Making it big : how characean algae use cytoplasmic streaming to enhance transport in giant cells

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SAMENVATTING

Levende organismen vertonen grote verschillen in afmetingen, maar bijna alle individuele cellen zijn kleiner dan 100 μm. De vraag waarom de grootte van een typische cel zo weinig variëert van soort tot soort is een van de grote fundamenteel onopgeloste problemen in de biologie.

Een verklaring voor dit relatieve gebrek aan variatie in celgrootte wordt vaak gezocht in de fysische beperkingen waaraan chemische reacties op cellulaire schaal onderhevig zijn. De verplaatsing van moleculen en eiwitten in cellen verloopt via een serie onvoorspelbare *diffusieve* bewegingen. De tijd die nodig is voor deze diffusieve verplaatsing neemt normaliter kwadratisch toe met de afstand. Dit betekent dat wanneer een cel 10 keer groter gemaakt wordt, de benodigde tijd voor verplaatsingen met een factor 100 toeneemt. Het feit dat zo weinig cellen groter zijn dan 100 μm zou dus een aanwijzing kunnen zijn dat diffusie overige grotere afstanden 'te' langzaam wordt, en daarmee een beperkende factor wordt voor het regulerende vermogen waarmee een cel *homeostase* handhaaft, de stabilisering van de stofwisseling onder variabel gebruik en beschikbaarheid van stoffen.

In de laatste tientallen jaren is het steeds duidelijker geworden dat veel transport processen in cellen niet geheel diffusief verlopen. Cellen bevatten een netwerk van moleculaire filamenten, het zogenaamde *cytoskelet*, dat hoofdzakelijk bestaat uit relatief stijve *microtubuli* en de meer flexibele *actine* filamenten. Door gebruik van *moleculaire motoren* kunnen cellulaire objecten langs dit netwerk van kabels verplaatst worden en het cytoskelet functioneert hiermee als de infrastructuur voor een groot aantal gerichte transport processen.

Deze door moleculaire motoren aangedreven transport processen zijn vaak het meest nadrukkelijk aanwezig in cellen met een uitzonderlijke grootte. In veel gevallen neemt het transport in dit soort cellen de vorm aan van een stabiele circulatie van de celvloeistof die *cyclose* (of in het Engels *cytoplasmic streaming*) genoemd wordt. Dit proefschrift onderzoekt de rol die deze circulatie kan spelen bij het verminderen van de traagheid van diffusief transport in grote cellen. Ons werk richt zich hierbij op het mogelijk meest bekende voorbeeld van dit proces: de cyclose die plaats vindt in de reusachtige cellen van de *characeae*.

De characeae, ook wel *kranswieren* genoemd, zijn algen die gevonden worden op de bodem van ondiepe meren en plassen. De scheuten van deze

plant-achtige algen zijn onderverdeeld in cylindrische segmenten, de zogenaamde *internodiën*. Deze internodiën zijn uitzonderlijk grote enkele cellen, die met hun lengte van soms meer dan 10 cm tot de grootste in de natuur behoren. De celvloeistof in de internodiën beweegt omhoog en omlaag langs twee banden op het oppervlak van de cel. Deze banden zijn doorgaans spiraalvormig waardoor het stromingspatroon op het oppervlak iets weg heeft van het rood-witte patroon dat men vaak zit bij kappers in anglo-saxische landen. Op moleculair niveau wordt deze beweging aangedreven door de verplaatsing van *myosine* motoren langs actine filamenten. Hiermee wordt de inhoud van de buitenste laag celvloeistof, het *cytoplasma*, langs de wand getrokken. Bijna alle cellulaire processen vinden plaats in deze dunne laag, die de structuur heeft van een soort dikke 'soep' van eiwitten en organellen. Het merendeel van het volume van de cel wordt echter ingenomen door het *vacuole*, een waterig compartiment in het midden van de cel dat op passieve wijze meebeweegt met het cytoplasma aan de wand.

In hoofdstuk 3 bestuderen we deze vloeistofbeweging met als doel te begrijpen hoe dit biologisch ontwerp precies het organisme tot nut is. Door te kijken naar de symmetrie van het probleem zien we dat de spiraalvorm van de banden, die eerder nog niet verklaard is, mogelijk een rol zou kunnen spelen in het versnellen van menging in de cel. De heliciteit beïnvloedt op subtiele wijze het stromingsveld, dat twee circulatieringen vertoont die afwezig zijn in een cel met een rechte, niet-spiraalvormige banden. De amplitude van deze secundaire component van het stromingsveld neemt toe naarmate de windingslengte van de banden korter wordt. Deze component is vergelijkbaar met een vorm van circulatie die in verschillende andere vloeistofstromingen wordt waargenomen en lijkt veel op de stroming die in het dagelijks leven zichtbaar is wanneer men in het midden van een bord soep blaast. Er treedt een stroming op door het midden, die zich splitst bij de wand en dan in twee richtingen terug beweegt naar de andere zijde van de cel.

Het patroon aan het oppervlak verandert gedurende de ontwikkeling van de cel. De scheut van characeae groeit door celdeling in de top. Een nieuwe internode maakt een buitengewone groei door, waarbij de grootte van de cel toeneemt van 20 μm tot enkele centimeters in een periode van ongeveer een week. De spiraalvormigheid van de banden neemt toe gedurende deze fase van snelle groei en neemt vervolgens weer af naar mate de cel volwassenheid bereikt. Doordat de meeste voedingstoffen verbruikt worden in groeiende cellen, lijkt het aannemelijk dat de circulatie

in volwassen cellen in de eerste plaats to doel heel het transport naar de top van de plant te bevorderen. Het feit dat de heliciteit van de cel juist het grootst is gedurende de fase van snelle groei suggereert dat deze eigenschap van de het stromingspatroon wellicht bijdraagt aan het handhaven van homeostase doordat de menging van stoffen in het vacuole wordt versneld.

De hypothese dat cyclose bijdraagt aan homeostase door menging van stoffen in de cel te bevorderen is vaak naar voren gebracht in de literatuur. In hoofdstuk 4 proberen we dit idee precies te maken voor de circulatie in de internodiën van characeae. Onze bevinding is dat de secundaire stroming die samengaat met de heliciteit van de stroming inderdaad diffusieve processen zou moeten versnellen, alhoewel zorgvuldige analyse nodig is als het er om gaat te bepalen in hoeverre dit de stofwisseling van de cel tot nut kan zijn. Om een zo simpel mogelijke maat te vinden voor de invloed op transporttijden kijken we naar de respons van de concentratie in het midden van de cel na een plotselinge verandering van de concentratie aan te buitenkant. De secundaire stromingscomponent duwt aan een zijde van de cel de naar binnen diffunderende stoffen tegen de wand, terwijl deze aan de andere zijde naar binnen worden getrokken. Samen resulteren deze twee effecten in een verscherping van de gradiënten in de concentratie bij de wand, wat een hogere flux van stoffen en daarmee een versnelling van de respons tot gevolg heeft. De grootte van de effect is echter betrekkelijk bescheiden. De secundaire circulatie zou daarom vooral verspreiding van zeer langzaam diffunderende objecten bevorderen, zoals relatief grote eiwitten. Het is hierdoor nog niet duidelijk in hoeverre de cel inderdaad baat kan hebben bij mechanismen die we hier geïdentificeerd hebben, met name ook omdat de precieze inhoud van het vacuole in de fase van groei niet bekend is.

Naast onze theoretische behandeling van de circulatie van het cytoplasma hebben we experimenten ontwikkeld om de vloeistofstroming en zijn invloed op transport te meten. De resultaten van deze experimenten zijn weergegeven in hoofdstuk 5. Onze op NMR methoden gebaseerde metingen laten vertonen een uitzonderlijk goede overeenkomst tussen de voorspellingen op grond van onze hydrodynamische analyse en het gemeten stromingsveld in het vacuole. Nog preciezere metingen in de buurt van de wand konden worden verkregen door injectie van fluorescente deeltjes. Het stromingsveld in deze metingen vertoont een afwijking van onze voorspelling voor een gewone vloeistof in de buurt van de wand, die mogelijk een afspiegeling is van de mechanische eigenschappen van het cy-

toplasma. Deze experimenten bieden uitzicht op toekomstig onderzoek naar de reologische eigenschappen van het cytoplasma, de onderliggende aandrijvingsprocessen van de circulatie, en de aard van diffusief transport in deze dichte omgeving. Uiteindelijk kunnen deze onderzoekingen ons inzicht bieden in de fysische eigenschappen van stoffentransport in cellen en ons dichter bij een antwoord brengen op de vraag welke evolutionaire processen geleid hebben tot de ontwikkeling van de celgroottes die we vandaag de dag in te natuur waarnemen.

SUMMARY

Whilst living organisms on this earth exist in a great variety of sizes, the vast majority of cells found in nature are smaller than 100 μm. Why this typical cell size is so similar across species is one of the fundamental unsolved problems in biology.

It has long been suggested that this relatively well-preserved length scale results from physical limitations on the chemical reactions that sustain cellular life. Molecules and proteins in a cell undergo a random motion known as diffusion. As the cell size increases, so does the time required for this random motion to transport a metabolite. Typically, this time scale increases quadratically with the length, so if the cell size increases by a factor 10, the time for diffusion increases by a factor 100. Thus the fact that few cells exceed a size of 100 μm could signify that diffusion becomes 'too' slow beyond this size, thereby hampering the precise control mechanisms that allow a cell to maintain *homeostasis*, the stabilisation of cellular processes under fluctuating availability and demand of metabolites.

In recent decades it has become increasingly apparent that many transport processes inside cells are in fact not purely diffusive. Cells possess a *cytoskeleton*, a mesh of molecular filaments whose main components are the relatively rigid *microtubules* and the more flexible *actin* filaments. This cytoskeleton forms the backbone for a variety of types of directed transport driven by *molecular motors*, specialised proteins that can transport structures through the cell by moving along these filaments.

It is precisely in cells of exceptionally large size that motor-driven transport tends to manifest most clearly. In many cases this transport takes the form of a continuous circulation known as *cytoplasmic streaming*. This thesis explores how this circulation can help mitigate the limitations of diffusive transport in large cells, by examining the hydrodynamics of what is perhaps the best known example of this phenomenon: the *rotational streaming* found in the giant cells of the *characean algae*.

The characean algae are weeds that grow on the bottom of shallow lakes and ponds. Their shoots are divided into cylindrically shaped segments known as *internodes*. These segments are giant single cells whose lengths can exceed 10 cm, placing them among the largest cells known in nature. The cellular fluid inside these cells moves up and down along two bands, which tend to spiral around each other, much like the red and white ribbon on a barber pole. At a molecular level, this motion is generated by

the movement of *myosin* molecular motors along actin filaments that line the cell wall. This process takes place inside a thin peripheral layer known as the *cytoplasm*, which has a structure somewhat like a dense 'soup' of proteins and organelles. While most of the metabolic processes take place in this outer layer, the bulk of the cellular volume is occupied by a central storage compartment known as the *vacuole*, whose watery contents exhibit a passive flow profile as a result of the motion at the periphery.

In chapter 3 we analyse this fluid motion with the aim of understanding how its design provides benefit to the organism. Examination of the symmetry of the flow problem reveals that the twist in the bands, whose existence is otherwise unexplained, may serve to improve mixing in the cell. The helical twist has a subtle effect on the flow field, which exhibits two secondary circulation loops whose strength increases with the helical pitch. This circulation moves through the centre of the cell, splitting and reversing along the boundary. This basic pattern of flow occurs in a variety of fluid problems and can be observed in every day life as the circulation that results from blowing into the centre of a plate of soup, or a cup of tea.

The pattern of flow in internodes evolves over the course of cellular development. Characean shoots grow by cell division at the tip. A newly formed internode undergoes an extraordinary expansion from a length of 20 μm to several centimetres in the space of about one week. During this phase of rapid growth a twist develops in the bands that slowly unwraps again as the cell matures. Since most nutrients are consumed in growing cells, a likely purpose of streaming in mature cells is to simply act as a *conveyor belt* of sorts that serves to enhance the flow of nutrients towards the tip. The fact that the helical pitch increases precisely during growth suggests that this feature of the flow may aid homeostasis by homogenising concentrations in the bulk of the cell.

The hypothesis that streaming enhances homeostasis by improving intracellular mixing has often been raised in literature. In chapter 4 we aim to quantify this notion in the case of the secondary circulation predicted in the characean internode. We find that this circulation should indeed be expected to enhance diffusive transport, but that careful analysis is required to determine the extent of the benefits it may confer to a cell. As a simplest measure of the effect on transport rates, we look at the time it takes for the concentration in the centre of the cell to adjust to a change in concentration at the boundary. The effect of the circulation is that material diffusing into the cell is pushed against the boundary on one side of the cell, and carried into the centre at the other side. Together, these two

effects help maintain concentration gradients that are higher than those present in cells with straight non-twisting bands, where the secondary circulation is absent. Since the flux of nutrients is directly proportional to the concentration gradient, this results in an enhanced response. However, the magnitude of this effect is modest. The circulation should therefore be expected primarily to play a role for very slowly diffusing structures, such as large proteins. Thus, it is not yet clear to what extent the cell is able to derive benefit from the mechanisms identified in chapter 4, particularly since the exact contents of the vacuole during development are poorly known.

In parallel to our theoretical treatment of cytoplasmic streaming, we have developed experiments to measure the flow profiles inside cells and study its effect on transport. The results of these experiments are presented in chapter 5. Flow measurements based on NMR methods reveal an extremely good correspondence between our hydrodynamic predictions and the measured flow field in the vacuole. Even more detailed localised measurements can be obtained by the injection of fluorescent microspheres. In the flow near the boundary, these measurements a deviation from profile predicted for a normal viscous fluid. We hypothesise this to be a signature of the viscoelastic properties of the outer layer of cytoplasm. These experiments lead into future investigations of the mechanic properties of the cytoplasm, the generation of the streaming motion, and the nature of diffusive motion in this crowded environment. Ultimately, this can inform us about the physical limitations of metabolite diffusion inside cells, allowing us to begin to identify and understand the mechanisms that have governed the evolution towards the typical cell sizes we observe in nature today.

PUBLICATIONS

1. Jan Willem van de Meent, Andy J. Sederman, Lynn F. Gladden and Raymond E. Goldstein, 'Measurement of cytoplasmic streaming in single plant cells by magnetic resonance velocimetry', *Journal of Fluid Mechanics*, **642**:5-14, 2010.

2. Jan Willem van de Meent, Idan Tuval and Raymond E. Goldstein, 'Nature's Microfluidic Transporter: Rotational Cytoplasmic Streaming at High Péclet Numbers', *Physical Review Letters*, **101**(17):178102, 2008.

3. Raymond E. Goldstein, Idan Tuval and Jan Willem van de Meent, 'Microfluidics of cytoplasmic streaming and its implications for intracellular transport', *Proceedings of the National Academy of Sciences of the United States of America*, **105**(10):3663-7, 2008.

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CURRICULUM VITAE

I was born in Delft on the first of October, in 1980. After a year in Athens, GA (USA), where I attended *Clarke Middle School*, I completed my high-school education at the *Werkplaats Kindergemeenschap* in Bilthoven. Upon obtaining my VWO diploma in 1999, I enrolled in the Classics program at *Leiden University*, passing my propedeutical exam before commencing my studies in Physics at the same university. Whilst pursuing my degree I worked on granular flows in the lab of Martin van Hecke in Leiden, and studied the effect of weak agitations on packings of rings in the lab of Eric Clément at the *École Supérieure de Physique et de Chimie Industrielles* in Paris. In 2006 I was awarded a degree in Theoretical Physics for my thesis entitled *Onset of Turbulence in a Model Geometry; An Investigation of the Formation of Turbulent Structures in Plane Couette Flow using Dissipative Particle Dynamics Modeling*, a computational study of the formation of turbulence in compressible fluids, under the supervision of Alexander Morozov and Wim van Saarloos.

With the gracious support of Leiden I moved to the lab of Ray Goldstein at the *University of Cambridge* in 2006, where I embarked on a research project under joint supervision from Wim van Saarloos in Leiden. My investigations of the circulation process known as cytoplasmic streaming in the giant cells of *Chara* would keep me in Cambridge for most of the duration of my PhD. In addition to attending a number of courses, conferences and schools, I supported the Darwin College Bar as treasurer and joined Cambridge University Entrepreneurs as vice-president, leading their entrepreneurship competition at the university. In the final year of my PhD I returned to Leiden, where I helped introduce and supervise the course *Diffusion and Dissipation* with Martin van Hecke.

ACKNOWLEDGEMENTS

This collaborative project owes its inception to the constructive thinking of my supervisors as well as the administrations at Leiden and Cambridge. I have been exceptionally lucky with the supervision of Wim van Saarloos, who for many years now has been an unfailing source of guidance and sound advice despite his at times most challenging personal circumstances. My career owes a great deal to the opportunities he has created for me. In making this project a scientific success, Ray Goldstein's intuition for the field and eye for key problems has been a great asset. It has been both a pleasure and a privilege to work in his lab at DAMTP.

The Leiden and Cambridge administration have been instrumental in making this collaboration a reality. In particular, I would like to acknowledge the role of Peter Kes and Jan van Ruitenbeek, who as scientific directors at LION have generously supported this effort by providing full stipendiary funding in the form of a departmental PhD position. I would also like to express my appreciation to Peter Haynes, who in his role as head of department at DAMTP arranged further support in the form of an EPSRC scholarship covering tuition fees. The flexible mindset and exceptionally supportive attitude of these individuals has been invaluable in keeping administrative red tape to a minimum, leaving us free to focus on the work and the science.

My time at Cambridge was enriched by interactions and discussions with a remarkable group of colleagues and collaborators. My office mates Marco Polin and Kyriacos Leptos were a steady source of stimulating conversation and sage advice. Sujoy Ganguly taught me much of what I know about working on biology in an experimental setting. I greatly enjoyed working with Idan Tuval, with whom I spent many hours working through the hairy details of our theoretical models. I would like to highlight the role of Cyril Picard, whose creative thinking and broad knowledge were a driving force in our experimental efforts, and who became a true friend in the period we worked together. Vasily Kantsler made key improvements to the injection protocol near the end of the project, resulting in detailed measurements of the flow profile near the wall. Finally I would like to thank Andy Sederman, who patiently schooled me in the physics of MRI velocimetry and whose mastery of pulse-sequence design allowed us to obtain flow measurements with a level of detail rarely seen before at this scale.

I feel that particular recognition is due to the workshop technicians at DAMTP. David Page-Croft, Neil Price and Trevor Parkin have played an integral role in the development of nearly all experimental set-ups in our lab. Their knowledge, technical skill and can-do attitude has been invaluable in finding solutions to experimental problems, and their workmanship has without exception been impeccable.

Finally, to my family and friends, I warmly thank you all for your good company and perspective in this period of learning and experience.