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bot²

Estimating xylem vessel length distributions

4th Xylem International Meeting (Padua)

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University of Würzburg

September 25, 2019

Vessel length: the neglected dimension

- "The neglected dimension" (Comstock and Sperry 2000)
- Related to **hydraulic conductivity**
  - controls contribution of pit membranes to total flow resistance[1]
- Related to **embolism resistance**
  - longer vessels → more potential nucleation sites for emboli[1,2,3]
  - role in "embolism containment"[4]

⇒ **Important control variable for stability/efficiency trade-off**

- Putative role in length-related artifacts in hydraulic measurements[5,6]

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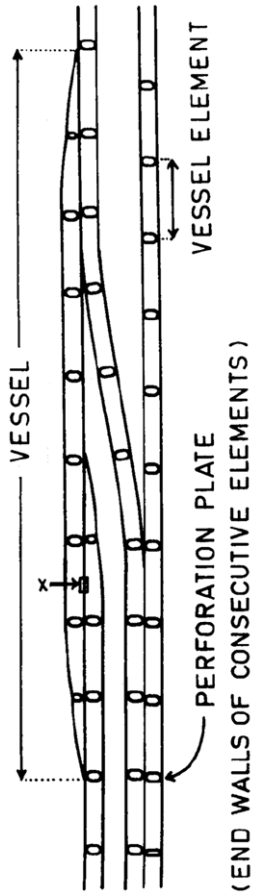

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  - not possible from longitudinal sections
  - not possible from macerations
- Instead: injection of a substance that passes through the lumen, but not pit membranes
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  $\Rightarrow$ vessels have to be cut to perform measurement

$\ldots$ true length distribution inferred from cut-off vessels

Figure: Zimmermann & McDonough (1978); in: Cai and Tyree (2014)

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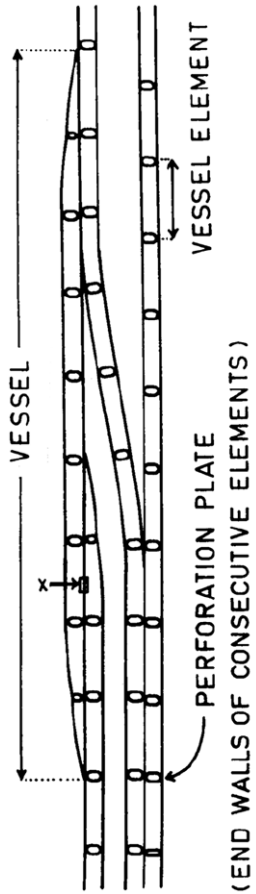

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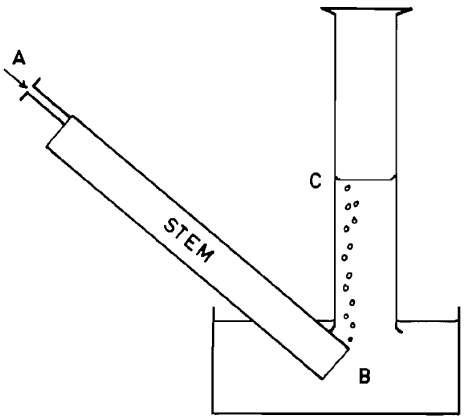

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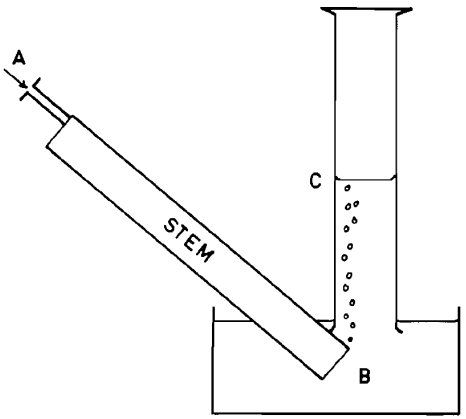

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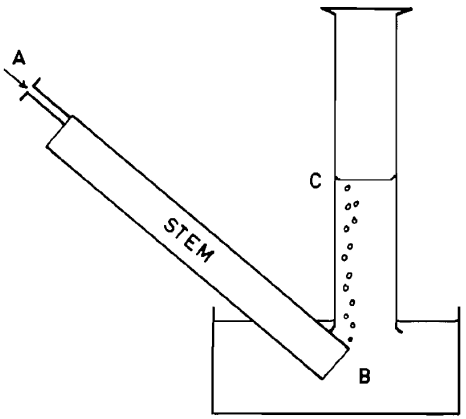

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Minimum set of assumptions* for VL estimates from silicon injection

1. vessels run in parallel and are unbranched
2. uniform distribution of end points along the stem
3. vessel lengths i.i.d. and independent of position
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Importance of simulation

- Indirect measurement that interferes with object of research
  - → validation with "true" data impossible
- Preparation for own measurements for PhD project
  - Simulation to establish minimum sample size / number of vessels
  - But: results do not add up...

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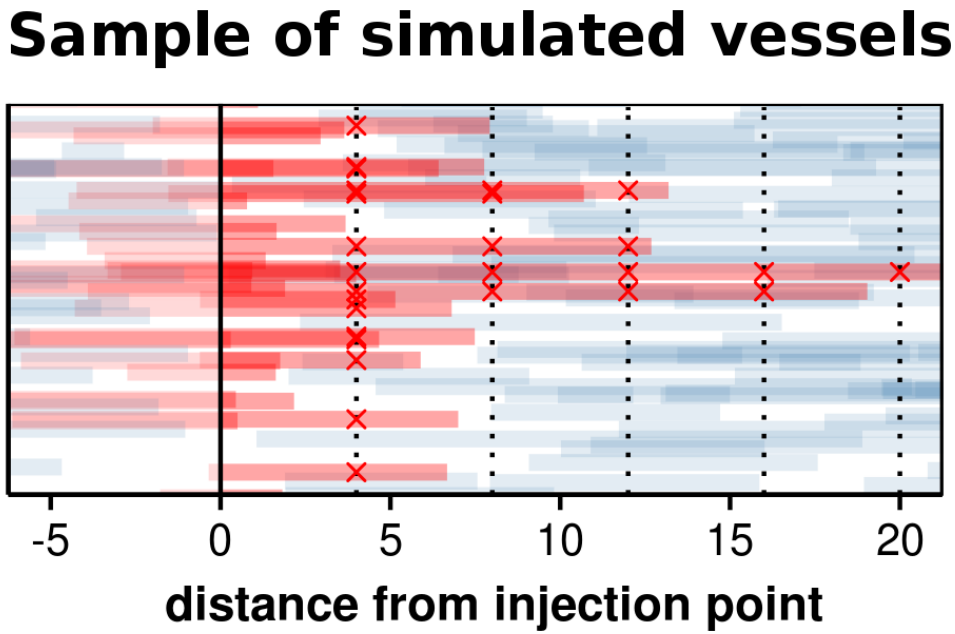

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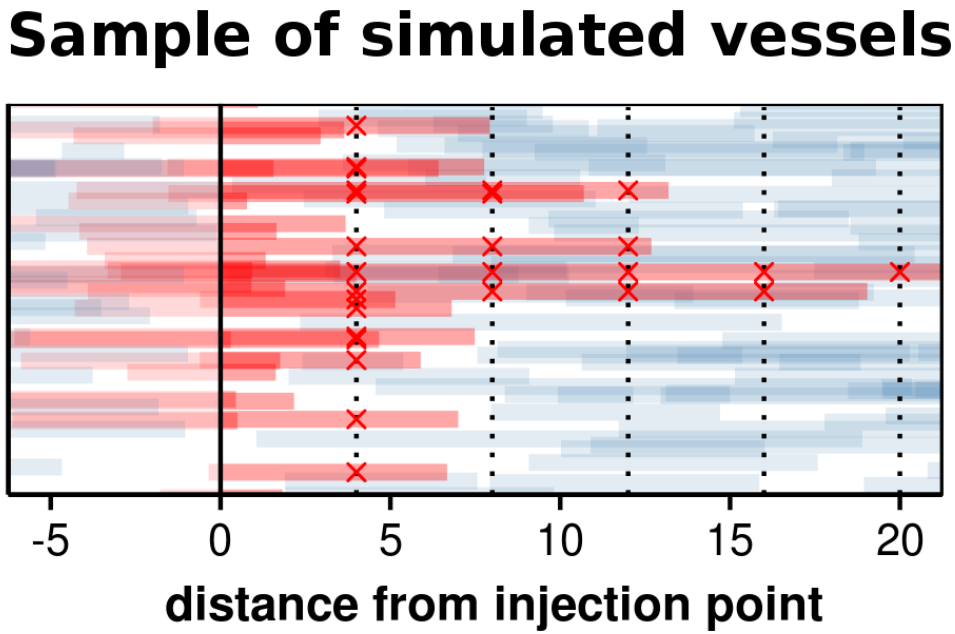

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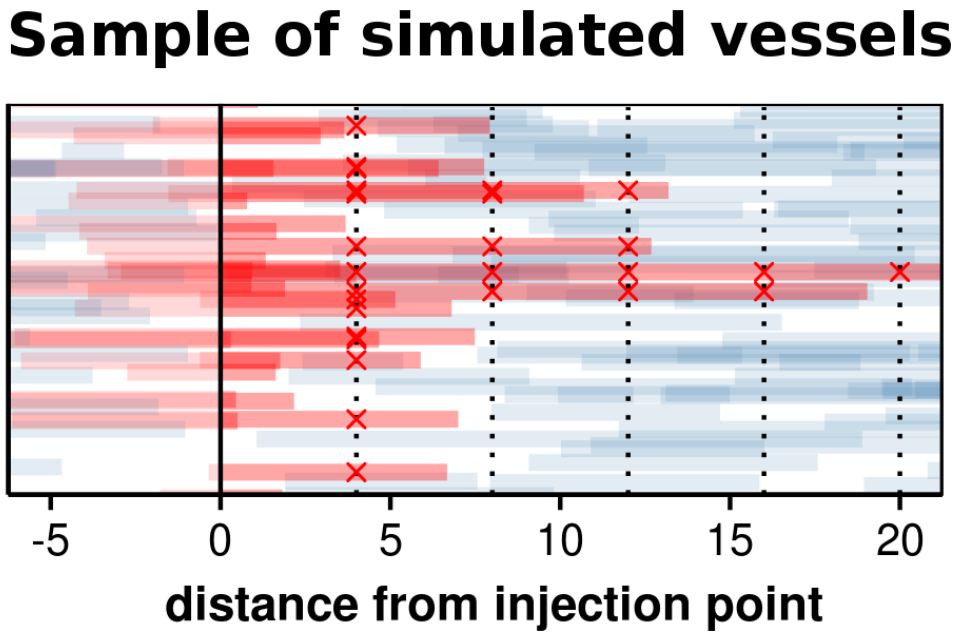

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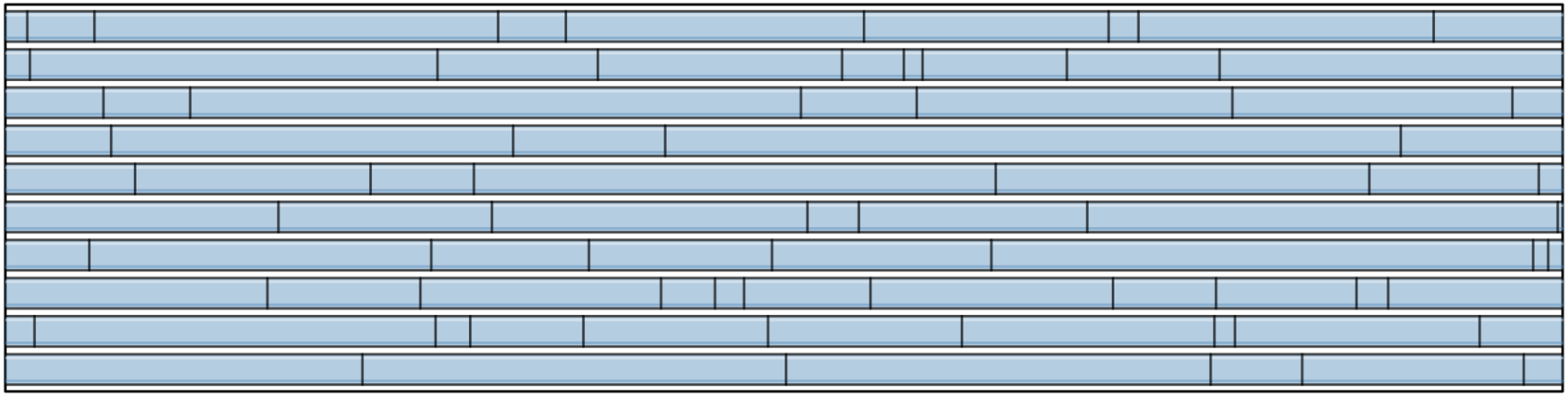
Four different ways to look at vessel length



- What's there
- Distribution of the length of all vessels in the wood sample irrespective of their position

$\Rightarrow$ **marginal vessel length distribution**

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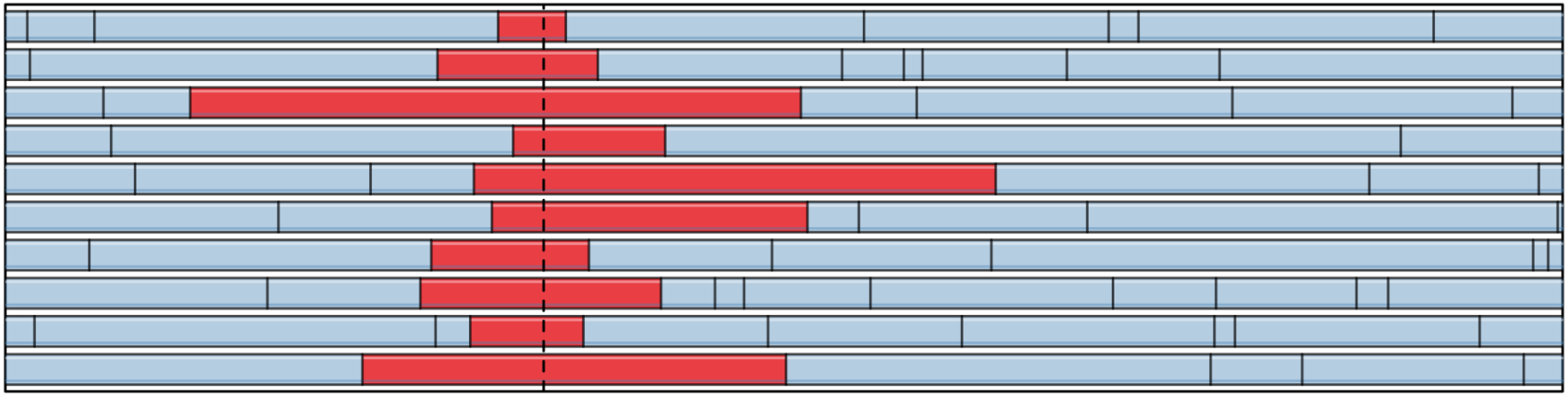

- What's in a cross-section
- Probability of a vessel to be cut depends on its length
- Resulting conditional length distribution of vessels in a cross-section:

$\Rightarrow$ **"Size-biased" length distribution** (Cox 1969)

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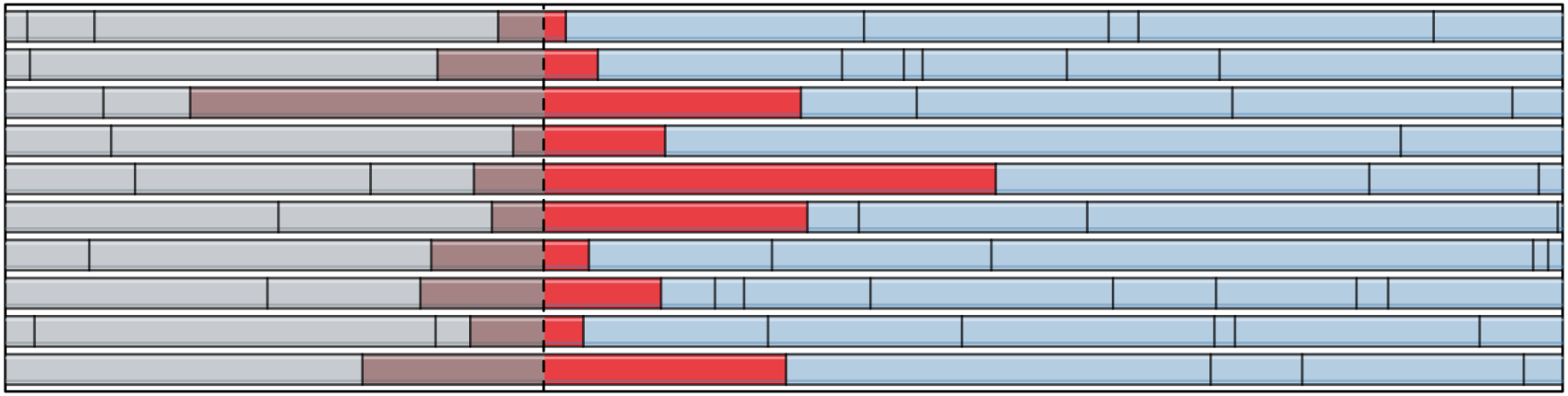

- What's left after cutting
- only a random fraction of the unknown original length

$\Rightarrow$ **length of cut-off vessel fragments**

Four different ways to look at vessel length

- What we actually measure
- Counts of stained vessels in each of a series of consecutive cuts

$\Rightarrow$ **Injection profile**

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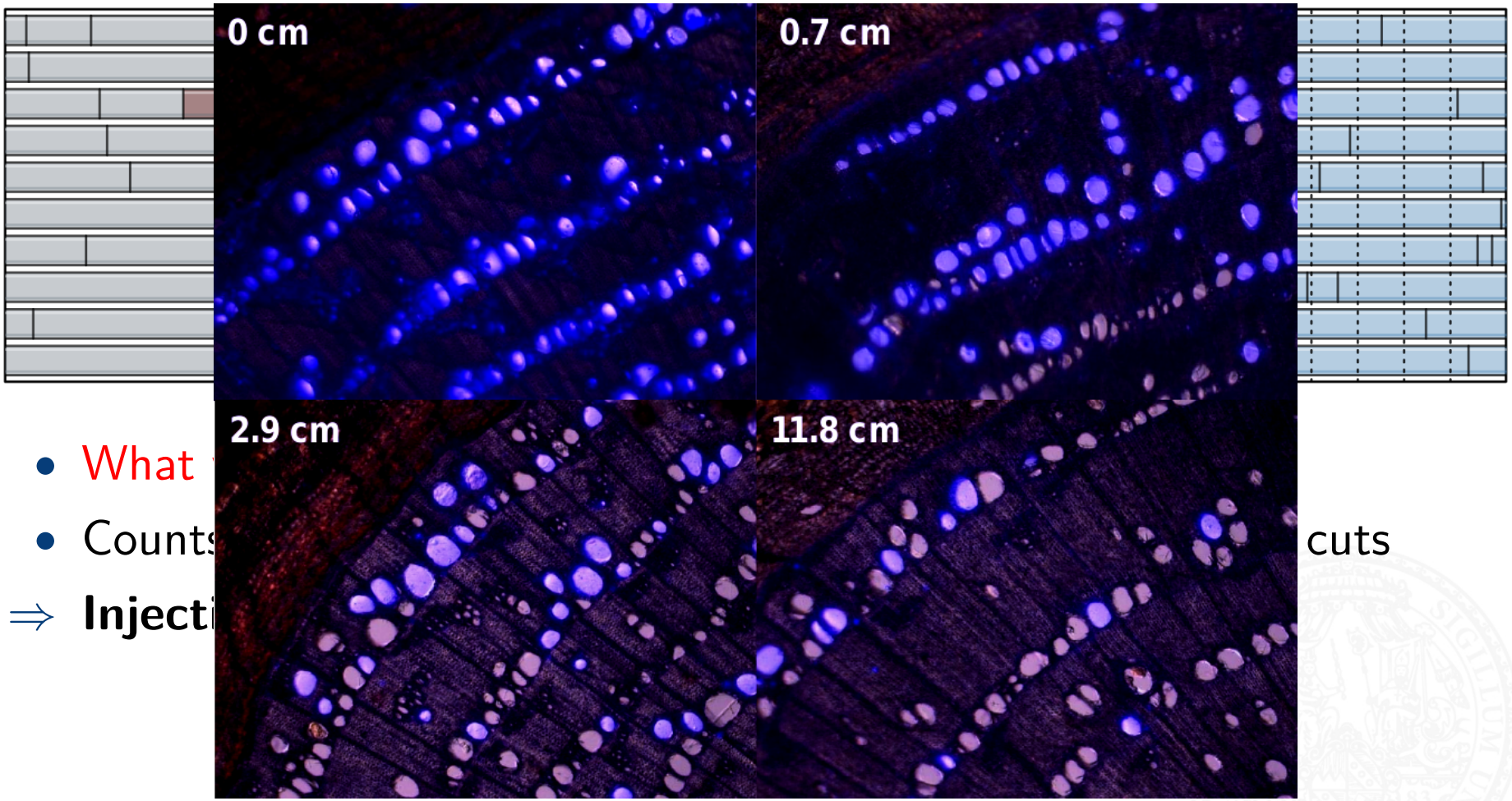

- What
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Foto: Jacobsen (2011), lab webpage (modified)

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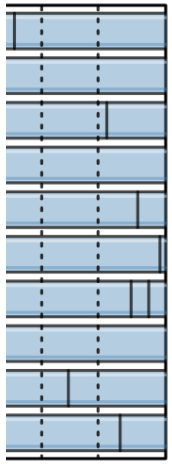

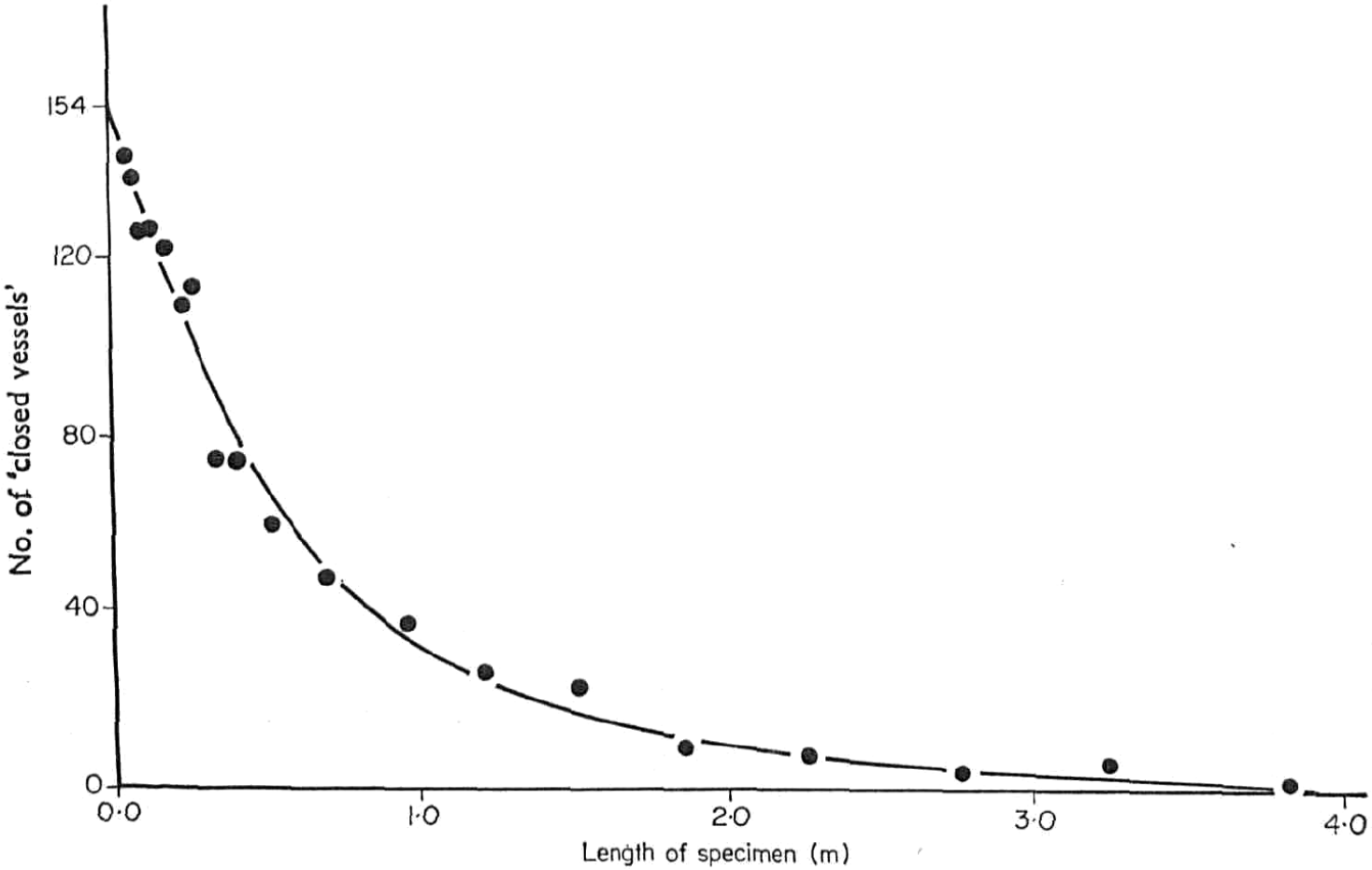

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Figure: modified from Milburn and Covey-Crump (1971)

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Literature survey:

- The most commonly used methods all estimate the **size-biased distribution**
  - Graphical method (Milburn and Covey-Crump 1971)
  - Double-difference algorithm (Zimmermann and Jeje 1981)
  - Differential form of DD algorithm (Cohen 2003)
- Very few **exceptions**[1,2,3]

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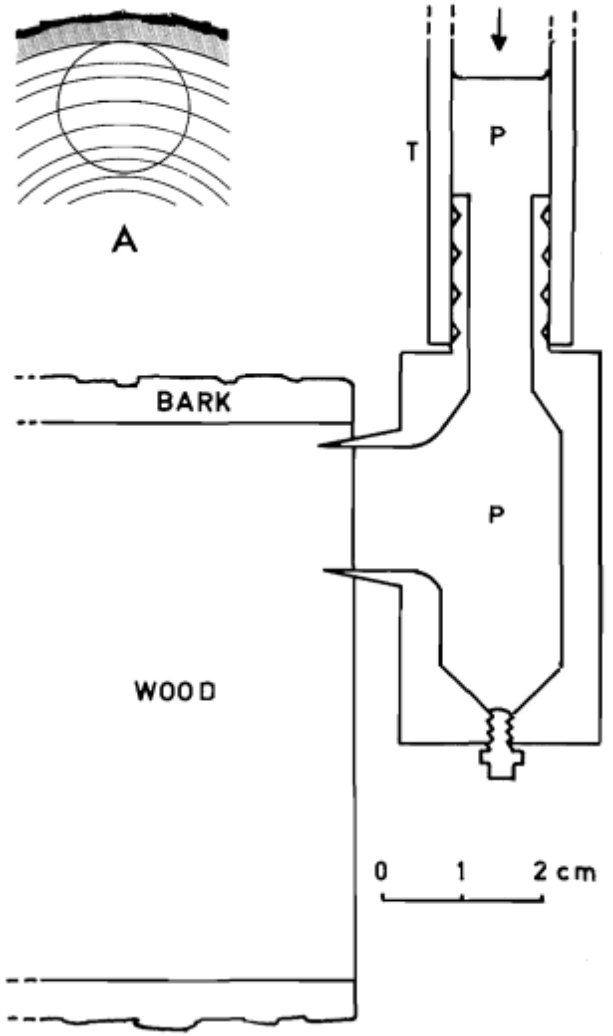

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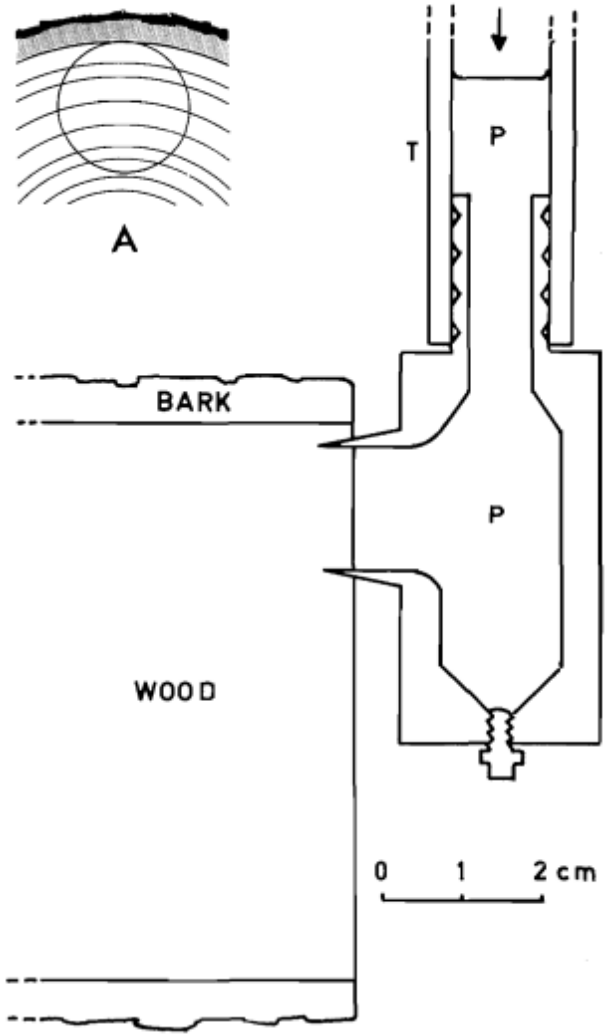

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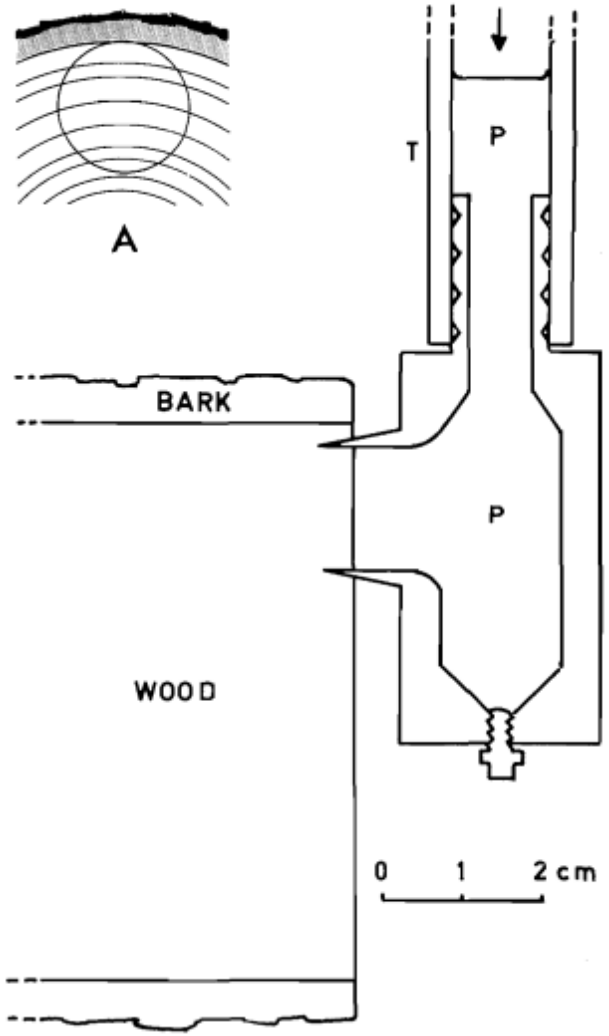

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- The average length of the marginal and size-biased VL distribution differ by up to a factor of 2!
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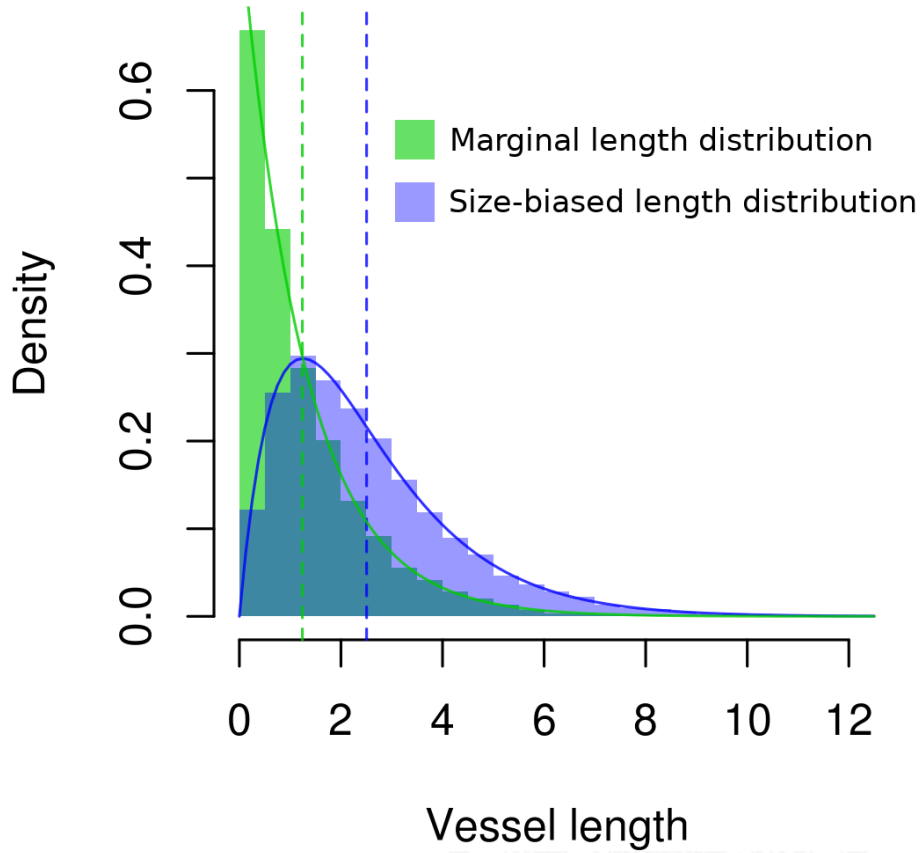
  - **Marginal distribution:** useful when focusing at the vessel level
  - **Size biased distribution:** useful when comparing VL to properties measured from cross-sections



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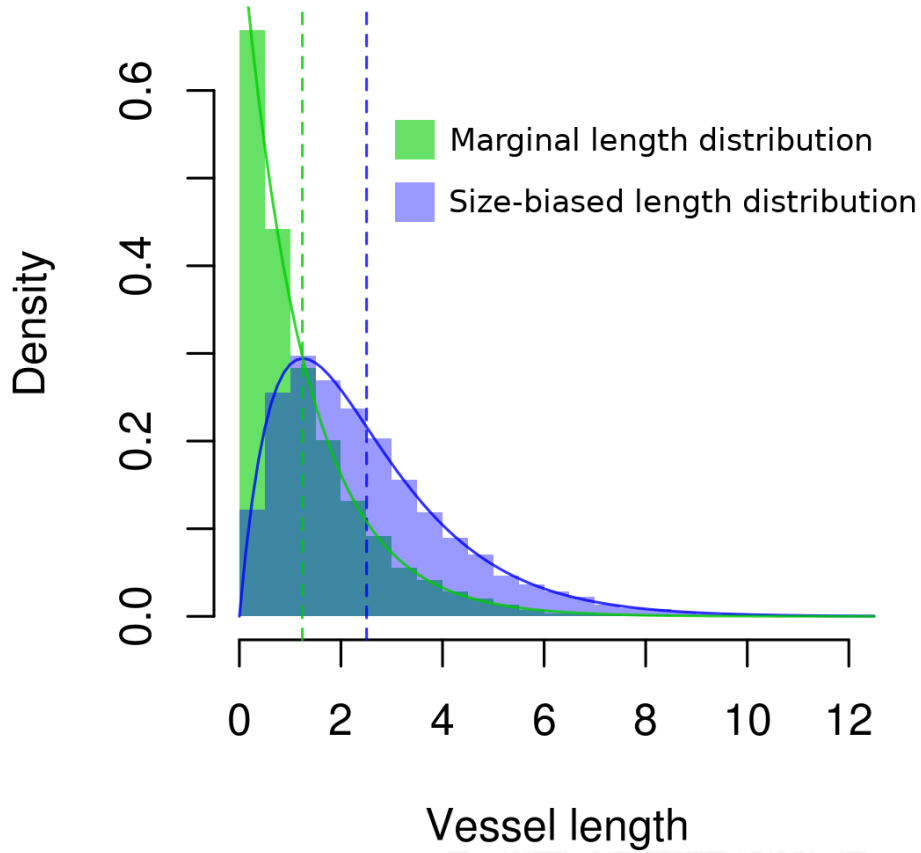

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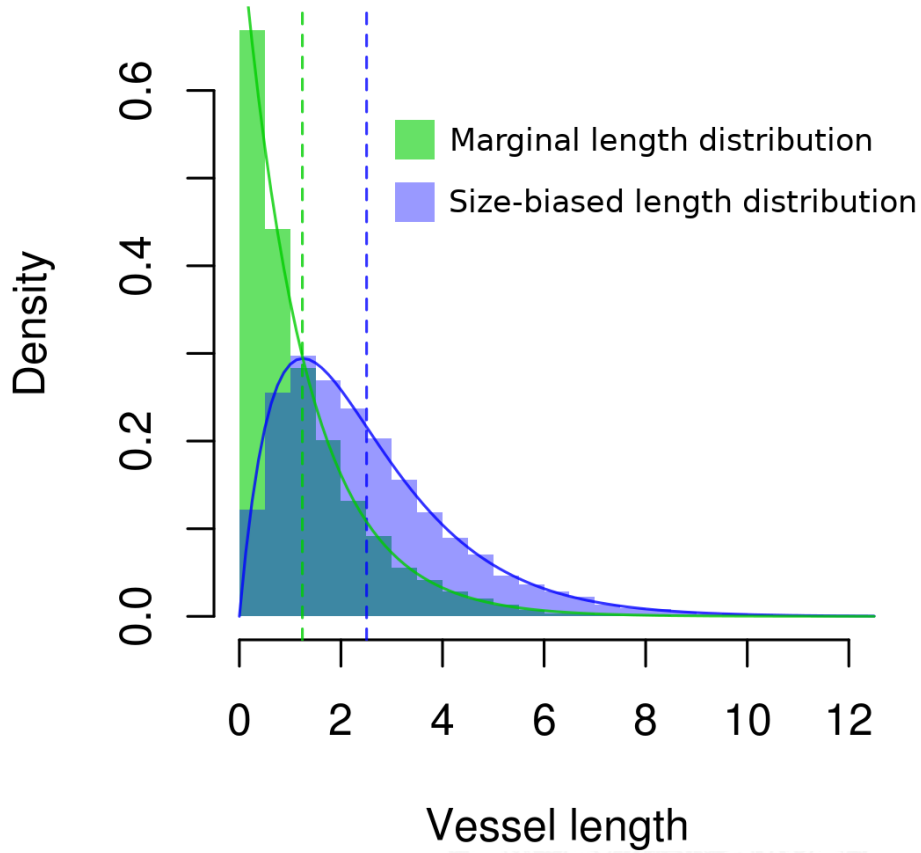

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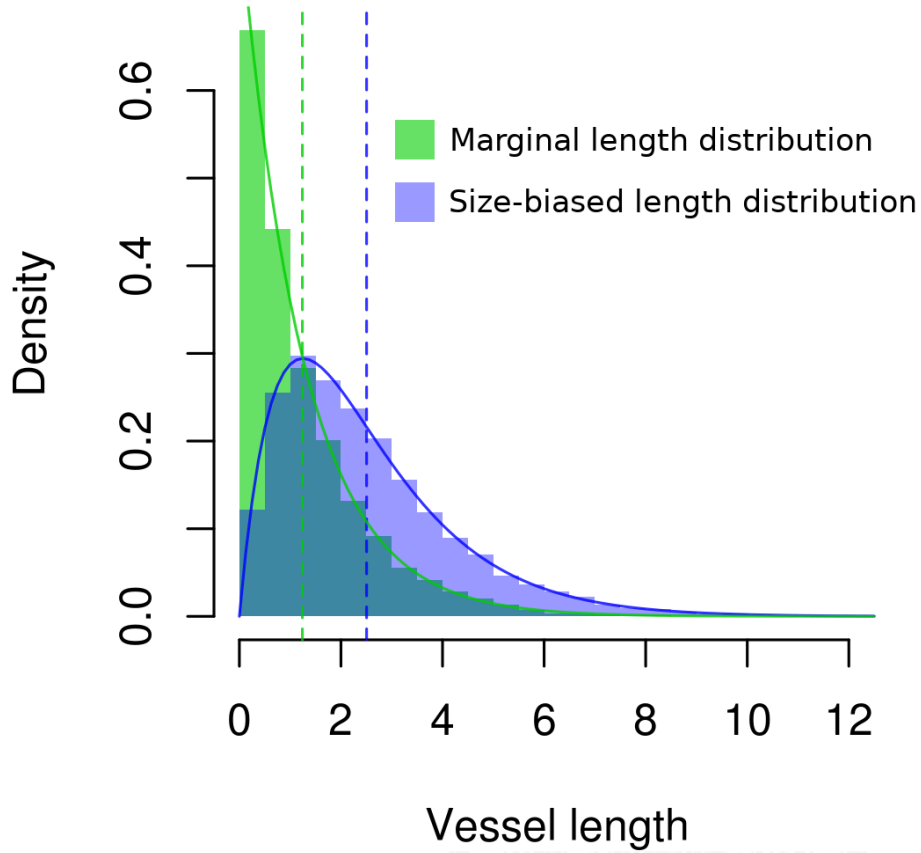

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- Estimators for two different counting methods incl. R-code

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   - example: allometric diameter-length scaling laws affect all vessels, not just the sample situated in a cross-section
   - wrong reference frame can obscure or even invert relationships
2. What **scale** is relevant for the processes you are studying?
   - example: allometric constraints act at the single-vessel level
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Important corollary

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→ Estimates of average vessel diameter etc. are potentially size-biased

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Summary

- **Vessel length can be characterized by different distributions**
  - Marginal distribution: focus on vessel level
  - "Size-biased" distribution (e.g. DD algorithm): focus on cross-sections

  → Choice of focus has important implications
- **Theory and tools for vessel length estimation: Link et al. (2018)**
- **Possible directions for future studies**
  - Model extension: more realistic model of vessel length
  - Analyses of bivariate length-diameter-distributions

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Thank you!
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Twitter: @RomanMLink

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