Biological flow networks: The absolute basics

Eleni Katifori

Department of Physics and Astronomy, University of Pennsylvania, Philadelphia, PA 19104, USA

E-mail: katifori@sas.upenn.edu

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Abstract. These notes are intended as a brief introduction to flow networks, with motivation and emphasis in biological applications. We introduce basic circuit theory and proceed to discuss questions related to optimization, adaptation, and more. The work is intended for college seniors and graduate students in the beginning of their careers, or post-docs with no previous exposure to circuit theory.

1. Introduction

Transport networks appear in a variety of forms, and serve indispensable functions. They deliver load in the form of nutrients or information and help rid of waste. The xylem and phloem in plants, the system of arteries, veins, and lymphs in animals, mycelia in fungi are just a few of the many complex biological flow systems that life has engineered to optimize flow and allow for organisms to grow beyond the limits set by diffusion. Transport networks are a necessary ingredient of all multicellular life, but also of human life. Road networks, irrigation and other water delivery systems, power grids, are several examples of how transport networks permeate all aspects of human life.

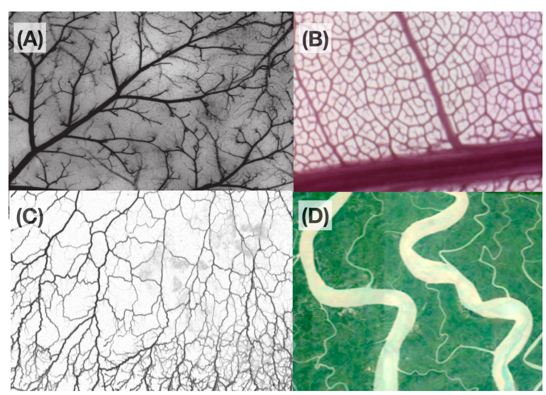

Figure 1: Examples of physical, spatially embedded, constrained degree networks. (A) Animal vascular network from the murine cortex (image by Patrick Drew). (B) Dicotyledonous leaf vascular network (image by EK). (C) Physarum polycephalum, (image adapted from [1]). (D) Channel network from the Ganges Brahmaputra Delta.

The study networks in their most general form can be traced at least as back as Euler, and his forays into graph theory, as exemplified by the problem of the seven bridges of Koenigsberg [2]. The history of the study of networks in mathematics and graph theory is long, and a lot of that interest has continued in physics and engineering in the form of circuit theory, random resistor networks and percolation theory [3]. In the 90's a series of seminal papers by Barabasi, Newmann and several others brought network science into the forefront, and introduced the idea that the architecture of networks is something that warrants exploration as a means to understand interconnected systems and human behavior [4, 5]. Examples include the internet, airport connectivity, friendship networks, citation networks, even biological examples such as gene networks and the brain connectome. Several metrics such as degree distribution, clustering, betweenness centrality were introduced and popularized. Classes architectures of complex networks were extensively studied and understood, such as Erdos-Renyi, small world, Watts-Strogatz.

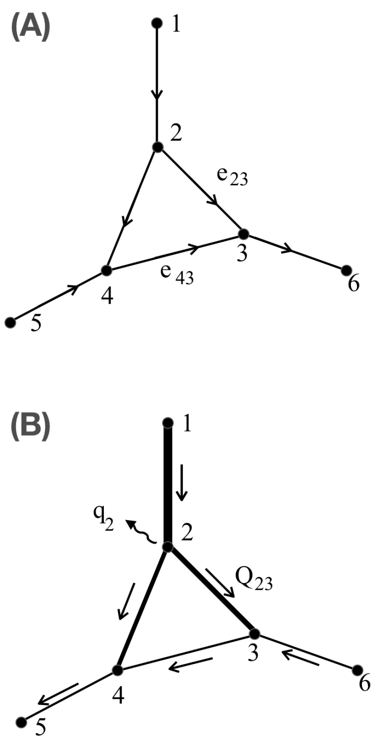

Figure 2: (A) A graph as a set of nodes and oriented edges. The orientation of the edges is displayed by the arrow. (B) A flow field is defined on the edges of the graph. The arrows now represent the orientation of the flow along the link.

The networks that we will be discussing in this review belong in this broad class of complex network systems, so a lot of the tools that we will present should apply beyond the specific examples that we present here. However, the networks in this review come with their own set of challenges. They are embedded in space, which imposes several constraints in the architecture, that non-embedded, abstract networks do not have. For example, geometrically embedded networks of the class we will focus in this review are typically, but not always, of low node degree. They have no hubs, and typically they are not strongly clustered, so a lot of the popular tools for complex systems to examine them are not adequate. Also, unlike information or neuronal networks, they transport a physical quantity that is conserved at the nodes, unless the node acts as an explicit source, injecting flow in the system, or a sink, removing flow.

The proper function of biological flow systems, such as the ones we will focus in these notes, is necessary for the survival and fitness of organisms [6]. Deviations from the intended design and operation signifies disease. However their biological importance is not by any means the only motivation to study them. Exploring the physics of biological flow networks is an excellent way to think about problems in discrete calculus, graph theory and gain practice using many other tools that are transferrable to a broad array of problems.

These lecture notes will start with an introduction to some basic circuit theory and the physics of flow networks. Then, I will talk about optimization, adaptation, and their relevance to biological systems and finally discuss aspects from topology and graph theory. The tone throughout the notes will be informal and educational, with several worked examples and references, so that the interested reader can delve into more rigorous derivations.This is the first version of this document, so please forgive the abundant typos.

Interwoven in each chapter there will be homework exercises, some requiring simple analytic calculations and some programming. They may vary in difficulty, and I strongly recommend that you at least attempt all of them. The computational exercises were designed with a programming language like Python in mind (and the associated toolboxes line NetworkX), but in practice any language you are sufficiently familiar with will do.

For students interested in performing the computational exercises, but have no relevant software (Python, Matlab etc) already installed, an easy way to get started is to install the open source Anaconda distribution `https://www.anaconda.com/distribution/`. Then, the Jupyter notebooks is a very convenient "Mathematica" style environment to do your claculations.

2. Circuit theory and flow networks

2.1. Definitions

We represent our circuit as a graph consisting of a set of N nodes $\mathcal{V}$ and M edges $\mathcal{E}$ (see Fig. 2(A)). An edge (otherwise called link) is a vessel that connects two nodes and has some resistance to the flow of current, and the nodes (or vertices) are the junctions between the links. An edge $e_{ij} \in \mathcal{E}$ can be represented by the ordered pair $\{v_i, v_j\}$, where $v_i \in V$. The orientation of the edge determines which direction of the flow (discussed below) is considered positive of negative. An *oriented* edge is different than a *directed* edge, otherwise known as a diode, which permits current flow only in one direction. Unless otherwise noted, we will be considering networks, or graphs, that form a single component, namely where you can hop from one node to any other node using the edges.

We can represent the relationship between oriented edges and nodes with the incidence matrix. The incident matrix encodes which nodes belong to which end of the each oriented edge. The incidence matrix $\hat{\Delta}^T$ is an $N \times M$ matrix with elements $\Delta^T_{i,k} = 0$ if node i is not part of the edge e_k, $\Delta^T_{i,k} = -1$ if node i if edge e_k is oriented out of the vertex i, and $\Delta^T_{i,k} = 1$ if node i if edge e_k is oriented into the vertex i.

If the edges of the graph shown in Fig. 2(A) are $e_1 = \{1, 2\}, e_2 = \{2, 3\}, e_3 = \{2, 4\}, e_4 = \{4, 3\}, e_5 = \{5, 4\}, e_6 = \{3, 6\}$, then the incidence matrix of the graph is:

$$\hat{\Delta}^T = \begin{bmatrix} -1 & 0 & 0 & 0 & 0 & 0 \\ 1 & -1 & -1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 1 & 0 & -1 \\ 0 & 0 & 1 & -1 & 1 & 0 \\ 0 & 0 & 0 & 0 & -1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix} \tag{1}$$

Note that $\sum_{i=1}^{N} \hat{\Delta}^T_{ij} = 0$.

Problem 1. *In your favorite programming language, plot the graph of Figure 2. Also, plot a* 10×10 *square grid. The purpose for this exercise is that you get familiarized with constructing a graph in the computer and plotting it. Note that the Python module NetworkX has several functions that automate this process.*

Now assume that this network is transferring some sort of load. This load can be blood, in the case of the animal circulatory system, or sap, in the case of plants. To describe the flow of that load from node to now, we consider the field Q_{ki}, which represents the current from node k to node i. The current is defined positive when the current flows in the same direction as that of the oriented edge the boundaries of which are the nodes k and i. In Fig. 2(B) the arrows now represent the flow direction. The flow Q_{23} through oriented edge e_{23} is positive. The flow Q_{43} through oriented edge e_{43} is negative, as the orientation of the edge $e_{43} = \{4, 3\}$ is opposite that of the current. However, the flow Q_{34} is positive, as the current flows in the same direction as that of the oriented edge $\{3, 4\}$. The $N \times N$ matrix $\hat{Q}$, defined by the entries Q_{ki} is thus antisymmetric. Mass conservation at each node implies $\sum_k Q_{ki} = 0$, unless there is net loss of current at that edge, and the edge is considered a "sink", or net input at that edge and the edge is considered a source. We define at each vertex i the net current q_i, that is zero if there is strict current conservation at that node, positive if the source is a sink and negative if it is a source. So finally

$$\sum_k Q_{ki} = q_i \tag{2}$$

Note that I can define a $M \times 1$ vector $\vec{Q}$ whose kth element is the current through the kth edge $e_k = \{i, j\}$. I can also define a $N \times 1$ vector $\vec{q}$ whose jth element is the net current q_j through the jth node. With these definitions, the current conservation equation 2 can be written in a simple algebraic form:

$$\hat{\Delta}^T \vec{Q} = \vec{q}. \tag{3}$$

Quantity	**Symbol**
Current through edge ij	Q_{ij}
Net current at node i	q_i
Conductance of edge ij	C_{ij}
Pressure at node i	p_i
Pressure drop between nodes i and j	$\Delta p_{ij} \equiv p_i - p_j$

Table 1: Symbols.

A quick note to the undergraduates: Knowing the net currents q_i at all nodes is not sufficient to uniquely determine the all flows in the system. Imagine a simple network in the form of two resistors connected in parallel, where one of the terminals (terminal 1) in the current source and the other (terminal 2) is the current sink. The current from the source is split in the two parallel branches A and B of the network, but without any extra information any splitting would satisfy the boundary conditions. We obviously need extra information to determine the flows, in the form of a constitutive relation.

This constitutive relation in its simplest form can be intuited as follows. Consider the two aforementioned parallel paths A and B. Now assume that each of the two routes has a certain conductance C_A (respectively C_B), or a degree of "ease" with which each link can carry flow. Now assume that the current Q that takes each path is proportional to the conductance of that path, or $Q_A/C_A = Q_B/C_B$. If we define a field p defined on each node 1 or 2, then the previous proportionality relationship can in general read $p_i - p_j = \frac{Q_{ij}}{C_{ij}}$ or

$$Q_{ij} = (p_i - p_j)C_{ij} \tag{4}$$

This field is the pressure, and this relation tells us simply that if the pressure drop between two nodes is $p_i - p_j$, with $p_i > p_j$, then the current Q_{ij} will be positive and flow from i to j, and its magnitude will be equal to $C_{ij}(p_i - p_j)$. The conductances can be written as a symmetric matrix with elements C_{ij} in row i and column j.

This probably sounds all too familiar. The physics of linear flow networks maps one to one with that of electric circuit theory. The voltage is now the pressure, the the electronic current flow is now the fluid flow and the electrical conductance is the flow conductance.

Note that we can write Eq. 4 in matrix form using the incidence matrix. Consider a diagonal matrix $M \times M$ where the C_{mm} diagonal element is the mth element of the vector $\vec{C}$. We will denote this matrix as $\mathrm{diag}(\vec{C})$. With this definition, Eq. 4 reads:

$$\vec{Q} = -\mathrm{diag}(\vec{C})\hat{\Delta}\vec{p} \tag{5}$$

Bear in mind that Eq. 4 can be derived by a Taylor expansion from any pressure drop relationship of the form $\Delta p = f(q)$ if $f(q) = f(-q)$, if the function f is odd. In the next paragraph we will derive the pressure flow relationship of Eq. 4 in the case of laminar flow through a pipe, known as Poisseuille flow.

2.2. Poisseuille flow

Consider a smooth pipe that carries laminar flow of low Reynolds number, with non-slip boundary conditions at the wall. The fluid is incompressible. The pipe has radius R and length L. There is a pressure drop Δp between the two ends of the pipe. The pressure gradient "pushes" the fluid and results in fluid flow. Because of the no slip boundary condition at the wall, the flow speed is zero there and increases towards the center of the pipe. In general, if two layers of fluid are moving at different speeds, as shown in Fig. 3(A), there is a frictional shear force

$$F = -\mu A \frac{dv_x}{dy} \tag{6}$$

assuming that the fluid is moving in the x direction and the gradient of the speed is along the y axis. Here, A is the area of contact between the two layers, and μ is the fluid viscocity. Each layer of fluid is experiencing two frictional forces, one from each side of the layer. The force is opposite to the direction of motion from if the contact fluid layer is slower, and in the direction of fluid motion if it is faster. The net frictional force will determine if the fluid layer will accelerate or decelerate.

To overcome this frictional force and maintain the fluid velocity we need a net force along the direction of fluid motion. In the case of a cylindrical geometry, as that of the pipe shown in Fig. 3(B), we calculate the net force in each cylindrical shell dr, and equate that with the net force $\Delta p 2\pi r dr$ pushing that shell. Eventually:

$$\Delta p = -\mu L \frac{1}{r}\frac{d}{dr}\left(r\frac{dv}{dr}\right) \tag{7}$$

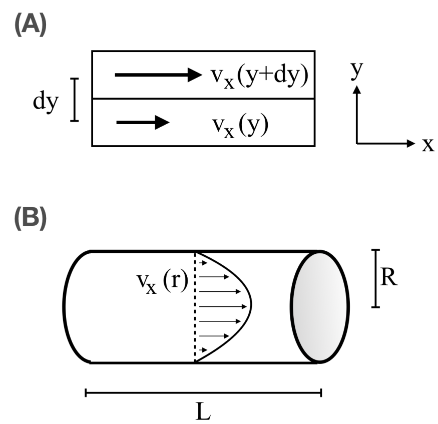

Figure 3: (A) Shear in the velocity gradient. (B) Parabolic laminar flow profile in a cylindrical pipe.

Integrating this equation one can find the fluid flow at each distance r from the center of the pipe:

$$v = \frac{1}{4\mu}\frac{\Delta p}{L}\left(R^2 - r^2\right) \tag{8}$$

The profile is parabolic, as shown in Fig. 3(B).

The total flow in the pipe is

$$Q = \int_0^R v(r) 2\pi r dr = \frac{2\pi \Delta p}{4\mu L} = \int_0^R (R^2 - r^2) r dr = \frac{\pi R^4}{8L\mu}\Delta p \tag{9}$$

If we identify $C \equiv \frac{\pi R^4}{8L\mu}$, then we pressure flow relationship assumes the form of the linear constitutive relation $Q = C\Delta p$ of Eq. 4. The conductance scales as the fourth power of the pipe radius, a fact that has major implications for several structural aspects of our circulatory system, and something we will revisit in subsequent sections.

Problem 2. *Assume now that the fluid is complex and that the effective fluid viscosity is now dependent on* r*, via some complicated interaction of the fluid with the wall. What is the fluid velocity* $v(r)$ *dependence on the distance to the center of the pipe and what is the dependence of* $C(R)$ *on the radius of the pipe if (a)* $\mu = b_1 r$ *and (b)* $\mu = b_2/r$ *. Is either a physical scenario?*

2.3. The Laplacian operator

So far we have established the basic nomenclature for the network topology and pressure flow function. In what follows we will see how we can determine all the network flows, through each link of the network. First, we will derive the basic equations without explicit using any matrix formalism.

Remember the flow conservation boundary condition Eq. 2 and pressure flow relationship Eq. 4. To determine the pressures p_i we plug in the latter into the former, and we have $\sum_i C_{ij}(p_i - p_j) = q_j$. We can massage the left hand side to

$$\sum_i C_{ij}(p_i - p_j) = \sum_i (C_{ij}p_i) - (\sum_i C_{ij})p_j \tag{10}$$

$$= \sum_i (C_{ij}p_i) - \sum_i [(\sum_k C_{jk})\delta_{ji}]p_i \tag{11}$$

$$= \sum_i [C_{ji} - (\sum_k C_{jk})\delta_{ji}]p_i \tag{12}$$

Now define a matrix $\hat{L}$ with elements

$$L_{ij} = -C_{ji} + (\sum_k C_{jk})\delta_{ji}. \tag{13}$$

This is the weighted Laplacian of the network. This is a symmetric positive semidefinite matrix. With the introduction of this matrix, the equation for p can be written as

$$\hat{L}\vec{p} = -\vec{q}. \tag{14}$$

Note that we could have equally simply used the matrix form of the flow conservation boundary condition Eq. 3 and pressure flow relationship Eq. 5. To determine the pressures $\vec{p}$ we plug in the latter into the former, and we have $\Delta^T \tilde{C} \Delta \vec{p} = -\vec{q}$. If we identify $\hat{L} \equiv \Delta^T \text{diag}\vec{C}\Delta$ we recover Eq. 14.

Problem 3. *Prove that* $[\Delta^T \text{diag}\vec{C}\Delta]_{ij} = -C_{ji} + (\sum_k C_{jk})\delta_{ji}$.

You are probably already wondering why the operator defined in Eq. 13 is called a *Laplacian* and how it is related to the Laplacian operator ∇^2 you know from calculus. The usage of the same name is not a coincidence; the Laplacian operator defined in Eq. 13 (which, if we wanted to minimize confusion, we should call the *discrete* Laplace operator) is an matrix operator that has the exact same properties as the continuum Laplacian operator, but operating on a network rather than a continuous field. This is a fact of paramount importance, as it is at the core of the connection of circuit theory to discrete calculus. We will not discuss this further, but instead refer the mathematically inclined reader to the book [7].

To provide some intuition here we will show how the discrete Laplacian operator on a square grid is connected to the continuous Laplace operator in the long wavelength limit. Note that the discrete Laplacian operator should not be confused with the discretized Laplacian operator [7]. The discrete Laplacian operator, unlike the discretized one is the correct generalization of the continuous one.

Consider a square grid of conductances C, equal for all the links, as shown in Fig. 4. Now the nodes i are represented with the coordinates on the grid, aka $i = (x, y)$. Equation 14 for the node (x, y) reads

$$[\hat{L}p]_{x,y} = -(C(p_{(x,y+\Delta y)} + p_{(x+\Delta x,y)} + p_{(x,y-\Delta y)}) + p_{(x-\Delta x,y)}) + 4Cp_{(x,y)} \tag{15}$$

After a Taylor expansion:

$$\begin{aligned}[\hat{L}p]_{x,y} &= C(\Delta y \left.\frac{dp}{dy}\right|_{x,y+\Delta y/2} - \Delta y \left.\frac{dp}{dy}\right|_{x,y-\Delta y/2} + \Delta x \left.\frac{dp}{dx}\right|_{x+\Delta x/2,y} - \Delta x \left.\frac{dp}{dx}\right|_{x-\Delta x/2,y}) \\ &= C(\Delta y^2 \frac{d^2p}{dy^2} + \Delta x^2 \frac{d^2p}{dx^2})\end{aligned} \tag{16}$$

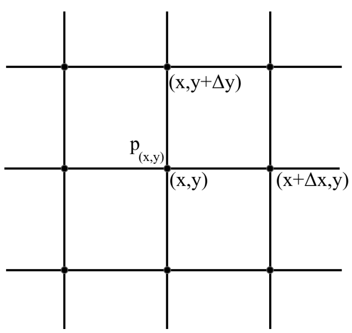

Figure 4: A network as a discretization of the continuum.

So finally, if $\Delta x = \Delta y$, Eq. 16 in the continuum limit reads $\nabla^2 p = \frac{q(x,y)}{C\Delta x^2}$. This is Poisson's equation from electromagnetism, where $\Delta^2 V = -\rho/\epsilon$, where here V is the voltage and ρ is the charge. Note that the negative sign is missing in our derivation. Can you think why?

Before we leave the discussion of the discrete Laplacian operator, we need to mention a few words about the incidence matrix. As some of you might have already guessed, there is something highly "suspicious" representing the incidence matrix as the transpose Δ^T of a matrix Δ. This $M \times N$ matrix Δ is actually a matrix with direct physical meaning: it is a boundary operator, which, when acts on a $N \times 1$ vector assigning a field on each network node, for example the pressures $\vec{p}$, returns a $(M \times 1)$ vector of the differences of the field values between the end nodes of each oriented edge.

2.4. Determining the pressure and flows

To solve for $\vec{p}$ and eventually all the Q, we would simply need to invert the matrix $\hat{L}$.

$$\hat{L}\vec{p} = -\vec{q} \Rightarrow \vec{p} = -\hat{L}^{-1}\vec{q} \tag{17}$$

However, $\mathrm{Det}|\hat{L}| = 0$, as $\sum_i L_{ji} = -\sum_i C_{ji} + (\sum_k C_{jk}) \sum_i \delta_{ji} = 0$, so the Laplacian is not invertible. This is intimately related to the fact that the pressure, like the voltage in an electrical circuit, is gauge invariant, and it can only be determined by differences. How can we then determine the pressures?

We can explore three different ways to solve this problem.

(a) Fix the pressure in one node, akin to grounding a node in a circuit. We can then remove the grounded node from $\vec{p}$, and the circuit, replacing its value with the imposed value in the equations that determine the pressure flow relationship. Ultimately, we rewrite $\hat{L}$ as a non-degenerate $(N-1 \times N-1)$ matrix so that it is non-degenerate. This is approach is in some ways the most straghtforward, but in many cases somewhat cumbersone to implement.

(b) We can use the pseudoinverse, which is typically computed via singular value decomposition.

(c) Last, there is a nice trick, that provides the correct result but avoids the issues with either (a) or (b). You can add a small constant α to the first diagonal element of the Laplacian L_{11}, i.e. $L_{11} \to L_{11} + \alpha$. This is simple and obviously makes the Laplacian invertible, but how does it eventually provide the correct pressure differences and flows?

To see why and how method (c) works, augment the circuit you are trying to solve by adding a node 0 with $q_0 = 0$, and connect it with a finite $C_{01} > 0$ to node 1. Note, no current can go through edge $\{0, 1\}$, so there is no pressure drop between the nodes 0 and 1.

The new Laplacian L' of the matrix with the added node reads:

$$\hat{L}' = \begin{bmatrix} C_{01} & -C_{01} & 0 & \dots & 0 \\ -C_{01} & \sum_{j=1}^{N} C_{1j} + C_{0,1} & -C_{12} & \dots & -C_{1N} \\ 0 & -C_{12} & \sum_{j=1}^{N} C_{2j} & \dots & -C_{2N} \\ \dots & \dots & \dots & \dots & \dots \\ 0 & -C_{1N} & -C_{2N} & \dots & \sum_{j=1}^{N} C_{N,j} \end{bmatrix} \tag{18}$$

and the new pressure vector $\hat{p'}$ is

$$\hat{p'} = \begin{bmatrix} p_0 \\ \vec{p} \end{bmatrix} \tag{19}$$

Finally, since the added no has no net current, the new net current vector is:

$$\hat{q'} = \begin{bmatrix} 0 \\ \vec{q} \end{bmatrix} \tag{20}$$

We now apply Eq. 14, we see that the equations for the first two rows read

$$p_0 - p_1 = 0 \tag{21}$$

$$C_{01}p_0 - (\sum_{j=1}^{N} C_{1j})p_1 - C_{01}p_1 + \sum_{j=2}^{N} C_{1j}p_j = q_1. \tag{22}$$

The rest of the equations for the remaining nodes are exactly as the ones of the original graph, before the addition of node 0. Now set $p_0 = 0$ (equivalent to connecting the 0 node in an electrical circuit to be the ground). Eq. 22 becomes $[-(\sum_{j=1}^{N} C_{1j}) - C_{01}]p_1 + \sum_{j=2}^{N} C_{1j}p_j = q_1$. The system of equations for the augmented circuit is therefore exactly the same as the original one, and adding a constant on the diagonal element $(1, 1)$ of $\hat{L}$, is equivalent to fixing the gauge.

Once the pressures are determined by any of the methods mentioned above, all the other attributes of the system, like the edge flows, can be trivially derived. So given the conductances C and net currents $\vec{s}$, we can determine $\vec{Q}, \vec{p}$ for any network! Note that we can also set pressure boundary conditions by fixing p in some nodes, and setting q_j as unknowns.

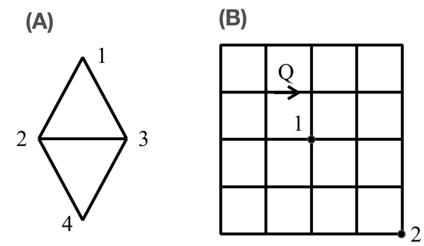

Figure 5: Practice examples

The following (fairly easy) problems are intended to build intuition about the behavior of linear circuits.

Problem 4. *Can you have* $\sum_{i=1}^{N} q_i > 0$*?*

Problem 5. p_1 *is the maximum node pressure in the network in Fig. 5 (A),* p_4 *is the minimum. If all conductances are* $C = 1$*, what is the current in each link? What if* $C_{12} = 2C_{13} = C_{23} = 2C_{24} = C_{34}$*?*

Problem 6. *The only thing you know about the circuit in Fig. 5 (B) is that* $p_1 = p_2$*, and that* $s_j = 0$ *for every* j *that is not 1 or 2. The net currents* q_1, q_2 *are unknown. What is the current* Q*? .*

2.5. Dissipation and effective resistance

In this section we will show some useful identities and derivations regarding dissipation, average pressure drop and effective resistance of linear flow networks.

The dissipation P of a linear flow network is the power that is lost due to friction in moving the fluid through the network. The total dissipation of the entire network is the sum of the dissipation at each link $P = \sum_e P_e = \sum_e \Delta p_e Q_e = \sum_e \Delta p_e^2 C_e$. This can be written in a more compact form:

$$\sum_{j>k} C_{jk}(p_j - p_k)^2 = \vec{p}^T \hat{L} \vec{p}. \tag{23}$$

The proof is simple

$$\vec{p}^T \hat{L} \vec{p} = \sum_{i,j} p_j [(\sum_k C_{jk})\delta_{ji} - C_{ji}] p_i \tag{24}$$

$$= \sum_j (\sum_k C_{jk}) p_j^2 - \sum_{ji} C_{ji} p_j p_i \tag{25}$$

$$= \sum_{j>k} C_{jk}(p_j^2 + p_k^2) - 2 \sum_{j>k} C_{jk} p_j p_k \tag{26}$$

$$= \sum_{j>k} C_{jk}(p_j - p_k)^2 \tag{27}$$

Problem 7. *Equation 23 can proven in half a line using the incidence matrix. Try it!*

Note also that $\vec{p}^T \hat{L} \vec{p} = -\vec{p}^T \vec{q}$. This is a simple manifestation of energy conservation: the total energy dissipated at the network is equal to the energy "injected" in the system by the source $(-\vec{p}^T \vec{q})$. To see this more clearly, consider a network with one source at v_1 and one sink at v_N. The, if q_o is the total injected current, $-\vec{p}^T \vec{q} = (p_1 - p_N) q_o$. If we identify $p_1 - p_N$ as the pressure drop imposed by the hydraulic equivalent of an electric EMF, then we see how this trivially maps to very well known identities from freshman E&M.

Problem 8. *Revisit the example of Fig. 5(B). Use* $\vec{p}^T \vec{s} = \sum_{j>k} C_{jk}(p_j - p_k)^2$ *to show that the pressures at all nodes are equal.*

A very useful concept of circuit theory is that of the effective resistance. The effective resistance $\tilde{R}_{ij}$ between two nodes i and j is the potential difference between the two nodes when a unit current q is injected in node i (node i is a current source) and collected from node j (node j is a current sink).

$$\tilde{R}_{ij} \equiv \frac{p_i - p_j}{q} \tag{28}$$

The effective resistance satisfies the triangle inequality $R_{ik} \leq R_{ij} + R_{jk}$, so it defines a metric on the graph called the resistance distance. This is a very useful tool to quantify transport networks, with some very cool properties that you can read in [8, 9].

Problem 9. *Find a simple closed form for the average pressure of a network of* N *nodes with current boundary conditions* $q_j = 1 - N\delta_{j1}$ *when node* 1 *is grounded.*

Bibliography

[1] W Baumgarten and M J B Hauser. Detection, extraction, and analysis of the vein network. *Journal of Computational Interdisciplinary Sciences*, 1:241–249, 2010.

[2] Reinhard Diestel. *Graph Theory*. Springer-Verlag, 2005.

[3] Sidney Redner. Fractal and Multifractal Scaling of Electrical Conduction. In *Encyclopedia of Complexity and System Science*, pages 446–462. 2007.

[4] R Albert and A L Barabasi. Statistical mechanics of complex networks. *Reviews Of Modern Physics*, 74(1):47–97, 2002.

[5] M E J Newman. The Structure and Function of Complex Networks. *SIAM*, 45(2):167–256, 2003.

[6] M LaBarbera. Principles of design of fluid transport systems in zoology. *Science*, 249(4972):992–1000, 1990.

[7] Leo J. Grady and Jonathan R. Polimeni. *Discrete calculus*. Springer, 2010.

[8] D J Klein and M Randi. Resistance distance. *Journal of Mathematical Chemistry*, 12:81–95, 1993.

[9] W. Ellens, F. M. Spieksma, P. Van Mieghem, A. Jamakovic, and R. E. Kooij. Effective graph resistance. *Linear Algebra and Its Applications*, 435(10):2491–2506, 2011.