}|$ has two different peaks at $V \to 0$ and a finite $V$ value and that the quantity $h(V_z)$ for $|V_z|$ along the longitudinal direction is also nontrivially influenced by the Brownian force. Moreover, we study the effects of the circular motion of boundary fluid on streaming and find that circular motion enhances the speed of fluid particles inside the plant cells.

I. INTRODUCTION

The size of plant cells, such as Nittela flexilis, in water ranges up to 1 (mm) in diameter, and flows in cells called protoplasmic streaming have recently attracted considerable interest from biological and agricultural technological viewpoints [1–3]. It is well known that the flows are driven by a so-called molecular motor in which a myosin molecule moves along actin filaments. Hence, flow activation shares the same mechanism with animal cells [4–7]. Recently, Tominaga et al. reported that plant size depends on the streaming speed, implying that the velocity of myosin molecules determines plant size [3]. Therefore, protoplasmic streaming has been extensively studied by experimental and theoretical techniques, including fluid dynamical simulations [8–13].

Kamiya and Kuroda first measured the flow velocity along the longitudinal direction of a cell by an optical microscope ($V_z$ for $\theta = 0$ in Fig. 1(a)) [14, 15]. The corresponding physical quantities, such as kinematic viscosity, were also reported [16–18]. Later, by magnetic resonance velocimetry on whole points of a cylinder section, Goldstein et al. measured the velocity and reported the position dependence on several different lines on the section [10].
The authors of Ref. [10] also theoretically studied the flow field by combining the Stokes equation or the Navier–Stokes (NS) equation for low Reynolds numbers and an advection–diffusion equation for a new variable concentration. Their results are confirmed to be in good agreement with the experimentally obtained results [8, 9].

Approximately 25 years after Kamiya and Kuroda’s measurement, Mustacich and Ware observed streaming by the laser-light scattering technique [19–22]. They reported that the spectra of scattered light show two different peaks at \( V \to 0 \) and \( V \neq 0 \) (Fig. 1(b)). These peaks indicate that two different velocities of particles reflect streaming. The first peak at \( V \to 0 \) is caused by the Brownian motion of particles [22], and the second peak at \( V \neq 0 \) is due to the velocity of particles dragged by the molecular motor at the cell periphery (Fig. 1(a)).

Recently, the peaks were numerically reproduced in Refs. [23, 24] by simplifying the three-dimensional (3D) streaming to two-dimensional (2D) Couette flow and by using the Langevin Navier–Stokes (LNS) equation, which includes Brownian random forces. However, the 3D nature of streaming, such as the circulation on the cell boundary, is modified or neglected in 2D simulations. Therefore, for a better understanding of streaming, 3D simulations are preferable. In this paper, we simulate streaming by a 3D LNS simulation technique for the variable velocities and pressures on cylindrical lattices composed of regular cubes. The primary purpose is to find two different peaks in the distribution of velocities corresponding to experimentally observed velocities. Our purpose is also to clarify whether the circulation of particles at the cell boundary causes a nontrivial effect on streaming.

II. METHODS

A. Langevin Navier–Stokes equation and the discrete equation

The LNS equation is given by a set of coupled equations for velocity \( \vec{V} = (V_x, V_y, V_z) \) and pressure \( p \) such that

\[
\begin{align*}
\frac{\partial \vec{V}}{\partial t} &= -\left( \vec{V} \cdot \nabla \right) \vec{V} - \rho^{-1} \nabla p + \nu \Delta \vec{V} + \vec{\eta}, \\
\nabla \cdot \vec{V} &= 0,
\end{align*}
\]

(1)

where \( \rho \) and \( \nu \) denote the fluid density and viscosity, respectively [23, 24]. The final term \( \vec{\eta} \) on the right-hand side of the first equation corresponds to the Brownian random force per unit
FIG. 1. (a) Flow velocity $\vec{V}$ inside a cell and (b) normalized velocity distribution $h(V)$ [20]. The dashed lines in (a) denote the positions for numerical measurement of velocity $V$. The angle $\theta$ is assumed to be $\theta = 0^\circ, 35^\circ, 75^\circ$ [10]. The solid line in (a) denotes the indifferent zone, where two opposite boundary velocities contact each other.

density. Such a Langevin equation is used as a numerical technique in particle physics for functions on a lattice [25–27], and hence, we consider that Brownian forces can be combined with the NS equation for fluids. Thus, LNS simulations partly include a particle simulation scheme, as in the lattice Boltzmann simulation technique [28, 29].

To solve the LNS equation in Eq. (1) numerically, we multiply the divergence operator $\nabla \cdot$ from the left, and using the symbol $D = \nabla \cdot \vec{V}$, we have

$$\frac{\partial D}{\partial t} = -\nabla \cdot \left( \vec{V} \cdot \nabla \right) \vec{V} - \rho^{-1} \Delta p + \nu D + \nabla \cdot \vec{\eta}. \quad (2)$$

By replacing the time derivative $\partial D/\partial t$ with the discrete time difference $(D(t+\Delta t) - D(t))/\Delta t$ and imposing the condition $D(t+\Delta t) = 0$, we obtain Poisson’s equation for $p$ such that (see Ref. [24] for more detailed information)

$$\Delta p(t) = \rho \left[ \frac{D(t)}{\Delta t} - \nabla \cdot \left( \vec{V} \cdot \nabla \right) \vec{V}(t) + \nu D + \sqrt{\frac{2D}{\Delta t}} \nabla \cdot \vec{g} \right]. \quad (3)$$

The components of $\vec{g}$ are given by Gaussian random numbers of mean 0 and variance 1, and the relation between $\vec{g}$ and $\vec{\eta}$ is given by $\vec{\eta} \Delta t = \sqrt{2D \Delta t} \vec{g}$ (see Ref. [24] for further details in this part). This Poisson equation in Eq. (3) is solved by an iteration technique with the acceleration coefficient $A = 1.81$. The obtained convergent solution $p(t)$ is inserted in the discrete time evolution equation

$$\vec{V}(t + \Delta t) \leftarrow \vec{V}(t) + \Delta t \left[ \left( -\vec{V} \cdot \nabla \right) \vec{V} - \rho^{-1} \nabla p + \nu \Delta \vec{V} \right] + \sqrt{2D \Delta t} \vec{g}, \quad (4)$$
and we obtain a numerical solution $\vec{V}$ satisfying $\nabla \cdot \vec{V} = 0$ for a given set of Gaussian random random forces $\vec{\eta}$.

We assume the following convergent criteria for $\vec{V}$ and $p$ such that

$$\text{Max} \left[ |\vec{V}_{ijk}(t + \Delta t) - \vec{V}_{ijk}(t)| \right] < 1 \times 10^{-8},$$

$$\text{Max} \left[ |p_{ijk}(t + \Delta t) - p_{ijk}(t)| \right] < 1 \times 10^{-8},$$

and that of iterations for Poisson’s equation is

$$\text{Max} \left[ |p_{ijk}(n + 1) - p_{ijk}(n)| \right] < 1 \times 10^{-10},$$

where $n$ denotes the iteration step for solving Poisson’s equation. The suffix $ijk$ of $\vec{V}$ and $p$ denotes a lattice point inside the cylinder and on the boundaries $\Gamma_1$ and $\Gamma_2$, which are the nearest neighbors to each other by the periodic boundary condition.

The most time-consuming part is to solve Poisson’s equation for $p$, which is simulated by the Open Mp parallelization technique coded by Fortran. The mean value of physical quantity $\langle Q \rangle$ is obtained by

$$\langle Q \rangle = \frac{1}{n_s} \sum_{i=1}^{n_s} Q_i,$$

where $Q_i$ denotes the $i$-th convergent configuration corresponding to the $i$-th Gaussian random force $\eta_i$. The symbol $n_s$ is the total number of convergent configurations ranging from approximately $200 \leq n_s \leq 500$, which is dependent on $D$. For $D = 0$, $n_s$ should be $n_s = 1$ because no Gaussian random number is assumed in this case. For simplicity, the brackets $\langle \cdot \rangle$ are not used for the mean values henceforth.

**B. Lattices for simulations**

In Table I, we show the geometries of lattices A and B, of which more detailed information is given in Appendix A. In lattice A, the angle $\phi$ of the indifferent zone to the vertical direction is $\phi = 60^\circ$, while it is assumed to be $\phi = 90^\circ$ in lattice B to see the effects of the rotation of velocity on the boundary $\Gamma_3$ (Fig. 10(a) and (b)).

**C. Calculation details and input parameters**

Velocity $\vec{V}$ is numerically measured at the lines denoted in Figs. 1(a) and 2 with the angle $\theta = 0^\circ, 35^\circ, 75^\circ$ on the surface section at $z = L/2$ the middle point of the cylinder.
TABLE I. Two different lattice geometries for the simulations. The ratio \( L/R \) is approximately \( L/R \approx 11.2 \) in lattice A, while it is exactly \( L/R = 2 \) in lattice B, where \( L \) is the cylinder length and \( R \) is the radius (Fig. 10(a) and (b)).

| lattice | \( \phi \) | \( R \) | \( L \) | internal boundary |
|---------|---------|------|------|-----------------|
| A       | 60°     | 32   | 358  | 1153800         | 66240 |
| B       | 90°     | 40   | 80   | 406053          | 18468 |

FIG. 2. Lattice points on the lines of three different angles \( \theta \) for the calculation of \( \vec{V} \). The line at \( \theta = 0^\circ \) is the vertical line along the \( x \)-axis, while those at \( \theta = 35^\circ \) and \( \theta = 75^\circ \) are composed of two symmetric lines due to the reflection symmetry \( \theta \rightarrow -\theta \). The lattice section corresponds to lattice A, of which the radius is given by \( R = 32 \).

These angles are the same as those assumed in Ref. [10]. Only a single section is used for the numerical measurements because the boundary velocities are circulating, and there is no equivalent section along the longitudinal direction of the cylinder, although the sections at \( z = 0 \) and \( z = L \) are almost equivalent to each other by the periodicity of circulation (Fig. 10(a)). In the case of lattice B, whole surface sections are equivalent; however, we also use the section at \( z = L/2 \) to numerically measure \( \vec{V} \), as in the case of lattice A.

Here, we show the details on the normalization of the distributions or histograms \( h(V_z) \) of \( |V_z| \) and \( h(V) \) of \( V \) measured on these lines. The maximum speed \( |V_z|_{\text{max}} \) is obtained from the velocities for \( \theta = 0^\circ, 35^\circ, 75^\circ \) and normalized to \( |V_z|_{\text{max}} = 1 \). The maximum velocity \( V_{\text{max}} \) is also obtained from those for \( \theta = 0^\circ, 35^\circ, 75^\circ \) and normalized to \( V_{\text{max}} = 1 \). These \( |V_z|_{\text{max}} \) and
$V^{\text{max}}$ values correspond to the boundary velocity $\vec{V}_0$ if $D=0$; however, this correspondence is not always true for $D>0$ due to the Brownian random force.

The distributions $h(V_z)$ and $h(V)$ are also normalized such that $0 \leq h(V_z) \leq 1$ and $0 \leq h(V) \leq 1$ by obtaining $h(V_z)^{\text{max}}$ and $h(V)^{\text{max}}$, respectively. These $h(V_z)^{\text{max}}$ and $h(V)^{\text{max}}$ values are calculated for each $\theta=0^\circ, 35^\circ, 75^\circ$ in contrast to $|V_z|^{\text{max}}$ and $V^{\text{max}}$.

Physical parameters characterizing protoplasmic streaming are density $\rho_e$ (kg/m$^3$), kinematic viscosity $\nu_e$ (m$^2$/s), boundary velocity $V_e$ (m/s), and the diameter of the cell $d_e$ (m), which are given in Table II. These values are given in Refs. [14–18] and are the same as those assumed in 2D LNS simulations in Refs. [23, 24].

Using the numbers $\alpha, \beta, \lambda$ for the unit change (see Appendix B), we obtain the parameters in Table III in simulation units. These are used in the simulations in this paper. The strength $D$ of the Brownian force varies in the simulations since it is sufficient to observe the dependence of physical quantities on $D$ [23, 24].

| TABLE II. Physical parameters $\nu_e, V_e, d_e$ corresponding to the protoplasmic streaming in plant cells, expressed in physical units. |
| --- |
| $\rho_e$ (kg/m$^3$) | $\nu_e$ (m$^2$/s) | $V_e$ (µm/s) | $d_e$ (µm) |
| $1 \times 10^3$ | $1 \times 10^{-4}$ | 50 | 500 |

| TABLE III. Parameters assumed in the simulations; these values are given in the simulation units. |
| --- |
| Lattice | $\rho_0$ [kg/(µm)$^2$] | $\nu_0$ [(µm)$^2$/βs] | $V_0$ [µm/βs] | $\Delta x_0$ [µm] | $\Delta t_0$ [βs] |
| A | $1 \times 10^{-3}$ | $1 \times 10^6$ | 1 | 3.90625 | $5 \times 10^{-7}$ |
| B | $1 \times 10^{-3}$ | $1 \times 10^6$ | 1 | 3.125 | $5 \times 10^{-7}$ |
III. NUMERICAL RESULTS

A. Velocity distribution for $D=0$

First, we show the results for $D=0$ on lattice A. The distributions or histograms $h(V_z)$ of $|V_z|$ and $h(V)$ of $V$ are plotted in Fig. 3(a) and (b), where $|V_z|$ and $V$ are normalized as described in the preceding subsection. The plotted data are calculated from a single convergent configuration of $\vec{V}$. For this reason, small fluctuations are observed in the data. We find that the shape $h(V_z)$ vs. $|V_z|$ is almost but not exactly the same as that $h(V)$ vs. $V$. A peak can be observed in both $h(V_z)$ and $h(V)$ at $V \to 0$ for $\theta = 75^\circ$; however, this peak does not correspond to Brownian motion of fluid particles because no Gaussian random force is assumed. No peak is observed in either $h(V_z)$ or $h(V)$ at finite velocity for any $\theta$ for the same reason. Fig. 3(c) shows the dependence of $V_z$ on the distance $r$ from the center of the surface section.

The results obtained on lattice B are shown in Fig. 3(d)–(f). Both $h(V_z)$ and $h(V)$ for $\theta = 0^\circ, 35^\circ$ are almost flat or independent of $|V_z|$ and $V$, respectively, implying that the flow fields on these lines of the cylinder section resemble that of Couette flow without Brownian
force. We find no significant difference in lattice A and lattice B results for \( D = 0 \). This indicates that the flow field inside the cylinder is almost independent of the fluid circulation on the boundary, at least for \( D = 0 \) zero Brownian force.

The distributions \( h(V_z) \) and \( h(V) \) in Fig. 3(d) and (e) are almost the same because the boundary velocity is along the \( z \) direction on lattice B. In contrast, they are slightly different from each other in Fig. 3(a) and (b) on lattice A, as expected from the rotating boundary velocity around the cylinder. The position dependencies of \( V_z \) in Fig. 3(c) are close to those in Fig. 3(f), and these are almost the same as those reported in Ref. [10].

**B. Velocity distribution for \( D \neq 0 \)**

![Graphs](image)

**FIG. 4.** (a) \( h(V_z) \) vs. \( |V_z| \), (b) \( h(V) \) vs. \( V \), and (c) \( V_z(r) \) vs. \( r \) obtained on lattice A, and (d), (e), (f) those obtained on lattice B. \( D \) is fixed to \( D = 1 \).

The results corresponding to \( D = 1 \), which is nonzero, finite and small, are plotted in Fig. 4(a)–(c) as obtained on lattice A and in Fig. 4(d)–(f) for lattice B. We find that \( h(V_z) \) in Fig. 4(a) is close to \( h(V_z) \) at \( D = 0 \) plotted in Fig. 3(a); however, a nontrivial difference can be seen in \( h(V) \) plotted in Fig. 4(b) obtained on lattice A and \( h(V) \) in Fig. 4(e) on lattice B. Indeed, \( h(V) \) drops to \( h(V) \to 0 \) at \( V \simeq 0.9 \) in Fig. 4(b), or in other words, fluid particles of velocity \( V_{\text{max}} > V_{0,\text{max}} \) exist on lattice A, implying that the Brownian force changes the flow field to those different from Couette flow even though \( D \) is sufficiently small. In contrast,
$h(V_z)$ and $h(V)$ plotted in Fig. 4(d) and (e) remain unchanged from those in Fig. 3(d) and (e) obtained at $D=0$ on lattice B, implying that the nontrivial deviation from the Couette flow appears only on lattice A. The position dependence of $V_z$ is almost independent of lattices A and B, as plotted in Fig. 4(c) and (f).

![Graphs](image)

**FIG. 5.** (a) $h(V_z)$ vs. $|V_z|$, (b) $h(V)$ vs. $V$, and (c) $V_z(r)$ vs. $r$ obtained on lattice A, and (d), (e), (f) those obtained on lattice B. $D$ is fixed to $D=20$.

Now, we plot the results corresponding to $D=10$ obtained on lattices A and B in Fig. 5(a)–(c) and Fig. 5(d)–(f), respectively. In the case of relatively large $D(=10)$, we also find a nontrivial difference in $h(V)$ plotted in Fig. 5(b) and (e), where two vertical dashed lines are drawn at the two peaks. The peaks at smaller $V$ represent Brownian motion of fluid particles [22], and those at larger $V$ correspond to the boundary velocity. The positions $V$ of the peaks on lattice A are the same as those on lattice B. However, all curves $h(V)$ in Fig. 5(b) have a peak at the smaller velocity position, while $h(V)$ for $\theta = 75$ in Fig. 5(e) has no peak at the smaller velocity region, indicating that Brownian motion is not always reflected in $h(V)$ on lattice B. The fact that Brownian motion is reflected in small velocity fluid particles for all $\theta$ on lattice A indicates that the rotating boundary velocity effectively increases the strength of the Brownian force $D$. Recalling the formula $D \sim T/(\mu \tau_e^2)$ in Ref. [23], where $T$, $\mu$ and $\tau_e$ are the temperature, viscosity and macroscopic relaxation time [30, 31], respectively, we consider that the rotation of velocity effectively lowers the fluid
viscosity.

Note also that fluid particles appear, of which $V_{\text{max}}$ and $|V_z|_{\text{max}}$ are larger than the boundary velocities $V_0$ and $V_{0z}$ corresponding to the peak in the large velocity region. This appearance of large velocity particles is a nontrivial effect of Brownian random forces. The position dependence of $V_z$ is still almost independent of lattices A and B even for $D = 10$, as plotted in Fig. 5(c) and (f), and it is also independent of $D$ because no difference can be found $V_z$ in Fig. 5(c) and (f) and those in Figs. 3(c) and (f) and 4(c) and (f).

FIG. 6. $h(V)$ vs. $V$ for (a) $D = 20$, (b) $D = 100$, (c) $D = 1000$ obtained on lattice A, and $h(V)$ vs. $V$ for (d) $D = 20$, (e) $D = 100$, (f) $D = 1000$ obtained on lattice B.

To see the dependence on $D$, we further increase $D$ to $D = 20$, $D = 100$ and $D = 1000$ and plot $h(V)$ in Fig. 6(a)–(f). The effect of Brownian motion is now clearly visible even for $\theta = 75^\circ$ on lattice B (Fig. 6(d)); a peak appears for the small velocity region if $D$ is increased to $D = 20$. If $D$ is increased to $D = 100$, we find a nontrivial difference between Fig. 6(b) and (e) that the peak positions corresponding to the boundary velocity $\vec{V}_0$ in the large velocity region are different from each other. The fact that the position of the peak is located at a lower velocity on lattice A than that on lattice B means that $V_{\text{max}}$ is larger on lattice A than on lattice B, implying again that the circular velocity on the cylindrical surface effectively increases $D$ on lattice A. For a further increment of $D$, the second peak corresponding to the boundary velocity is expected to move left because $V_{\text{max}}$ becomes increasingly larger.
Thus, for sufficiently large $D$, two different peaks will be merged, as shown in Fig. 6(c) and (f), where $D = 1000$. In such a case of sufficiently large $D$, Brownian force is dominant for the activation force of fluid particles, and the boundary velocity is effectively neglected. As a consequence, the velocity distribution $h(V)$ shows ideal gas behavior \[23\].

Finally, in this subsection, we show the maximum velocities $V^{\text{max}}$ and $V_z^{\text{max}}$ obtained on lattices A and B in Fig. 7(a) and (b), where $V_z^{\text{max}}$ denotes the absolute maximum of the $z$ component of $\vec{V}$. These data are calculated on the lines for $\theta = 0^\circ, 35^\circ, 75^\circ$ on the cylinder section at $z = L/2$. We find from Fig. 7(a) that $V^{\text{max}}$ of lattice A becomes larger than that of lattice B at $D \geq 20$ even though these are almost the same for sufficiently small $D$. In Fig. 7(b), we find $V_z^{\text{max}}(B) > V_z^{\text{max}}(A)$ for a sufficiently small $D$ region. This comes from the fact that the boundary velocity rotates on lattice A while it is along the $z$ direction on lattice B. This magnitude relation is reversed at approximately $D = 100$. Thus, we confirm that the velocity of fluid particles is increased by Brownian random forces, indicating that the mixing of biological materials is enhanced by velocity circulation and Brownian motion.

C. Snapshots of velocity and pressure

We show snapshots of velocity and pressure obtained on the section of cylinder at $z = L/2$ of lattice A for several different $D$ values. The direction of the boundary velocity at $z = L/2$
FIG. 8. Snapshots of velocity and pressure obtained on lattice A at the section in the middle of cylinder $z = L/2 (= 159)$. Velocities corresponding to (a) $D = 0$, (b) $D = 20$, (c) $D = 100$, (d) $D = 1000$, and velocity with pressure corresponding to (e) $D = 0$, (f) $D = 20$, (g) $D = 100$, (h) $D = 1000$. Only velocities at every other vertex are shown.

is opposite to that on the boundaries $\Gamma_1$ at $z = 0$ and $\Gamma_2$ at $z = L$ (Fig. 10(a)). The velocities denoted by cones shown in Fig. 8(a)–(d) are of convergent configurations corresponding to (a) $D = 0$, (b) $D = 20$, (c) $D = 100$ and (d) $D = 1000$. For a clear visualization, only velocities at every other vertex are shown. The same velocities with pressures are shown in Fig. 8(e)–(h), where the pressures $p$ are normalized to $0 \leq p \leq 1$ and represented by the color gradation. In this normalization, the boundary pressure $p = 0$ changes to $p \simeq 0.5$. Since the $z$ component of velocity is negative $V_z < 0$ in the lower part of the section in Fig. 8(e)–(h), the velocities are hidden behind the sectional surfaces for the pressure visualization.

We find from Fig. 8(a) and (e) that the fluid regularly flows according to the boundary velocity and that the pressure $p$ remains almost unchanged from the boundary pressure $p(\simeq 0.5)$ at $D = 0$. It is also confirmed that the velocity and pressure are disturbed at nonzero $D$, and the disturbance becomes stronger with increasing $D$.

Note that the pressure at higher $D$ does not always smoothly vary but looks randomly distributed on the surface section. This condition of the pressure configuration is relatively
close to that of Couette flow in parallel plates obtained by 2D LNS simulations [24].

To see a difference in the velocity configuration \( \vec{V} \) between lattices A and B, we show snapshots of velocity \( \vec{V} \) and pressure \( p \) in Fig. 9(a)–(h) obtained on lattice B. Velocities in Fig. 9(a)–(d) are shown at every third vertex. Since \( p \approx 0.5 \) at every point on the section for \( D = 0 \) in the convergent configuration, we show snapshots of \( \vec{V} \) and \( p \) for \( D = 1 \) instead of those for \( D = 0 \) in Fig. 9(a) and (e). The velocity configurations on lattice B are clearly different from those on lattice A for all \( D \), as expected from the difference in the boundary condition for \( \vec{V} \).

**FIG. 9.** Snapshots of velocity and pressure obtained on lattice B at the section of the middle of cylinder \( z = L/2 (=40) \). Velocity corresponding to (a) \( D = 1 \), (b) \( D = 20 \), (c) \( D = 100 \), (d) \( D = 1000 \), and velocity with pressure corresponding to (e) \( D = 1 \), (f) \( D = 20 \), (g) \( D = 100 \), (h) \( D = 1000 \). Only velocities at every third vertex are shown.

**IV. SUMMARY AND CONCLUSION**

In this paper, we numerically study the velocity distribution of protoplasmic streaming in plant cells by using the LNS simulation technique on 3D cylinders discretized by regular cubic lattices. The purpose is to check whether experimentally observed and reported peaks
in the velocity distribution can be reproduced by LNS simulations, and at the same time, our interest focuses on whether the circular motion of fluid over the cell surface has nontrivial influences on the flows inside the cells.

The velocity distribution $h(V_z)$ of $|V_z|$ along the longitudinal direction of the cylinder and $h(V)$ of the magnitude of velocity $V$ are calculated on two different lattices A and B. The boundary velocity rotates on the cylindrical surface on lattice A, while lattice B’s boundary velocity is parallel to the longitudinal direction. The strength of Brownian random force $D$ is changed in the range $0 \leq D \leq 1000$ as an input parameter.

We find two different peaks in $h(V)$ at two different velocities $V_1$ and $V_2$ ($V_1 < V_2$) if $D$ is increased to $10 \leq D \leq 100$ or more, where $V_2$ corresponds to the boundary velocity. The Brownian motion of fluid particles is reflected in the emergence of the first peak in $h(V)$ at $V_1$, and it is also reflected in the second peak of $h(V)$ at $V_2$ such that the curve $h(V)$ has a tail at $V > V_2$. This appearance of fluid particles at a higher velocity $V > V_2$ than the boundary velocity $V_2$ is also a nontrivial effect of Brownian motion, which is expected to play a nontrivial role in enhancing mixing.

On the effect of circulation of boundary velocity, which is known to be activated by the so-called molecular motor, we find that circular motion increases the maximum velocity speed. This velocity increment implies that circular motion enhances the mixing of biological materials. Note that the enhancement of mixing is assisted by the Brownian motion of fluid particles.

V. DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Appendix A: 3D lattice and the boundary condition

FIG. 10. 3D cylindrical computational domains for (a) lattice A and (b) lattice B for streaming. The arrows in (a) and (b) indicate directions of boundary velocity, which activates the streaming inside the cylinder, and small cones represent the velocity directions. The length $L$ of the cylinder is determined such that the indifferent zone rotates once around the boundary $\Gamma_3$: $L = 2\pi(R+1)\tan\phi$, and consequently, the velocities and pressures on $\Gamma_1$ and $\Gamma_2$ are connected by a periodic boundary condition on lattice A. $L$ is fixed to $L = 2R$ on lattice B. The size or diameter of the cylinders in (a) and (b) is 4 times smaller than those used for the simulations to clearly visualize the cones.

In this Appendix, we show the details of lattice construction for a cylindrical domain for streaming in plant cells. The actual cell surface is soft and expected to be bending or fluctuating. However, it is relatively rigid compared with animal cell surfaces, and therefore, we assume that the cylinder surface is rigid for simplicity. Thus, for the computational domain, we assume a 3D cylinder of radius $R$ and length $L$ (Fig. 10). The regions indicated by the symbols $\Gamma_i, (i = 1, 3)$ in the figure denote the boundary surfaces.

The fluid is activated by molecular motors on the surface $\Gamma_3$, and the fluid particles
FIG. 11. Section of cylindrical lattice of size $R=8$. The total number of vertices is $N_S=241$, which includes $N_B=48$ boundary vertices. The radius $r$ of boundary vertices is given by $R-1 < r < R+1$, on which the velocity $\vec{V}$ and pressure $p$ are fixed, and $r$ of internal vertices is given by $r < R-1$.

are dragged on the boundary, as indicated by two large arrows in Fig. 10. The contact line in which two different velocities coexist is called the indifferent zone, dividing $\Gamma_3$ into two domains. The angle of the zone is fixed to $\pi/3$ (or $60^\circ$), on which the volume of the computational domain is dependent. For this reason, the angle $60^\circ$ is assumed to be smaller than the actual angle in plant cells to save computational time. The length $L$ of the cylinder is fixed such that the indifferent zone rotates once around $\Gamma_3$. Therefore, the boundaries $\Gamma_1$ and $\Gamma_2$ are connected by a periodic boundary condition such that velocities $\vec{V}$ and pressures $p$ on $\Gamma_1$ and $\Gamma_2$ are nearest neighbors to each other. Another boundary condition is $p=0$ at all points on $\Gamma_3$. From the computational viewpoint, $p$ should be fixed somewhere in the computational domain or boundaries, and since no difference is expected in points of $\Gamma_3$, we impose this condition on $p$.

To explain the lattice structure, we show a surface section of the cylinder (Fig. 11). The building block is the regular cube of side length $a(=1)$ the lattice spacing. For this reason, the boundary shape is not a circle. Let $r$ be the distance of a vertex from the center of the section. The vertices at the region $R-1 < r < R+1$ form the boundary, whereas those
$r < R + 1$ are internal points, where $R$ is the radius of horizontal and vertical lines passing through the center of the section. In Fig. 11, $R$ is given by $R = 8a$, which is 4 times smaller than that of the lattice used for the simulations.

**Appendix B: Physical units and simulation units**

In the simulations, the physical units (m, s, kg) are changed to simulation units ($\alpha$m, $\beta$s, $\lambda$kg) with positive numbers $\alpha, \beta, \lambda$. Using these numbers for $V_e, \nu_e, \rho_e$, we have the relations $V_e [\text{m/s}] = \nu_e \beta / \alpha [\text{am/(}\beta s)], \nu_e [\text{m}^2/\text{s}] = \nu_e \beta / \alpha^2 [(\alpha \text{m})^2/(\beta s)],$ and $\rho_e [\text{kg/m}^3] = \rho_e \alpha^3 / \lambda [\lambda \text{kg}/(\alpha \text{m})^3]$ in physical units. The right-hand sides of these relations can be written as $V_0 [\text{am/(}\beta s)], \nu_0 [(\alpha \text{m})^2/(\beta s)],$ and $\rho_0 [\lambda \text{kg}/(\alpha \text{m})^3]$ in simulation units. Therefore

$$\alpha = \frac{\nu_e V_0}{\nu_0 V_e}, \quad \beta = \frac{\nu_e}{\nu_0} \left(\frac{V_0}{V_e}\right)^2, \quad \lambda = \frac{\rho_e}{\rho_0} \left(\frac{\nu_e V_0}{\nu_0 V_e}\right)^3 \quad (B1)$$

In addition to these numbers, we need positive numbers $\gamma, \delta$ for lattice and time discretization such that $n_X \rightarrow \gamma n_X$ and $n_T \rightarrow \delta n_T$ for physical quantities to be independent of $n_X$ and $n_T$. In this expression, $n_X$ and $n_T$ are connected to lattice spacing $\Delta x (\text{m})$ and discrete time step $\Delta t (\text{s})$ such that $\Delta x (\text{m}) = d_e / n_X$ and $\Delta t (\text{s}) = \tau_e / n_T$, respectively, where $\tau_e$ is the relaxation time [30] [31]. In this paper, we do not go into detail on this problem on $n_X$ and $n_T$, and $\gamma, \delta$ are fixed to $\gamma = 1, \delta = 1$. We assume the numbers in Table [IV] for the unit change. Using the assumed numbers $\alpha, \beta,$ and $\gamma$ in Table [IV] we have $V_0 = V_e \beta / \alpha = (50 \times 10^{-6})(4 \times 10^{-2}) / (2 \times 10^{-6}) = 1[\text{am/(}\beta s)], \nu_0 = \nu_e \beta / \alpha^2 = (1 \times 10^{-4})(4 \times 10^{-2}) / (2 \times 10^{-6})^2 = 1 \times 10^{-6} [(\alpha \text{m})^2/(\beta s)],$ and $\rho_0 = \rho_e \alpha^3 / \lambda = (1 \times 10^3)(2 \times 10^{-6})^3 / (8 \times 10^{-12}) = 1 \times 10^{-3}[\lambda \text{kg}/(\alpha \text{m})^3].$

The lattice spacing $\Delta x_0$ in the simulation unit is given by $\Delta x_0 = \alpha^{-1} \frac{d_e}{n_X} = (2 \times 10^{-6})^{-1}(500 \times 10^{-6}) / (2R),$ where the diameter $2R$ of the cylinder is assumed to be $n_X$, which is the total number of discretizations introduced in the case of a regular square lattice of size $L \times L$ with $L = n_X \Delta x_0$. For $n_X = 2R = 64$ on lattice A ($n_X = 2R = 80$ on lattice B), we have $\Delta x_0 = 3.90625 \ (\Delta x_0 = 3.125).$

|   |   |   |   |   |   |
|---|---|---|---|---|
| $\alpha$ | $\beta$ | $\lambda$ | $\gamma$ | $\delta$ |
| $2 \times 10^{-6}$ | $4 \times 10^{-2}$ | $8 \times 10^{-12}$ | 1 | 1 |
The discrete time step $\Delta t_0$ can also be expressed by $\Delta t_0 = \beta^{-1} \tau_e$ using macroscopic relaxation time $\tau_e$ and the total number of time discretizations $n_T$. However, $\tau_e$ is not always given, and therefore, we simply assume $\Delta t_0 = 5 \times 10^{-7}$ for the simulation unit.

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