Thigmomorphogenesis: How trees respond to wind.

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Outline

• Brief historical overview of the past 205 years of thigmomorphogenetic research
• Comparison of Thigmomorphogenesis and Gravitropism in Woody Tissues
• Thigmomorphogenesis in Trees-
  – Wind drag and streamlining
  – Physiology and developmental anatomy
  – Biomechanics
• Applications in the urban forest
Trees can and will acclimate to prevailing windy conditions if given the chance! Trees can withstand heavy loading.
How do trees respond to wind and other mechanical stresses?

Trees can alter their canopy structure, growth rate, anatomy, morphology, and mechanical strength of their wood in response to wind.
Influence of mechanical stimuli on plants recognized at least since Theophrastus (300 B.C.E.)

Trees growing in windy environments were shorter in height, shorter internodes (more knots), less straight, closer grain, and harder wood.

“The region, in a word, must have good winds, this being not the same as to have no winds, and a windy region is definitely stunting to growth” (p215)

“…in windless and shaded places the trees always grow up erect and undistorted, with fewer knots and taller; whereas in well-ventilated, windward and sunny places, apart furthermore when among trees growing far apart, they do not do this to the same extent, since not only does lateral growth prevent height, but also the wind makes the trees rough, producing knots, because the winds check the movement of the food.” (pp 261-263)
First experiment with staked and free swaying apple trees (flexing: alternating tension and compression)

“If a tree be placed in a high and exposed situation, where it is much kept in motion by winds, the new matter which it generates will be deposited chiefly in the roots and lower parts of the trunk; and the diameter of the latter will diminish rapidly in its ascent. . . . the growth of the insulated tree on the mountain will be, as we always find it, low and sturdy, and well calculated to resist the heavy gales to which its situation constantly exposes it” p. 281
Metzger 1893

- Wind as the most significant or ‘Massgebender’ factor affecting growth of trees, regulating stem taper.
Schimper 1903

• “Vegetation of windy regions exhibits many peculiarities, which may be explained partly as due to direct action of the wind and partly as adaptations (acclimation) to withstand it”. Introduces the concept of elastic (growth response) and plastic (physical damage) strains
1954-1990: The ‘Renaissance’

- **Jacobs 1954**: Guying pines against wind sway, free swaying trees grew more in diameter over lower part of trunk than stayed trees.

- **Larson 1965**: Larch exposed to wind were shorter and thicker, also produced compression wood in some cases.
1954-1990:

- **Neel and Harris 1971**: Shaking stems of *Liquidambar* reduced growth by 70-80%.

- **Parkurst and Pearman 1972**: Height growth reductions could be due to cavitation, did not test.
Jaffe 1973:

- Tested 9 species, observed growth reductions in 6.
  - Coined the term **Thigmomorphogenesis** to describe the response as a way for plants to be protected from high winds and moving animals. (Cited 206 times)
  - Published a multitude of paper on thigmomorphogenesis during his career. Mostly on non-woody plants.
Stress and Strain relations in plants: Lessons from the world of mechanics

- Stress- applied force
- Strain- resultant deformation or change in the object or material being stressed (response)
- Tolerate the stress
- Avoid the stress
- Elastic deform.
- Plastic deform- Wounding
“We may say that the plant has the ability to respond to stress, but the notion stress is complex and will doubtless by future research be subdivided.” Newcombe 1895

<table>
<thead>
<tr>
<th>Pure Tension:</th>
<th>Pure Compression:</th>
<th>Sway:</th>
<th>Bending or displacement:</th>
</tr>
</thead>
<tbody>
<tr>
<td>pulling apart</td>
<td>pushing together</td>
<td>alternating compression and tension</td>
<td>Static compression and tension</td>
</tr>
<tr>
<td>Rare except in vines and tendrils</td>
<td>Self-loading-gravity on stem mass</td>
<td>Common due to wind induced sway</td>
<td>Common due to a number of environmental factors</td>
</tr>
</tbody>
</table>
External Mechanical Stress (load) compensated for by Internal Growth Strains:
A plant obtains an equilibrium with its mechanical environment.

After cutting, the stem was released from its mechanical equilibrium resulting in the trunk splitting.
Comparison of Thigmomorphogenesis and Gravitropism in Woody Tissues
Self-Loading: perceiving one’s own weight

**Euler’s Buckling**

\[ F = \frac{(K \pi^2 EI)}{l^2} \]

- \( F \) = maximum or critical force (vertical load on column)
- \( E \) = modulus of elasticity
- \( I \) = area moment of inertia
- \( l \) = unsupported length of column
- \( K \) = a constant for one end fixed and the other end free to move laterally \( K = 1/4 \);

**Critical Height**

\[ h_{\text{crit}} = \left( \frac{2.5Er^2}{\rho g} \right)^{1/3} \]

- \( \rho \) = density
- \( E \) = Young’s modulus
- \( r \) = radius vertical column of circular cross section

**Stem under compression load due to acceleration of Gravity**

**Stem failure (Euler’s Buckling) due to exceeding** \( h_{\text{crit}} \) (McMahon 1973)
Euler’s Buckling-

In *Larix* at Strbske Pleso after blowdown or windthrow event.
Self-loading and growth induced internal pressures (growth strains)

- Circumnutations- correction for self-support?
- Regulation of stem taper (allometry)
- Compressive force induce callus cell differentiation (Lintilhac & Vesecky, 1981; Barnett & Asante, 2000)
- Maintain organization of the vascular cambium (Brown & Sax, 1962; Makino et al., 1983)
- Induction of a vascular cambium and 2nd growth in Arabidopsis (Ko et al., 2004)
Gravitropism: sensing of differential loading on plasmamembrane?

Cell on tension side of stem

$T_A > T_B$

Cell on compression side of stem

$C_A < C_B$

Static load, or displacement meeting requirement of presentation time

Telewski 1993
Gravitropism: perceiving and reorientation with respect to the gravitational field

Statolith Hypothesis

Amyloplasts, starch grains, statoliths

Dr. Fred Sack, Ohio State University: www.biosci.ohio-state.edu/pcmb/osu_pcmb/people/fred_sack/sack_research_moss_grav_research.htm
Normal Angiosperm Wood

Tension Wood

Compression Wood
White Oak \((Quercus alba)\)

Eastern White Pine \((Pinus strobus)\)
Pressure Waves: Thigmorphogenesis

- Wind
- Water currents and tides
- Mechanical contact
  - Fungal penetration peg
  - Animals brushing past vegetation
  - Roots or stems pushing through soil
- Sound?
Pressure Waves: Thigmorphogenesis

Due to sway (damping) beyond vertical, presentation time requirement not met.

Thigmomorphogenesis in Trees-

- Wind drag and streamlining
- Physiology and developmental anatomy
- Biomechanics
Oaks in Lucca well exposed to wind
Mechanical Loads acting on a tree during winter

Evidence for a ‘long-term’ memory of loading during winter months (Valinger et al. 1994)

Telewski, F.W. 1982, Roan Mtn., N.C., U.S.A.
What is Streamlining?

• The ability of a tree to alter its canopy shape, either by breakage and loss of branches or by sweeping back of branches in response to a prevailing wind, thereby reducing drag upon the tree.
Not all species streamline alike!

• Streamliners (wind avoiders):
  – Eastern white Pine
  – Douglas fir
  – Ponderosa pine
  – True firs
  – Willow

• Non-streamliners (wind tolerators):
  – Austrian pine
  – Honey locust
### TABLE 2. Species comparison to greenwood biomechanical properties. Species are listed from most sensitive to least sensitive to crown deformation due to wind. Wood property data from Kretschmann [58]

<table>
<thead>
<tr>
<th>Species</th>
<th>Specific Gravity&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Modulus of rupture (kPa)</th>
<th>Modulus of elasticity (MPa)</th>
<th>Work to maximum load (kJ/m³)</th>
<th>Impact bending (mm)</th>
<th>Compression perpendicular to grain (kPa)</th>
<th>Shear parallel to grain (kPa)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Western Larch (&lt;i&gt;Larix occidentalis&lt;/i&gt;)&lt;sup&gt;c&lt;/sup&gt;</td>
<td>0.55-0.48</td>
<td>60,000-53,000</td>
<td>11,400-10,100</td>
<td>71</td>
<td>740</td>
<td>30,500-25,900</td>
<td>6,300-6,000</td>
</tr>
<tr>
<td>Tamarack (&lt;i&gt;Larix laricina&lt;/i&gt;)&lt;sup&gt;c&lt;/sup&gt;</td>
<td>0.48</td>
<td>47,000</td>
<td>8,600</td>
<td>-</td>
<td>-</td>
<td>21,600</td>
<td>6,300</td>
</tr>
<tr>
<td>Coastal Douglas fir (&lt;i&gt;Pseudotsugamenziesii&lt;/i&gt;)</td>
<td>0.45</td>
<td>53,000</td>
<td>10,800</td>
<td>52</td>
<td>660</td>
<td>26,100</td>
<td>6,200</td>
</tr>
<tr>
<td>Ponderosa pine (&lt;i&gt;Pinus ponderosa&lt;/i&gt;)</td>
<td>0.38</td>
<td>51,000</td>
<td>6,900</td>
<td>36</td>
<td>530</td>
<td>16,900</td>
<td>4,800</td>
</tr>
<tr>
<td>Balsam Fir (&lt;i&gt;Abies balsamea&lt;/i&gt;)</td>
<td>0.34</td>
<td>36,000</td>
<td>7,800</td>
<td>32</td>
<td>410</td>
<td>16,800</td>
<td>4,700</td>
</tr>
</tbody>
</table>

<sup>a</sup> Specific gravity is based on weight when oven-dry and volume when green.

<sup>b</sup> Modulus of elasticity measured from a simply supported, center-loaded beam, on a span depth ratio of 14/1. To correct for shear deflection, the modulus can be increased by 10%.

<sup>c</sup> Wade and Hewson [30] when discussing sensitivity to wind only reference <i>Larix</i> sp. but Owada [59] specifically studied <i>Larix leptolepis</i> (<i>L. kaempferi</i>). Unfortunately, greenwood data for this species was not presented in Kretschmann [58].

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Telewski 2012
Griggs-Putnam Index

Prevailing Wind Direction

I

II

III

IV

V

VI

Shrub-like Trees

VII
Different Frasier fir crowns exposed to different levels of wind on Roan Mtn., N.C.

Telewski & Jaffe 1986
Streamlining of crowns reduce wind loading by reducing the speed specific drag. Avoidance of stress by shedding the load.

Telewski & Jaffe 1986
THIGMOMORPHOGENESIS

Trees exposed to wind or flexed will not grow as tall, will have shorter branches and will have thicker stems and stronger roots.
Trees exposed to flexing are more wind firm
### Dose response to flexure or dynamic bending

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Leaf Area (cm²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Staked control</td>
<td>35.1 a</td>
</tr>
<tr>
<td>1 flexure</td>
<td>34.9 a</td>
</tr>
<tr>
<td>5 flexures</td>
<td>32.1 a</td>
</tr>
<tr>
<td>10 flexures</td>
<td>34.1 a</td>
</tr>
<tr>
<td>20 flexures</td>
<td>33.5 a</td>
</tr>
<tr>
<td>40 flexures</td>
<td>23.1 b</td>
</tr>
<tr>
<td>80 flexures</td>
<td>20.1 b</td>
</tr>
</tbody>
</table>

Telewski & Pruyn 1997 Tree Phys.
Mechanical Properties of Wood

• Strong in tension
• Weak in compression

• How do wood properties change in response to dynamic flexing (thigmo.) vs. static displacement (gravitropism)?
• Can wind induce reaction wood formation?
<table>
<thead>
<tr>
<th>Hybrid Treatment</th>
<th>Young’s Modulus</th>
<th>Second moment of area</th>
<th>Flexural stiffness</th>
</tr>
</thead>
<tbody>
<tr>
<td>47-174 Control</td>
<td>2.25 a</td>
<td>98.98 bc</td>
<td>2.46 bc</td>
</tr>
<tr>
<td>47-174 MP</td>
<td>2.02 b</td>
<td>191.60 a</td>
<td>3.76 a</td>
</tr>
<tr>
<td>H11-11 Control</td>
<td>2.51 a</td>
<td>81.48 c</td>
<td>1.98 c</td>
</tr>
<tr>
<td>H11-11 MP</td>
<td>2.33 ab</td>
<td>121.83 b</td>
<td>2.76 b</td>
</tr>
</tbody>
</table>
Flexure Wood in Conifers

- Intermediate between ‘Normal’ and Compression wood.
  - Increase in MFA
  - Increase in Wood Density
  - Sorter tracheid length
  - Slight increase in lignification

Telewski, F.W. 1989. Tree Physiology 5:113-121
Flexure Wood in Porous Wood
Angiosperms

• Will it be similar to Tension Wood? NO
  – Increase MFA angle (decrease in TW)
  – No significant change, slight increase in lignin content (decrease in TW)
  – No significant change in Glucose (cellulose) maybe slight decrease (increase in TW)
  – A few Gelatinous Fibers but not more than in control trees, but thicker fiber walls (increase in TW)
  – Reduced Vessel area (similar to TW)
  – Increase in Syringyl content (no change in TW)
Roots will respond to wind.

Photos: F.W. Telewski
The junction exposed to wind exhibited increased radial growth, with an increase in latewood density on the upwind side and an overall decrease in microfibrilar angle (increase flexibility) when compared to a junction from a less exposed site.

Jungnikl, Goebbels, Burgert & Fratzl
2009 Trees 23:605-610
Summary of structural changes in acclimation to windy environments

<table>
<thead>
<tr>
<th>Anatomy</th>
<th>Morphology</th>
</tr>
</thead>
<tbody>
<tr>
<td>• Increase in MFA</td>
<td>• Lower H:D (shorter-thicker stems) taper</td>
</tr>
<tr>
<td>• Increase in grain angle</td>
<td>• Smaller leaves</td>
</tr>
<tr>
<td>• Increased cell division in direction of</td>
<td>• Shorter internodes</td>
</tr>
<tr>
<td>flexing (increase I)</td>
<td>• Shorter branches</td>
</tr>
<tr>
<td>• Increased wood density</td>
<td>• Thicker branch junctions</td>
</tr>
<tr>
<td>• Increase lignification</td>
<td>• Streamlining</td>
</tr>
<tr>
<td>(increase S:G)</td>
<td>• Roots-</td>
</tr>
<tr>
<td>• Less stiff, more flexible</td>
<td></td>
</tr>
</tbody>
</table>
Applications in the Urban Forest
Incident Wind Speed = 10 m/s

MICHIGAN STATE UNIVERSITY

Min: 2.64E-02  Max: 2.61E+01
SW FLOW WIND VECTORS
400 x 400 metres
Height of *Gleditsia triacanthos* Around Michigan State University Library as a Function of the Predicted Mean Wind Speed

Tree Height = -1.38 * Wind Speed + 16.9

$R^2 = 0.63$
To Stake or Not to Stake?

Nursery stock?
To stake or not to stake?
Location, Location, Location?
Never say ‘NEVER’

• Never stake a tree
• Never leave a newly planted tree unstaked
How not to stake or guy a tree...

Don’t hold back!

Just in case gravity fails
Know the Facts:

- Site conditions
  - exposure
  - soil
- Species selection
- Nursery stock history
Site Conditions:

• Is the site exposed to wind?
• What is the prevailing wind direction?
  – If you select your own material from the nursery plots, mark the tree to identify the direction of the prevailing wind and align the tree in that direction when planting in the new site.
Site Conditions:

• Check soil type.
  – Sandy soils may be loose and will allow the root ball to rotate during strong winds.
  – Heavy soils may hold the ball well, but inhibit new root growth out of the ball.
  – Check the type of soil in the ball. Is the tree loose within the ball?
Species Selection

- Know what form you want in a mature tree canopy
  - Streamlined
  - Non-streamlined
- Select stronger wood varieties for windy locations
Nursery stock history

• Was the tree staked in the nursery?
• How ‘tightly’ were the trees planted in the field?
• How exposed was the nursery planting?
• What was the prevailing wind direction at the nursery?
• What type of soil was the tree grown in?
• Was the tree grown in a poly house or shade house for any period of time?
Ash and Honey Locust

Bradford Pear and Honey Locust

Prevailing wind

Bradford Pear

Photos: F.W. Telewski
Decision: To Stake

• If conditions require staking to prevent the root ball from rotating or to keep a weak nursery stock tree upright, the staking should be:
  – Loose to allow some stem movement to stimulate radial stem growth and root growth
  – Removed as soon as possible, preferably by the second growing season
Give the tree room to move in response to wind…
But not enough room so that it is blown over.

Check periodically for abrasion of the bark and remove guys as soon as roots have successfully anchored the tree.
What about cabling of trees? Does it impact biomechanics?
Acknowledgement

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