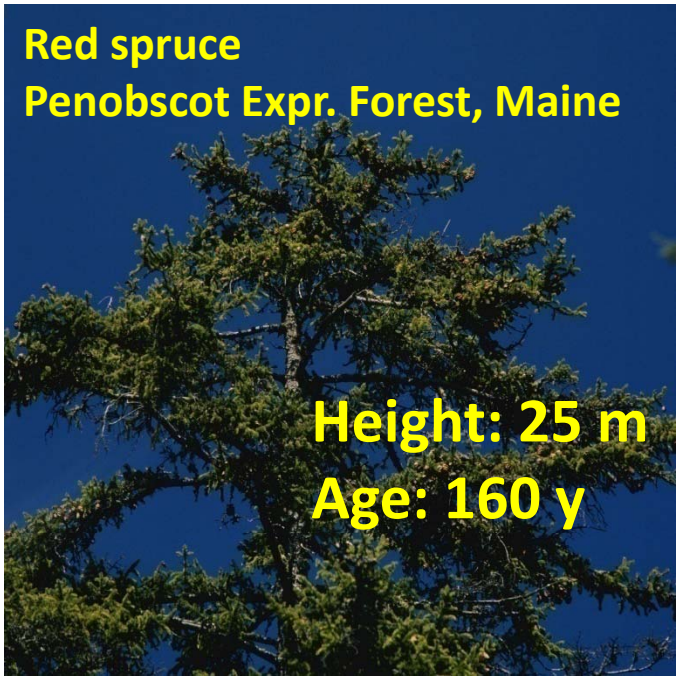
Development and growth-limits in temperate conifers: An evolutionarily stable perspective

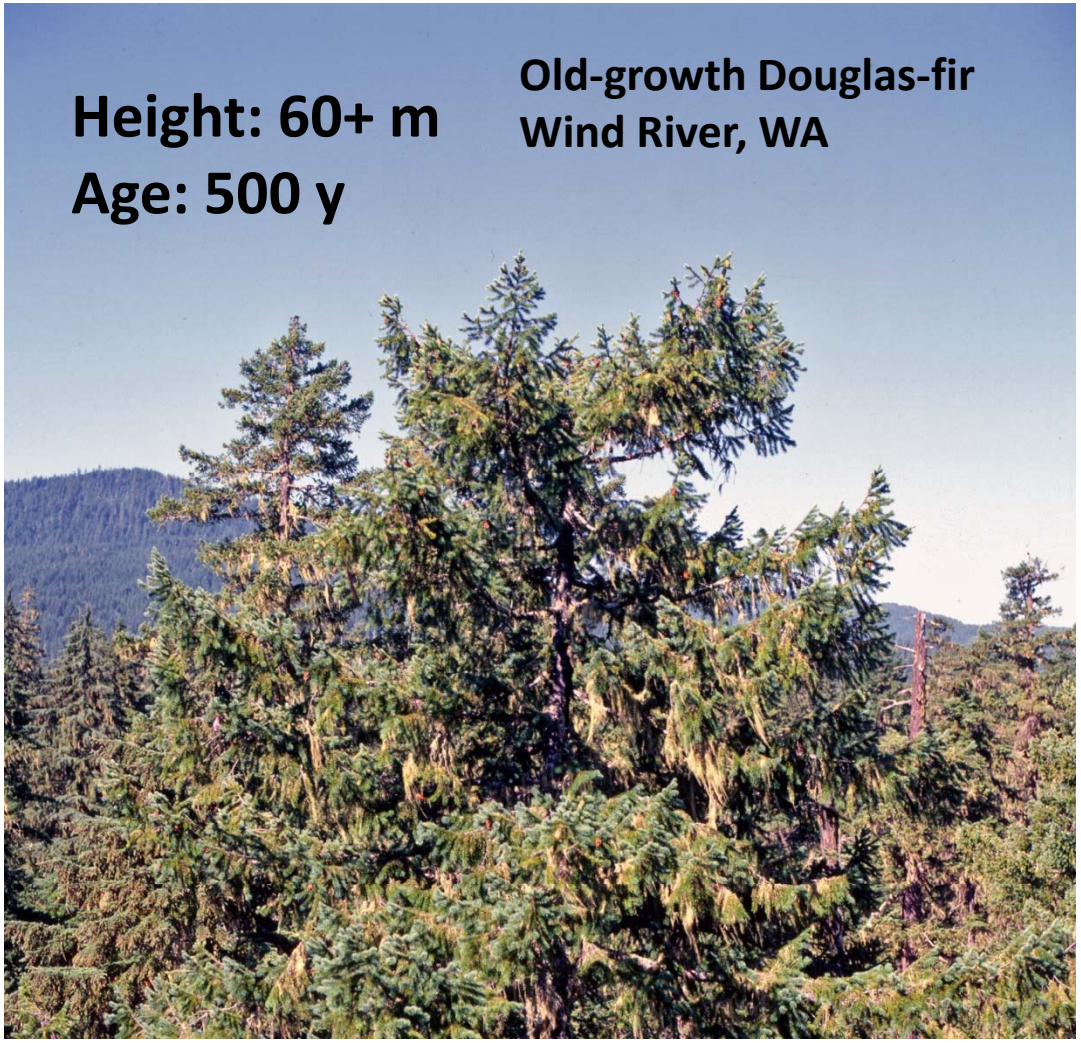
Michael E. Day
Michael S. Greenwood
Katherine S. Spencer

School of Forest Resources
University of Maine

Trees reach a point where *height growth* slows/ceases

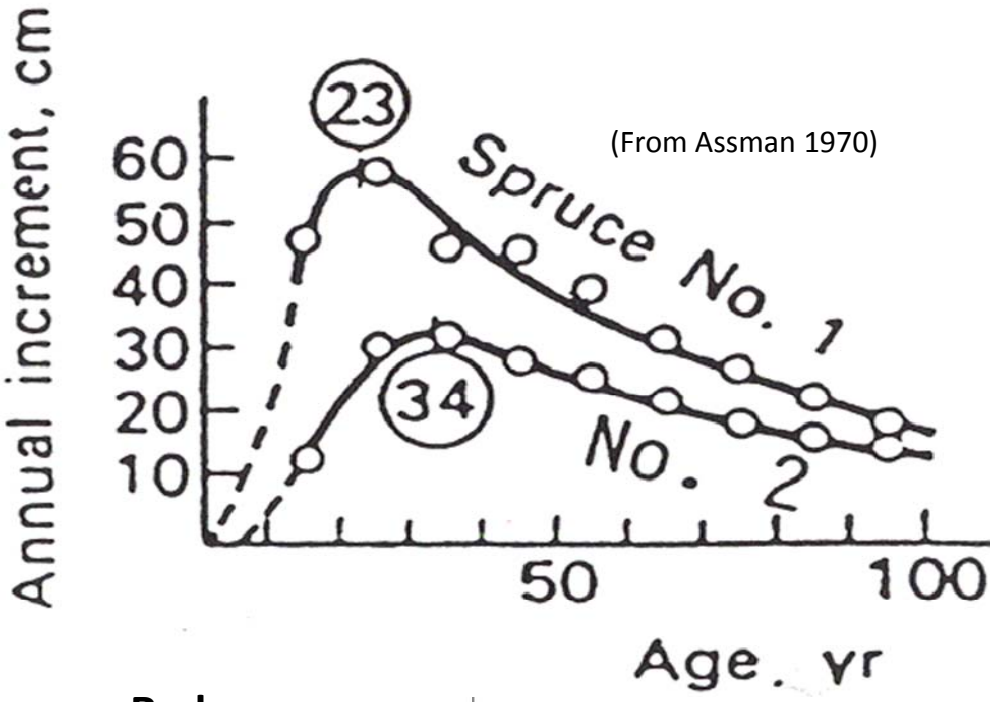
Tops characteristically flatten



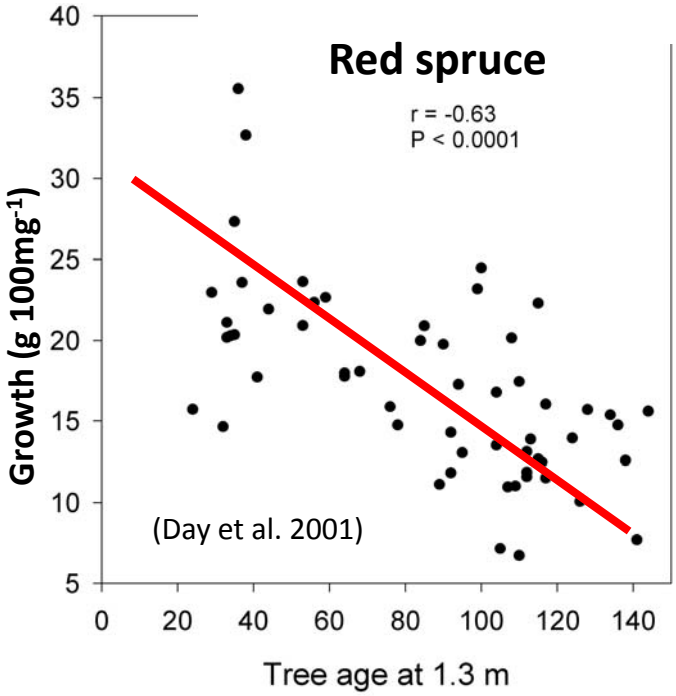


… as well as stem increment

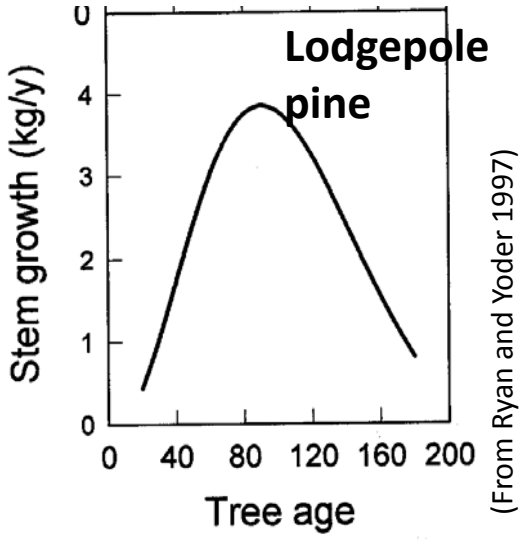
- Harvest age
- Carbon sequestration
- Woody tissue respiration?



(From Assman 1970)



(Day et al. 2001)

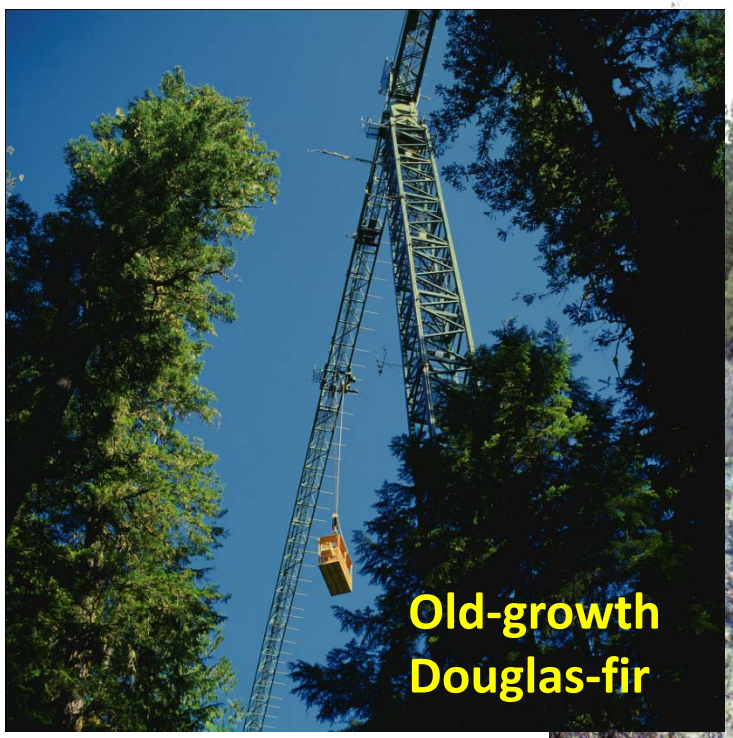


(From Ryan and Yoder 1997)

Supply-side explanations:

Physical or resource limitations

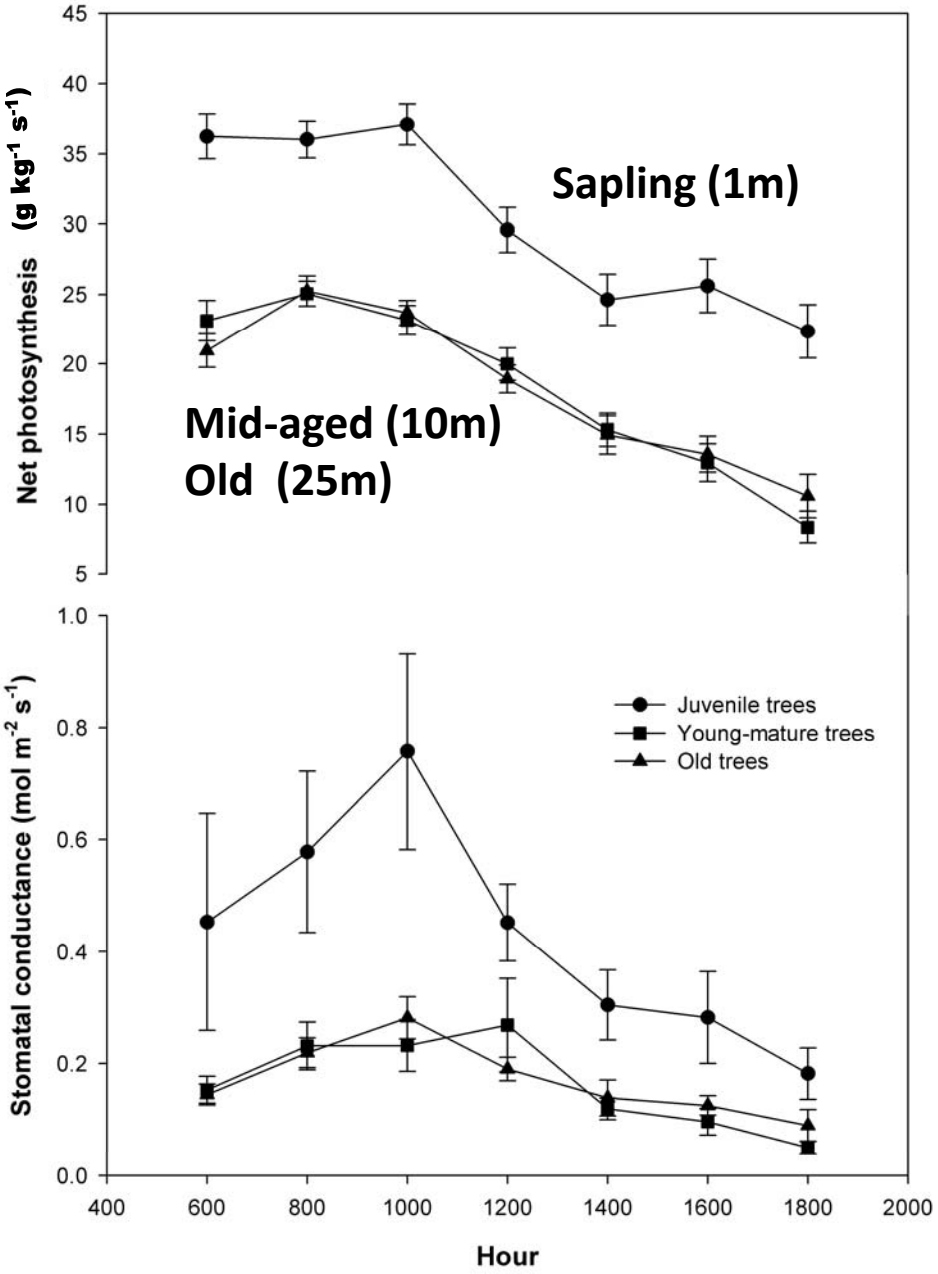
- Reduced nutrient supply
- Reduced photosynthesis (carbon supply)
- Hydraulic-limitations



Supply-side hypotheses in the Acadian Forest

Parameter	Juvenile	Mid-aged	Old
Foliar N (%)	1.0 [a]	0.94 [ab]	0.90 [b]
k_{tree} (µmol m^{-2} s^{-1} MPa^{-1})	3.9 [a]	2.1 [b]	2.3 [b]

Red spruce multi-cohort population
Penobscot Experimental Forest



Moving forward

Reciprocal grafting: a seven-year experiment

Exchanging scions between age classes to control for size & complexity effects

- **Extension growth was greater for all scions on mid-aged understock**
- **Branches cm^{-1} were greater for all scions on old understock**

Reciprocal grafting

- Old, mid-aged and young scions grafted into the tops of mid-aged and old trees took on the growth characteristic of the understock

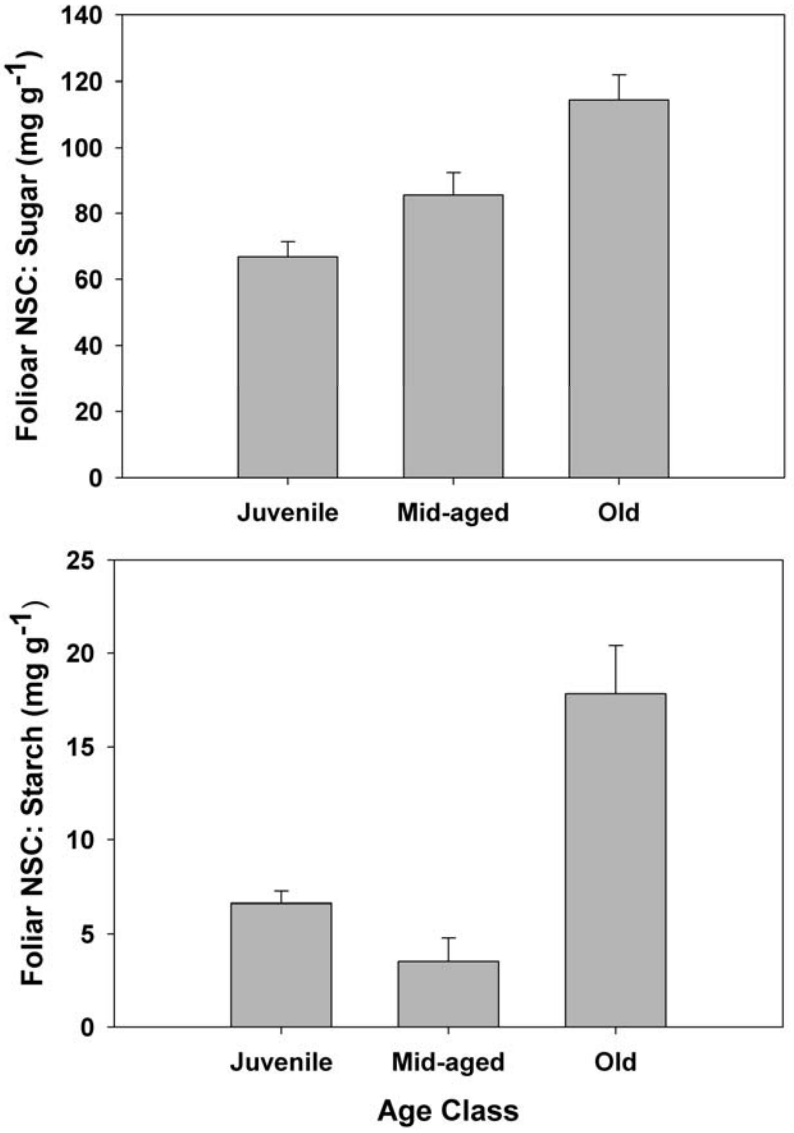
- Scions of all age classes grafted into tops of mid-aged and old trees exhibited equal biomass: identical growth potential

Natural branches on 165 y rootstock

Juvenile scions 7 y post-grafting

A look to the demand side

- **Non-structural carbohydrates (NSC) indicate C availability *relative to sink demand***
- **<u>And old trees show no indication of C-supply limitations</u>**

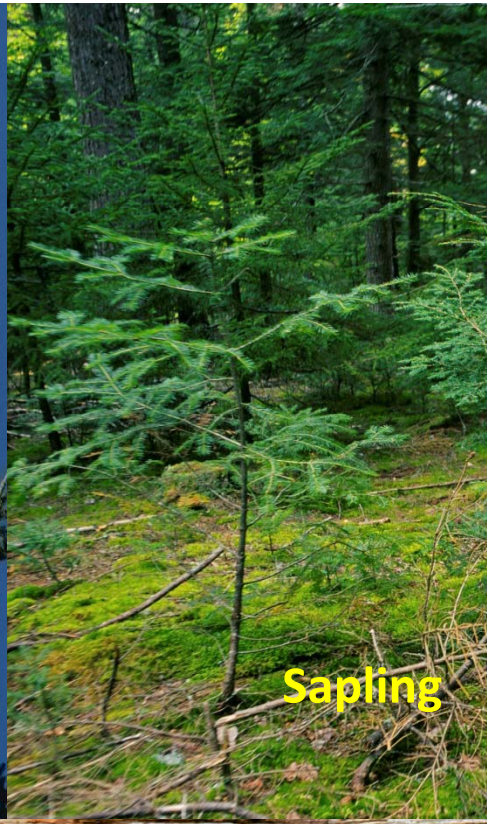


(From Day and Greenwood *In Press*)


Needed:
A new
paradigm
Cathedral Pines
Red pine
Eustis, Maine

Tree life stages and Evolutionarily / Ecologically Stable Strategies

- Germinant
- Seedling
- Sapling
- Mature
- Old-age



Germinants must find sources of water, nutrients and minimal light

- **Limited ability to sample environment**
- **Favors intrinsic genetic program**

Seedlings:

- **Maximize light capture**
- **Maintain understory carbon balance**
- **Resources allocated to branchiness**

Saplings:

- Gap detection
- Refocus allocation to main stem
- Branchiness greatly decreases
- ‘Low cost’ foliage

Mid-age:

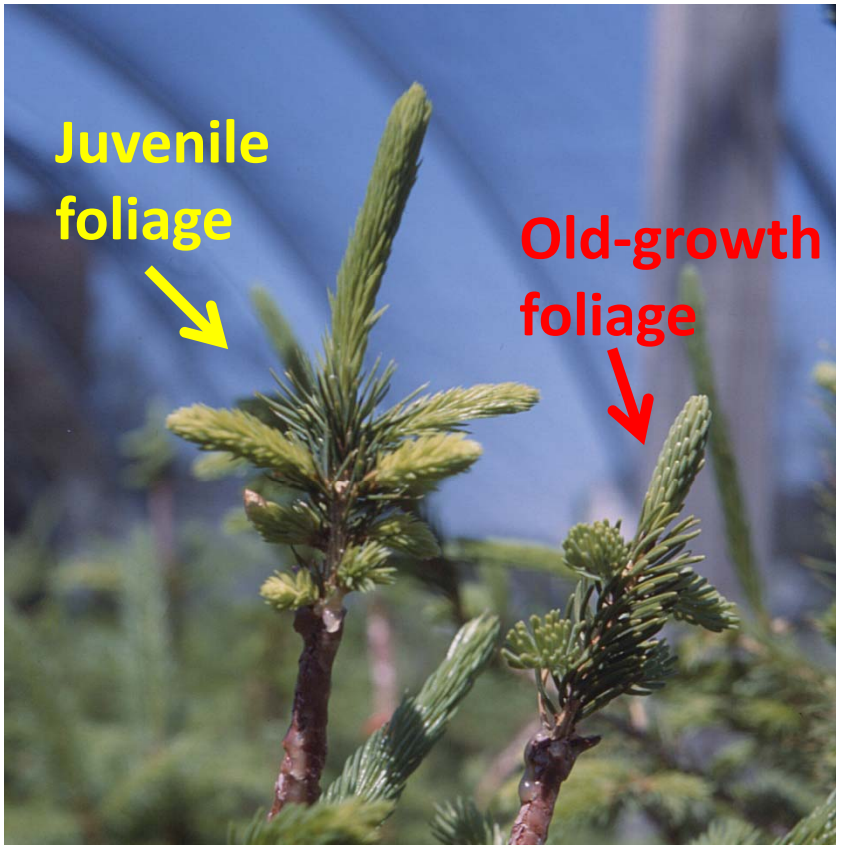
The race to the top

- **Resource allocation to height (extension) growth**

- **Bolewood production (PAI) at maximum**

Old age

- ‘Canopy-height’
- Extension growth slows



- Resource allocation
  - Branchiness
  - Robust foliage
  - Reserves

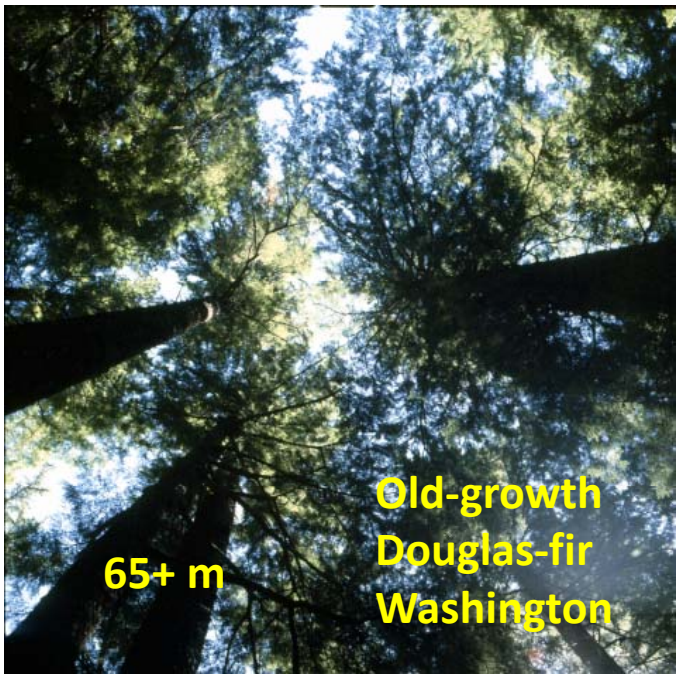
According to ESS height growth decreases:

- ‘Emergents’ face greater risk
- Minimizing strain minimizes stem cost
- ESS: tree maintains niche

Ecologically Stable Strategy model

- **Lower mutual canopies favored by *higher physical stress and higher probability of stochastic disturbance events***
  - **The feedback effect**

- **Height growth favored by 'run-away' *competition in relatively benign environments***
  - **The feed-forward effect**



Predictions of Ecologically Stable Strategy hypothesis:

- Trees have site-specific mean heights
- Maximizes long-term fecundity by lowering
  - competitive costs
  - risk to investment
- **Next chapter: Where does the carbon go?**

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