Hydraulic Design of Pine Needles

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3 Calculus of Variations
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Original Paper

This presentation for our AMATH 507 class and the Master's Symposium is based on the paper of M.A. Zwieniecki, H.A. Stone, A. Leigh, C. K. Boyce, N.M. Holbrook, (2006) Hydraulic design of pine needles: one-dimensional optimization for single-vein leaves. Plant, Cell and Environment 29, 803-809. The outline of this talk will be very similar to that of the paper, except that I supplemented math details about the second variation to justify that their solution is indeed a minimal to the optimization problem.

Water: the necessity of Life

- Why hydraulic design?
- Why pine needles?

Figure: The complex venation of a leaf. Photograph taken by Flickr user Surajram Kumaravel and found by Google Image Search.

Pine Needles: Single Vein Leaves

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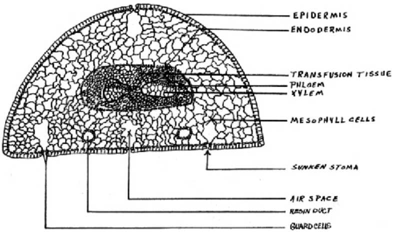

Figure: Cross section of a pine needle: sketch picture found by Google Image Search on the course page of BIO 1020 Spring 2009 in Volunteer State Community College

Why is pressure important?

- Pressure and turgor
- Stomata and transpiration

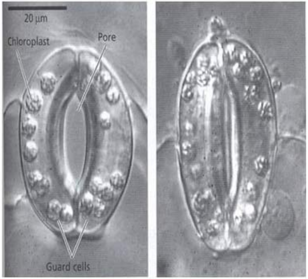

Image reproduced from Plant Physiology, Eds: L. Taiz and E. Zeiger, 2nd edition, Sinauer Associates, Inc. Publisher, Sunderland MA, USA. p. 523

Figure: Photo of closed and open stomata

Pressure Distribution Model: Boundary Conditions

- Take a needle as in Figure 1 and set up cylindrical coordinates, calling our axial variable z.
- Assume the pressure at the needle base is $p = p_{base}$. We assume that all water flowing into this single leaf has evaporated after traveling through distance l, meaning there is no fluid flux in the axial direction at the leaf tip, so we can prescribe that at $z = l$, $u = 0$, thus $\frac{dp}{dz} = 0$ by the Darcy's Law.

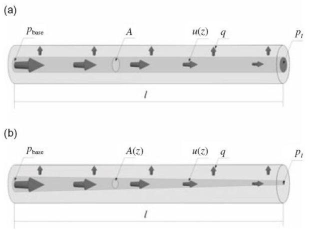

Figure 1. Model representation of a pine needle as a one-dimensional distribution system. (a) Control model of the needle with xylem cross-sectional area independent of length. (b) Model of the needle with xylem cross-sectional area functionally related to distance from the needle base. p_{base}, pressure at the needle base; A, cross-sectional area of the tracheid lumens; $u(z)$, fluid velocity; q, evaporation rate per needle length; p_l, pressure at the needle tip; l, needle length; $A(z)$, tracheid lumen cross-sectional area.

Initial Development

As an initial development, let the cross-sectional area of the tracheid lumens be a constant A. Denote the evaporation rate(per vein length) to be q, the water velocity(as a function of z) to be u. If we examine a section between z and $z + \Delta z$, the mass balance can be written as

$$A[u(z) - u(z + \Delta z)] - q\Delta z = 0$$

Dividing both sides by Δz and let Δz approach 0, we obtain

$$\frac{du}{dz} = -\frac{q}{A}$$

Let p(z) be the hydrostatic pressure, then Darcy's law gives the relationship between u and p:

$$\frac{dp}{dz} = -\frac{\mu u}{k}$$

where k is the xylem permeability and μ is the viscosity of the liquid.

Initial Development

Combining the two equations to eliminate u, assuming that q, A, μ and k are all constants, we obtain a differential equation about p: x

$$\frac{d^2p}{dz^2} = \frac{\mu q}{kA}$$

Integrating twice gives

$$p(z) = \frac{\mu q}{2kA} z^2 + c_1 z + c_2$$

Applying boundary conditions, we obtain

$$p(z) = p_{base} + \frac{\mu q l^2}{2kA}[(\frac{z}{l})^2 - 2\frac{z}{l}]$$

Generalized Model

We now allow for axial variation in cross-sectional area A of the xylem, so A is now $A = A(z)$. The evaporation rate (per needle length) q is still assumed to be a constant along the length of the needle. It would also be nice to variate the permeability parameter k, but the authors chose to assume that tracheid dimensions are uniform along the needle, meaning k remains a constant.
The mass balance equation now becomes

$$\frac{d}{dz}[A(z)u(z)] = -q$$

Integrating once gives

$$A(z)u(z) = -qz + c_3$$

Applying the same boundary conditions in the initial development, we obtain

$$A(z)u(z) = q(l - z)$$

or

$$u(z) = \frac{q(l - z)}{A(z)}$$

Generalized Model

Substituting into the equation of Darcy's Law, we have

$$\frac{dp}{dz} = -\frac{\mu q(l-z)}{kA(z)}$$

Integrating both sides give us the pressure drop along the needle

$$\Delta p = p_{base} - p_{tip} = \mu q \int_0^1 \frac{(l-z)}{kA(z)} dz$$

Since we have assumed tracheid dimensions are uniform, the cross-section area $A(z)$ is proportional to the number of tracheids at position z along the needle.

Optimal Strategy

The optimal hydraulic ”design” of the pine needle we are studying translates to the function $N(z)$, denoting the distribution of tracheids, that minimizes the pressure drop along the needle, given a fixed total number of tracheids. In Math language, if we peel off some constants from the expression of pressure drop, the functional we are minimizing is

$$\int_0^1 \frac{1-(s)}{N(s)} ds$$

where $s = z/l$ translates to the relative distance from the needle tip, and the constraint is

$$\int_0^1 N(s) ds = constant = c_0$$

The boundary condition is $N(1) = 0$.

Calculus of Variations: Type of Problem

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- It is a degenerate problem: both the integral and the isoperimetric constraint integrand are independent of $N^{'}(s)$.
- It is a problem with loose-end boundary conditions: the $s = 0$ end for $N(s)$ is not fixed.
- It is a "singular" problem: at $s = 1$ the boundary condition implies the functional is an improper integral.
- It has isoperimetric constraints: we might have trouble verifying that our extremal is indeed a minimal.

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Calculus of Variations: Euler-Lagrange Equation

- As shown in George's talk, the extremal of loose-end problems actually belong to the same family of solutions to the Euler-Lagrange equation for fixed-end problems.
- Using a constant Lagrange multiplier λ, let $F = \frac{1-(s)}{N(s)} - \lambda N(s)$, then we have our Euler-Lagrange Equation

$$\frac{\partial}{\partial N}\left(\frac{1-(s)}{N(s)} - \lambda N(s)\right) = 0$$

- Solving this algebraic equation, we obtain

$$N(s) = \left(\frac{1-s}{-\lambda}\right)^{1/2}$$

- Substituting into the isoperimetric constraint, we obtain

$$\lambda = -\frac{4}{9(c_0)^2}$$

- The extremal candidate we obtain is

$$N(s) = \frac{3c_0}{2}(1-s)^{1/2}$$

Is this candidate really qualified?

- As we mentioned, we need to check if the boundary condition is satisfied. In this case, $N(1) = 0$ is satisfied.
- We then check if the candidate allows the target functional to be well-defined. In this case, we are relieved to see that the functional is convergent.

Is this really a minimal?

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- First of all, it is not a maximal: comparison with uniformly distributing tracheids along the needle shows the amount of improvement.
- The pressure drop for the uniform distribution $N_{uniform} = c_0$ is

$$\Delta p_{uniform} = \frac{\mu q l^2}{c N_{uniform}} \int_0^1 (1-s) ds = \frac{\mu q l^2}{2 c c_0}$$

  where c is the constant proportion between number of tracheids $N(s)$ and cross-section area $A(s)$
- The pressure drop for the minimal candidate distribution is

$$\Delta p_{min} = \frac{2\mu q l^2}{3 c c_0} \int_0^1 (1-s)^{1/2} ds = \frac{4\mu q l^2}{9 c c_0} = \frac{8}{9} \Delta p_{uniform}$$

- So we have reduced the pressure drop by about 10 percent.

Is this really a minimal?

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- Recall the way we attacked the isoperimetric constraints for a first variation: to find an extremum of the functional

$$J[y] = \int_a^b f(x, y, y^{'})dx$$

subject to restriction

$$K[y] = \int_a^b g(x, y, y^{'})dx = l$$

we introduced in class two small variation terms

$$y(x) = \hat{y}(x) + \epsilon_1\eta_1(x) + \epsilon_2\eta_2(x)$$

- In our class we let $I = J - \lambda K$, $F = f - \lambda g$ where λ is a Lagrange multiplier, and transformed the functional problem into a finite-dimensional calculus problem of optimizing $I(\epsilon_1, \epsilon_2)$ and letting

$$\frac{\partial I}{\partial \epsilon_1} = \frac{\partial I}{\partial \epsilon_2} = 0$$

to obtain our Euler-Lagrange equation as a first variation result.

Is this really a minimal?

- In the same finite-dimensional calculus framework, we notice that if we can prove

$$A = \frac{\partial^2 I}{\partial(\epsilon_1)^2} \tag{1}$$

$$= \int_a^b \left(\frac{\partial^2 F}{\partial y^2}(\eta_1)^2 + 2\frac{\partial^2 F}{\partial y \partial y'}\eta_1(\eta_1)' + \frac{\partial^2 F}{\partial y'_2}(\eta_1)'^2\right)dx \tag{2}$$

$$B = \frac{\partial^2 I}{\partial \epsilon_1 \partial \epsilon_2} \tag{3}$$

$$\tag{4}$$

$$= \int_a^b \left(\frac{\partial^2 F}{\partial y^2}\eta_1\eta_2 + \frac{\partial^2 F}{\partial y \partial y'}\eta_1(\eta_2)' + \frac{\partial^2 F}{\partial y \partial y'}\eta_2(\eta_1)' + \frac{\partial^2 F}{\partial y'_2}(\eta_1)'(\eta_2)'\right)dx$$

$$\tag{5}$$

$$C = \frac{\partial^2 I}{\partial(\epsilon_2)^2} \tag{6}$$

$$= \int_a^b \left(\frac{\partial^2 F}{\partial y^2}(\eta_2)^2 + 2\frac{\partial^2 F}{\partial y \partial y'}\eta_2(\eta_2)' + \frac{\partial^2 F}{\partial y'_2}(\eta_2)'^2\right)dx \tag{7}$$

satisfy $A > 0$ and $AC - B^2 > 0$, then our solution of the Euler-Lagrange equation is garanteed to be a minimal.

Is this really a minimal?

- Notice that we did not use any fixed boundary condition in writing out A, B and C.
- In our degenerate case:

$$A = \int_a^b \frac{\partial^2 F}{\partial y^2} (\eta_1)^2 dx \tag{8}$$

$$B = \int_a^b \frac{\partial^2 F}{\partial y^2} \eta_1 \eta_2 dx \tag{9}$$

$$C = \int_a^b \frac{\partial^2 F}{\partial y^2} (\eta_2)^2 dx \tag{10}$$

- Substituting in the specific functions we have

$$A = \int_0^1 \frac{2(1-s)}{N^3} (\eta_1)^2 ds \tag{11}$$

$$= \int_0^{1-\epsilon} \frac{2(1-s)}{N^3} (\eta_1)^2 ds + \int_{1-\epsilon}^1 \frac{2(1-s)}{N^3} (\eta_1)^2 ds > 0 \tag{12}$$

This also justifies that at least our minimal candidate is not a maximal.

Is this really a minimal?

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- Proposition: In our case, $AC - B^2 > 0$ for any η_1, η_2 in the Hilbert space $L^2[0,1]$.
- Proof: Given any f, g in $L^2[0,1]$, define an inner product $(f,g) = \int_0^1 F_0 fgds$ where $F_0 = \frac{2(1-s)}{N^3}$.
- Check that this is indeed an inner product:

$$(i)(\alpha f, g) = \int_0^1 F_0 \alpha fgds = \alpha(f,g)$$

$$(ii)(f+g,h) = \int_0^1 F_0(f+g)hds = \int_0^1 (F_0 fh + F_0 gh)ds$$

$$= (f,h) + (g,h)$$

$$(iii)(f,g) = \int_0^1 F_0 fgds = (g,f)$$

$$(iv)(f,f) = \int_0^1 F_0 f^2 ds > 0$$

The last inequalify holds because of nonnegativity of F_0 and similar argument to $A > 0$.

Is this really a minimal?

- After defining this inner product, the inequality

$$0 \leq AC - B^2$$

follows from the Cauchy-Schwartz inequality

$$(f, g)^2 \leq (f, f)(g, g)$$

But the equality in Cauchy-Schwartz inequality only holds when

$$f = g$$

and in our case η_1 cannot equal η_2 because they were designed as correction terms to each other so as to fit the isoperimetric constraint. Thus we get our positivity.

- Since $C[0, 1]$ is contained in $L^2[0, 1]$, and we are only considering weak variations, the solution to the Euler-Lagrange equation in this case is indeed a minimal.

Mother Nature thinks so too

- The minimal distribution allows the needle to be longer if the pressure drop along the needle length is fixed:

$$\Delta p = \frac{\mu q (l_{uniform})^2}{2cc_0}$$

$$\Delta p = \frac{4\mu q (l_{max})^2}{9cc_0}$$

$$\frac{l_{max}}{l_{uniform}} = (\frac{9}{8})^{1/2}$$

- This result gives an optimal length increase of about 6 percent, allowing precious space for photosynthesis.

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Mother Nature thinks so too

P.Palustris, Greenwood Plantation, Thomasville, GA, USA.

Figure: P.Palustris, or Long-leaf Pine

Pinus Ponderosa, Arnold Arboretum, Harvard University, Jamaica Plain, Boston, MA, USA.

Figure: Pinus Ponderosa

P.rigida, Arnold Arboretum, Harvard University, Jamaica Plain, Boston, MA, USA.

Figure: P.rigida, or Pitch-Pine

Mother Nature thinks so too, sometimes

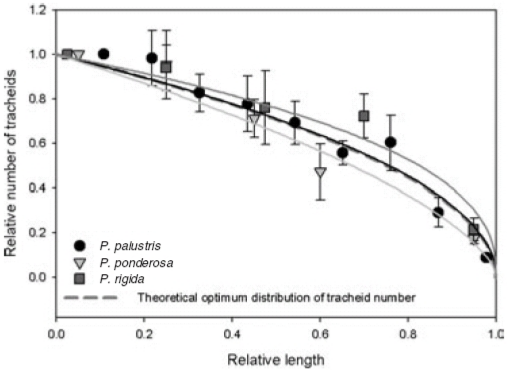

Figure 4. Measured axial distribution of tracheid number with fitted function based on Eqn 17. Optimum theoretical distribution is plotted as a reference line. The values were normalized to those of the leaf base ($z = 0$), where the absolute values for *Pinus palustris*, *Pinus ponderosa* and *Pinus rigida* were 290, 337 and 211, respectively. Error bars represent SD.

Summary

- The authors used calculus of variations to derive a model describing the investment strategy of water permeability along pine needles
- Based on their analysis of necessary conditions of an extremal, I discussed the justification of the solution being a minimal in a restricted function space
- The theoretical solution was compared with field study, and obtained amazingly good results

References

- M.A. Zwieniecki, H.A. Stone, A. Leigh, C. K. Boyce, N.M. Holbrook, (2006) Hydraulic design of pine needles: one-dimensional optimization for single-vein leaves. Plant, Cell and Environment 29, 803-809
- Boyer J.S. (1985) Water transport. Annual Review of Plant Physiology 36, 473-516
- Esau K. (1977) Anatomy of Seed Plants, 2nd edn, John Wiley & Sons, New York, USA.

Thank you!

Please cherish water.

Figure: Google logo on the World Water Day