# The production ecology of forests: how species differ

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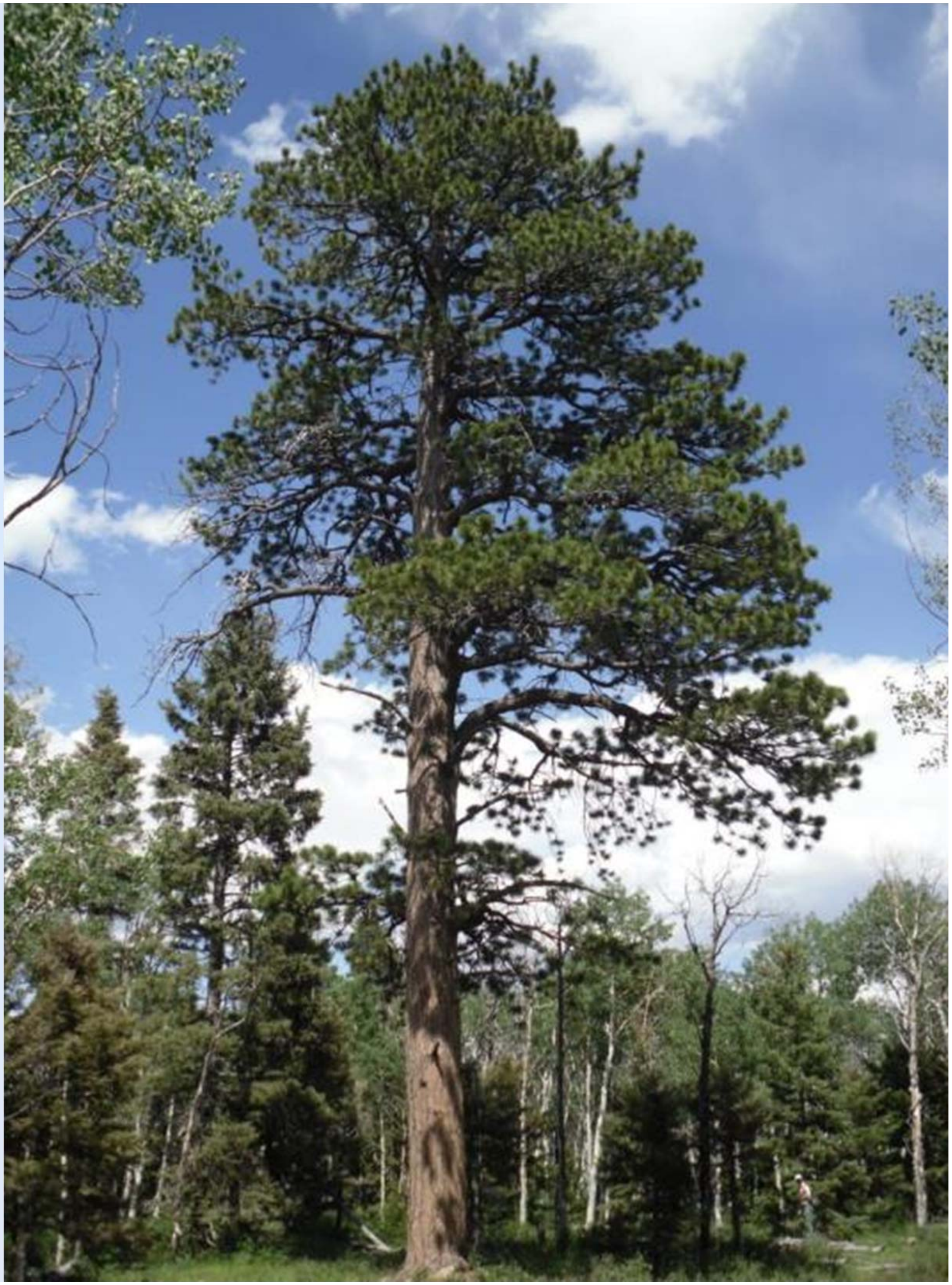
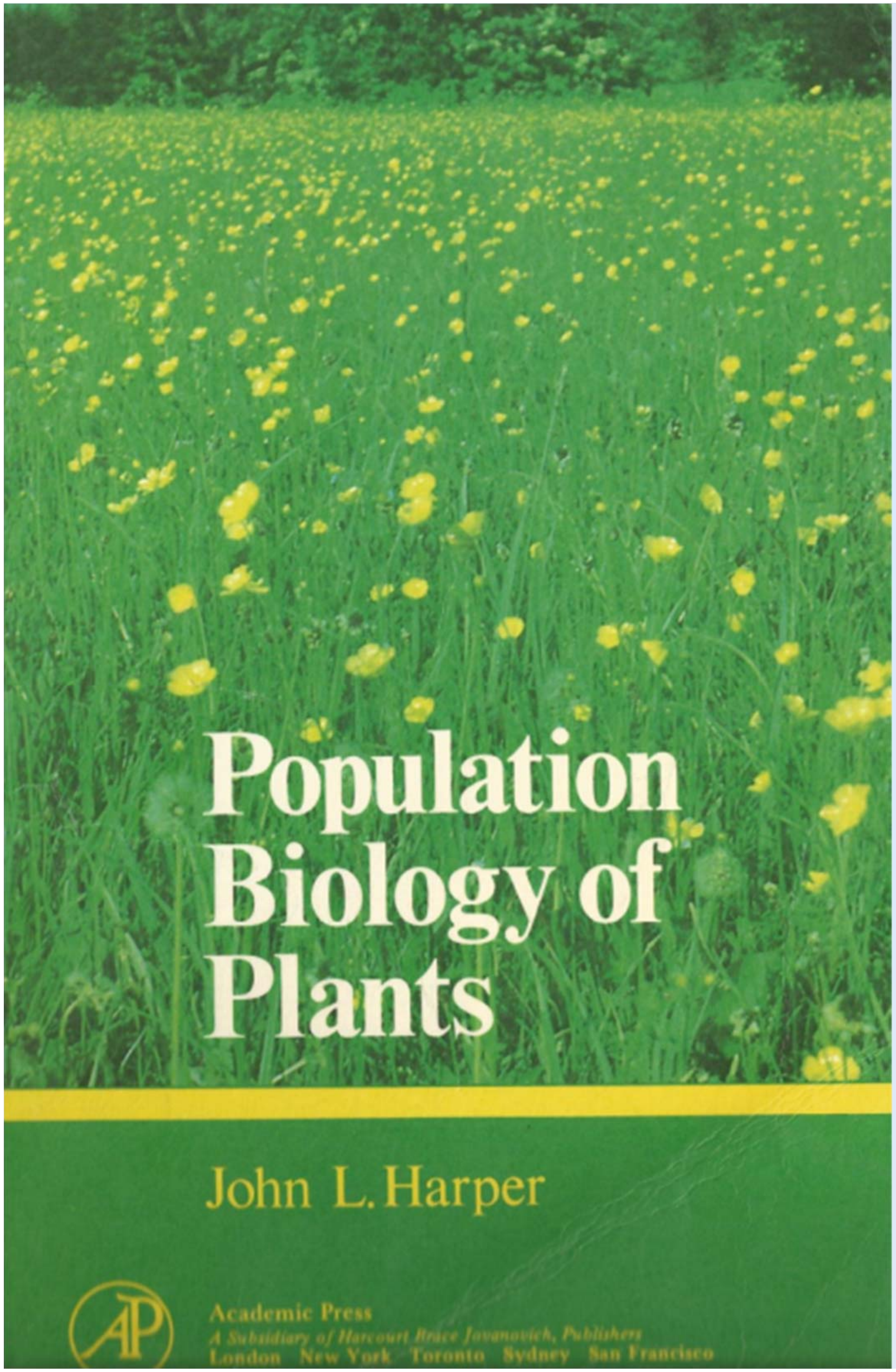
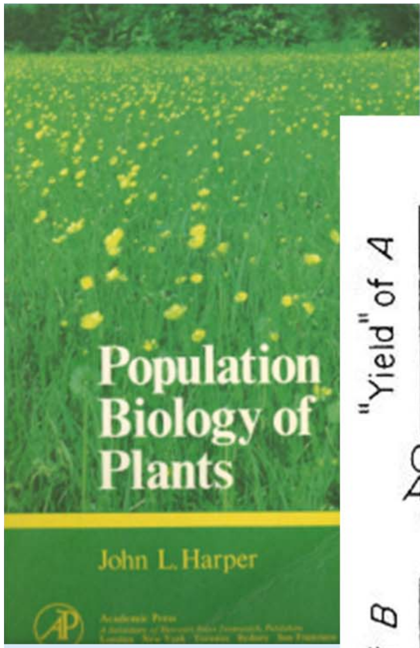


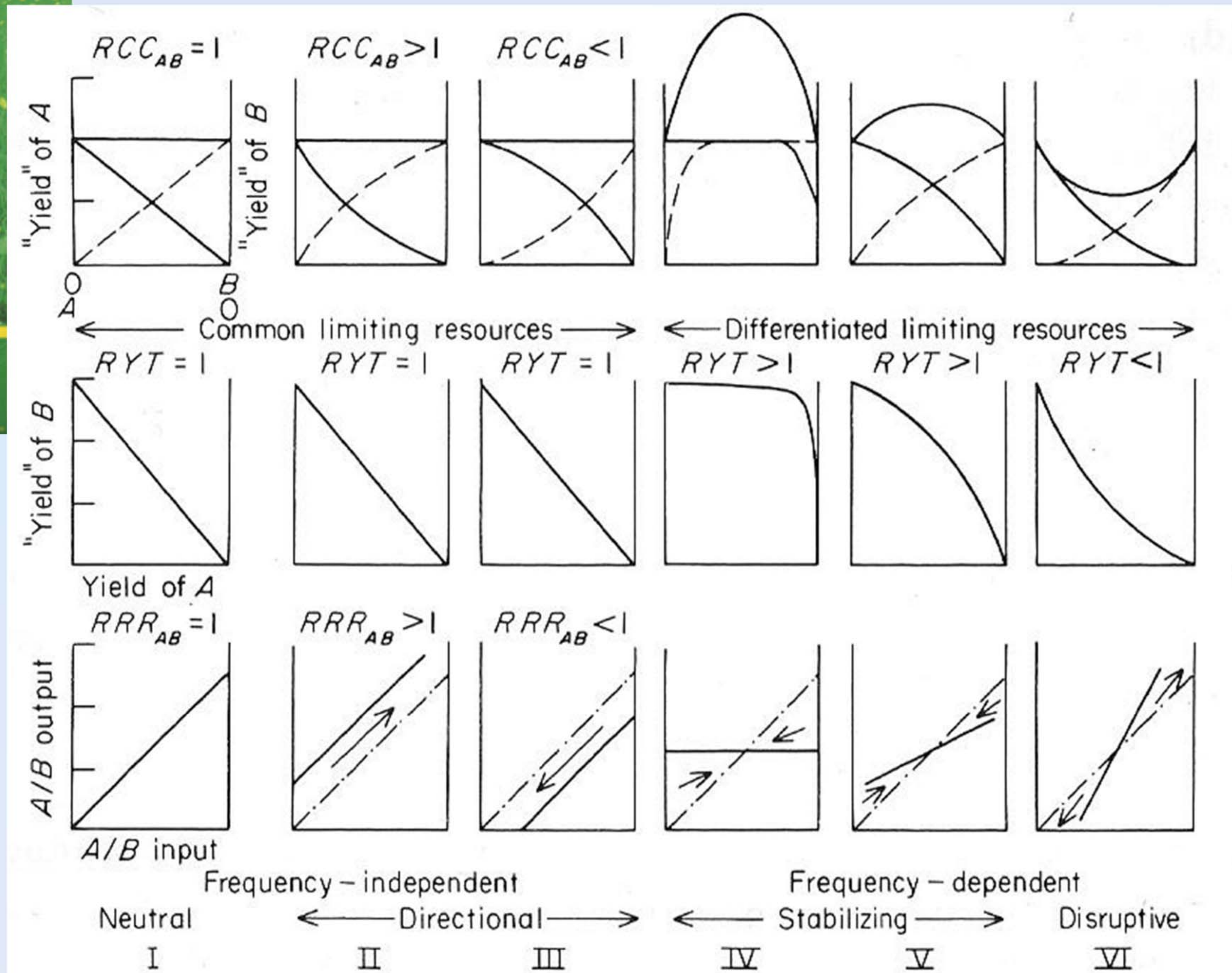
Road map:

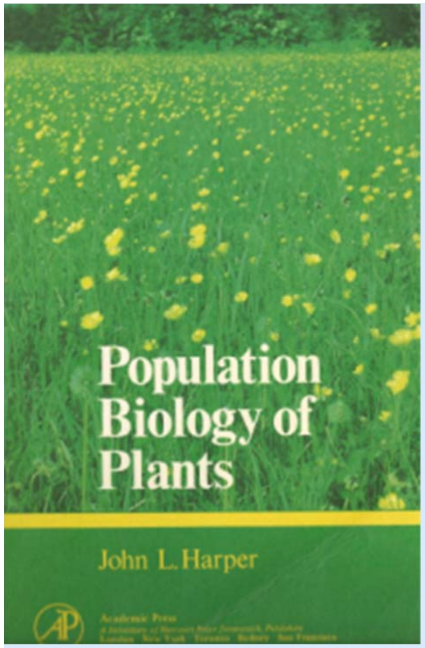
- Classic replacement series patterns
- Correlation leads to experimentation leads to confidence
- Why the production ecology equation is central
- Time to put the equation to use in analyzing mixtures




The productivity of mixtures has a rich history of experimentation in botany

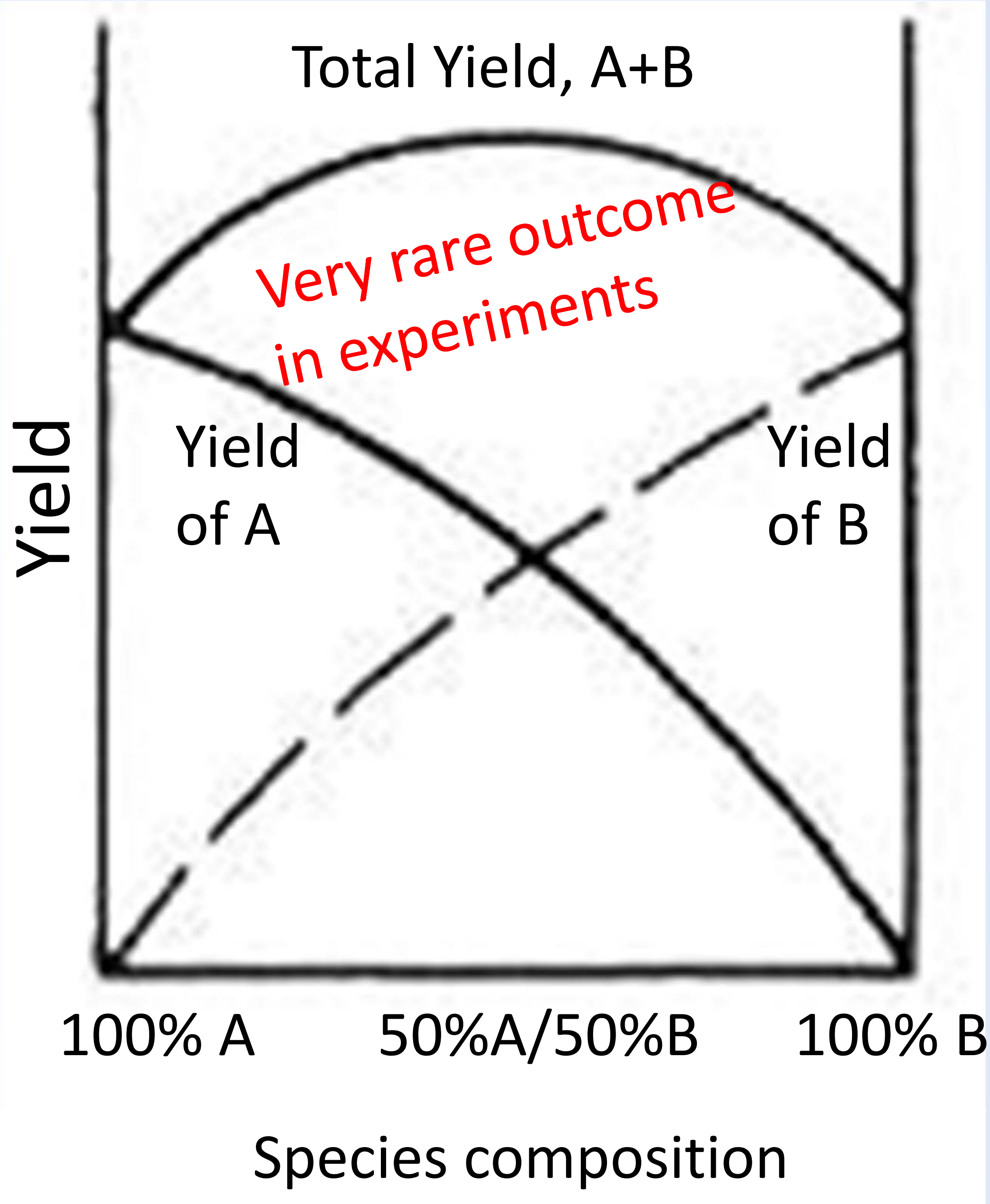

Population Biology of Plants
John L. Harper
Academic Press


$RCC_{AB}=1$
$RCC_{AB}>1$
$RCC_{AB}<1$
"Yield" of A
"Yield" of B
O
A
B
O
← Common limiting resources →
← Differentiated limiting resources →
$RYT=1$
$RYT=1$
$RYT=1$
$RYT>1$
$RYT>1$
$RYT<1$
"Yield" of B
Yield of A
$RRR_{AB}=1$
$RRR_{AB}>1$
$RRR_{AB}<1$
A/B output
A/B input
Frequency – independent
Frequency – dependent
Neutral
← Directional →
← Stabilizing →
Disruptive
I
II
III
IV
V
VI

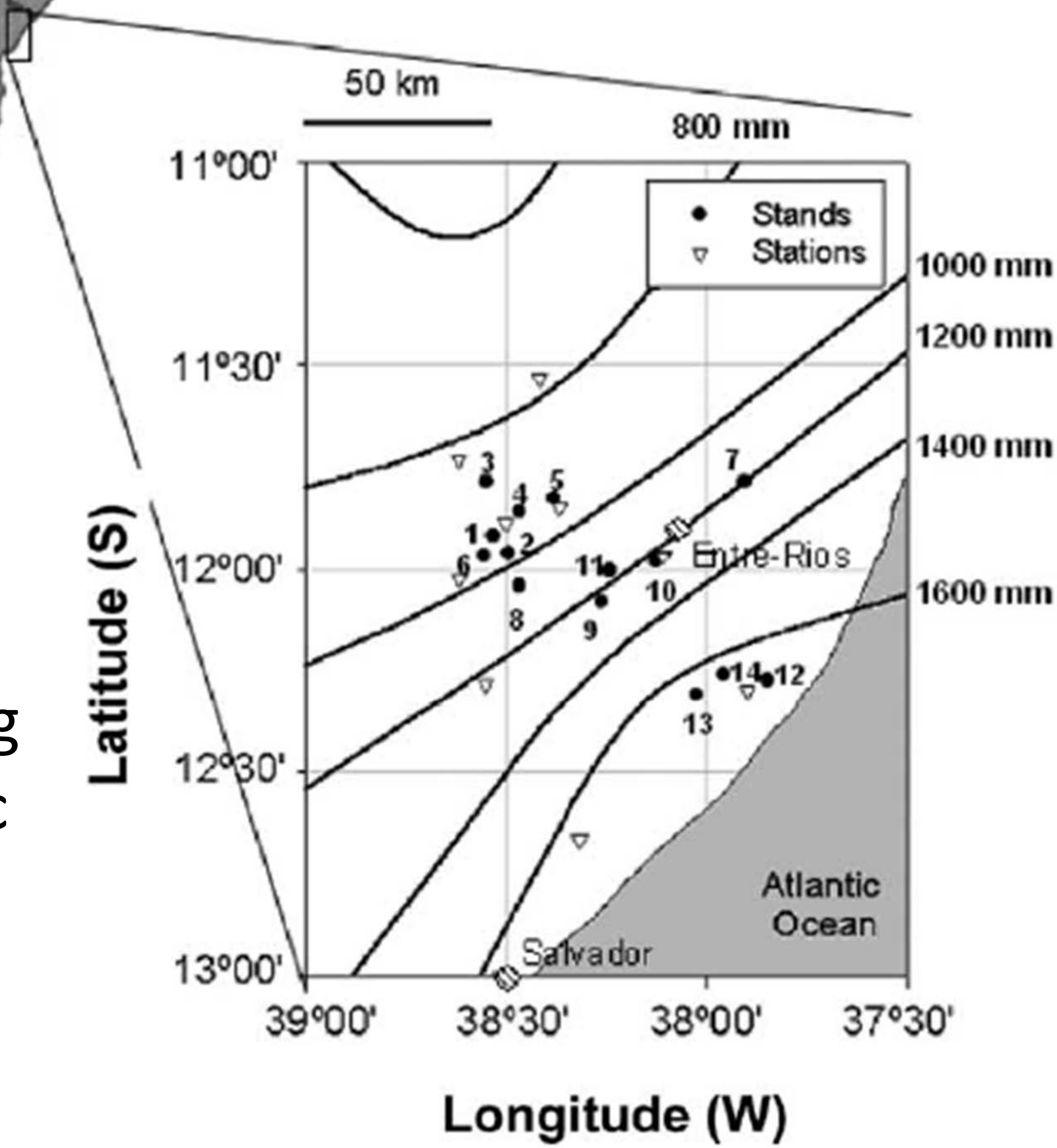



The fascinating case:

Transcendent yields of mixtures



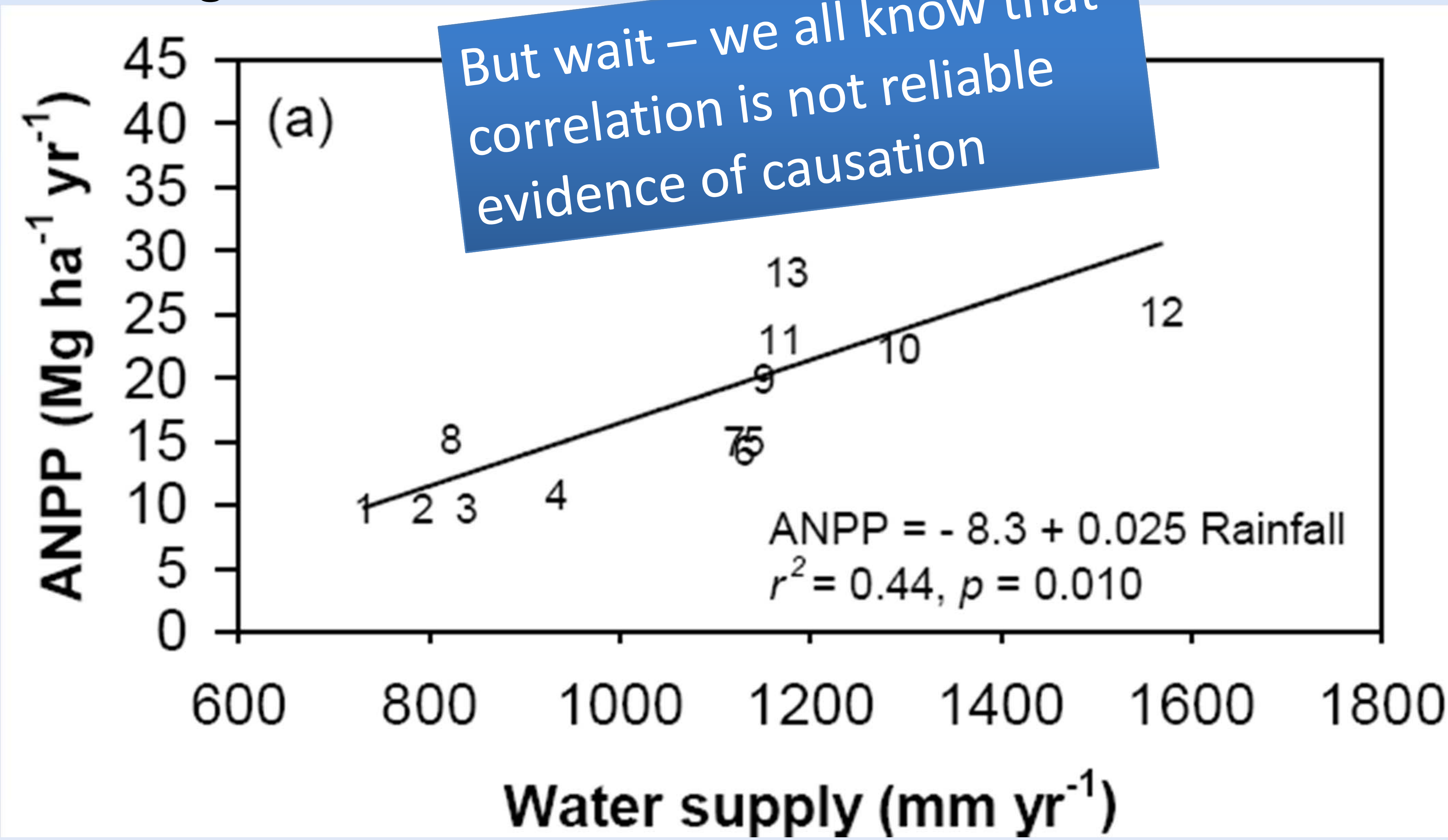
# Correlation leads to experimentation leads to confidence


Why does forest growth differ along geographic gradients?

Stape, Binkley, Ryan 2004

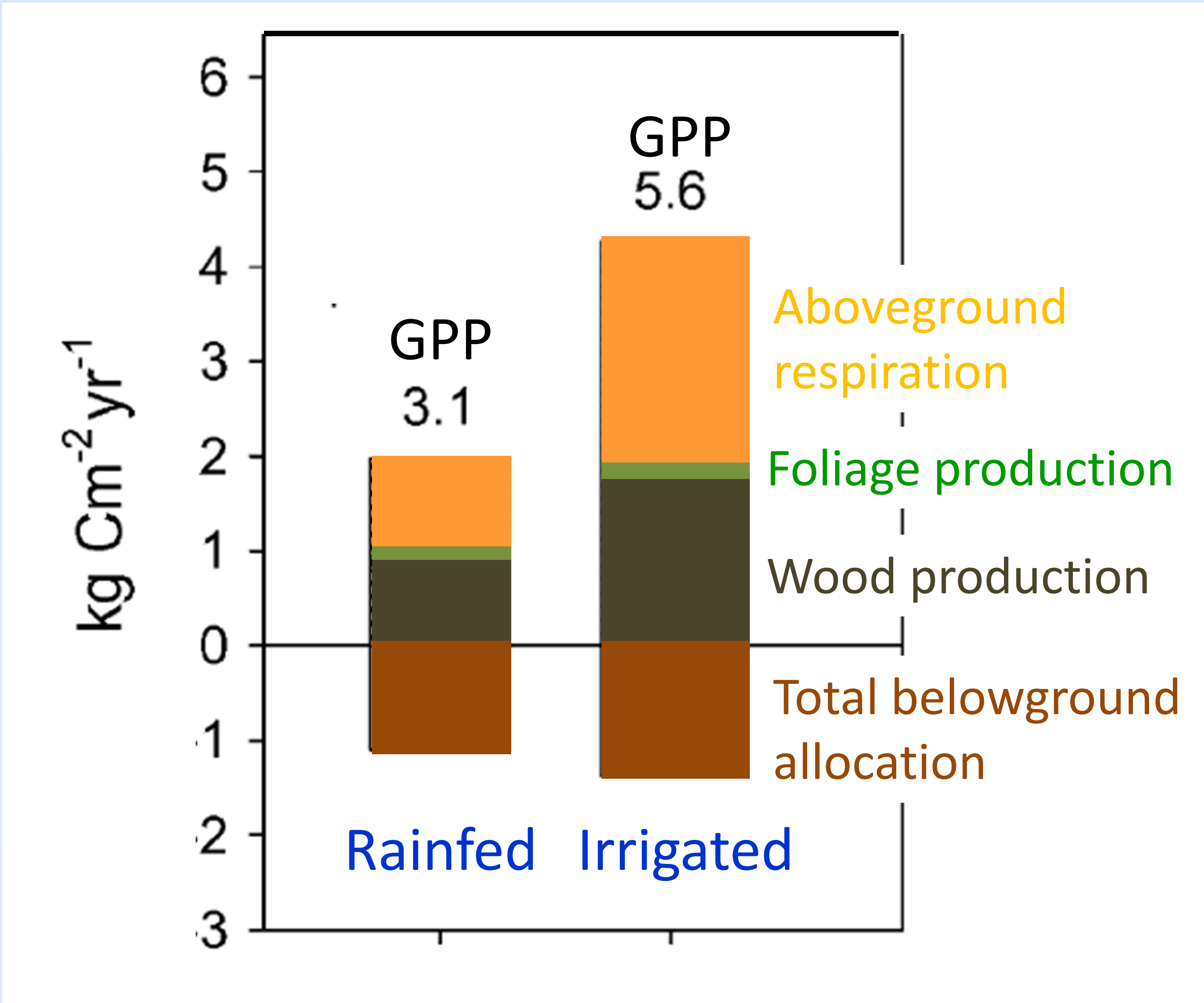
Well, we can look at water supply – faster growth occurs with higher rainfall:



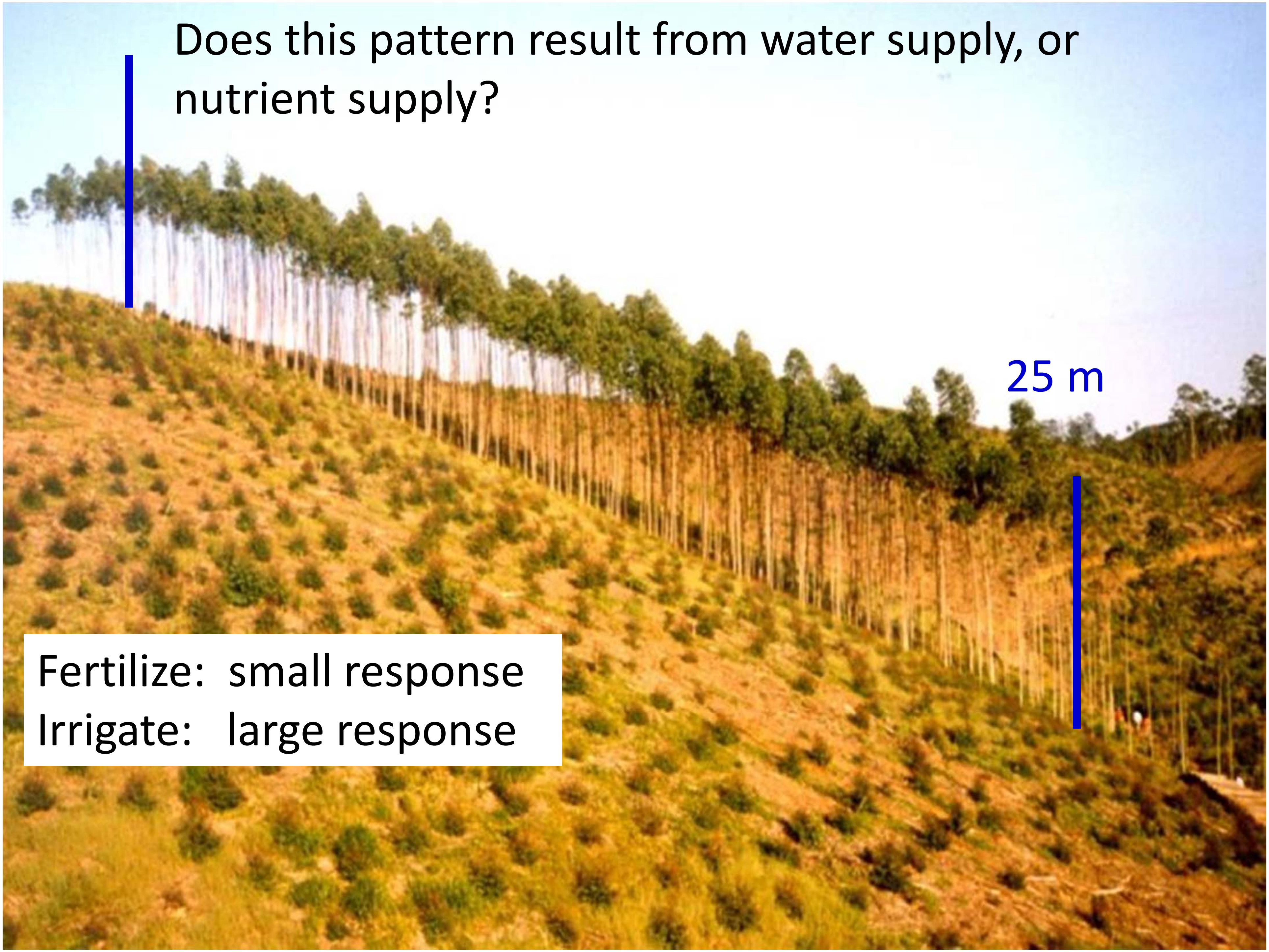

But wait – we all know that correlation is not reliable evidence of causation

Stape, Binkley, Ryan 2004

We need to challenge ideas (correlations) with experiments to develop confidence in process explanations:



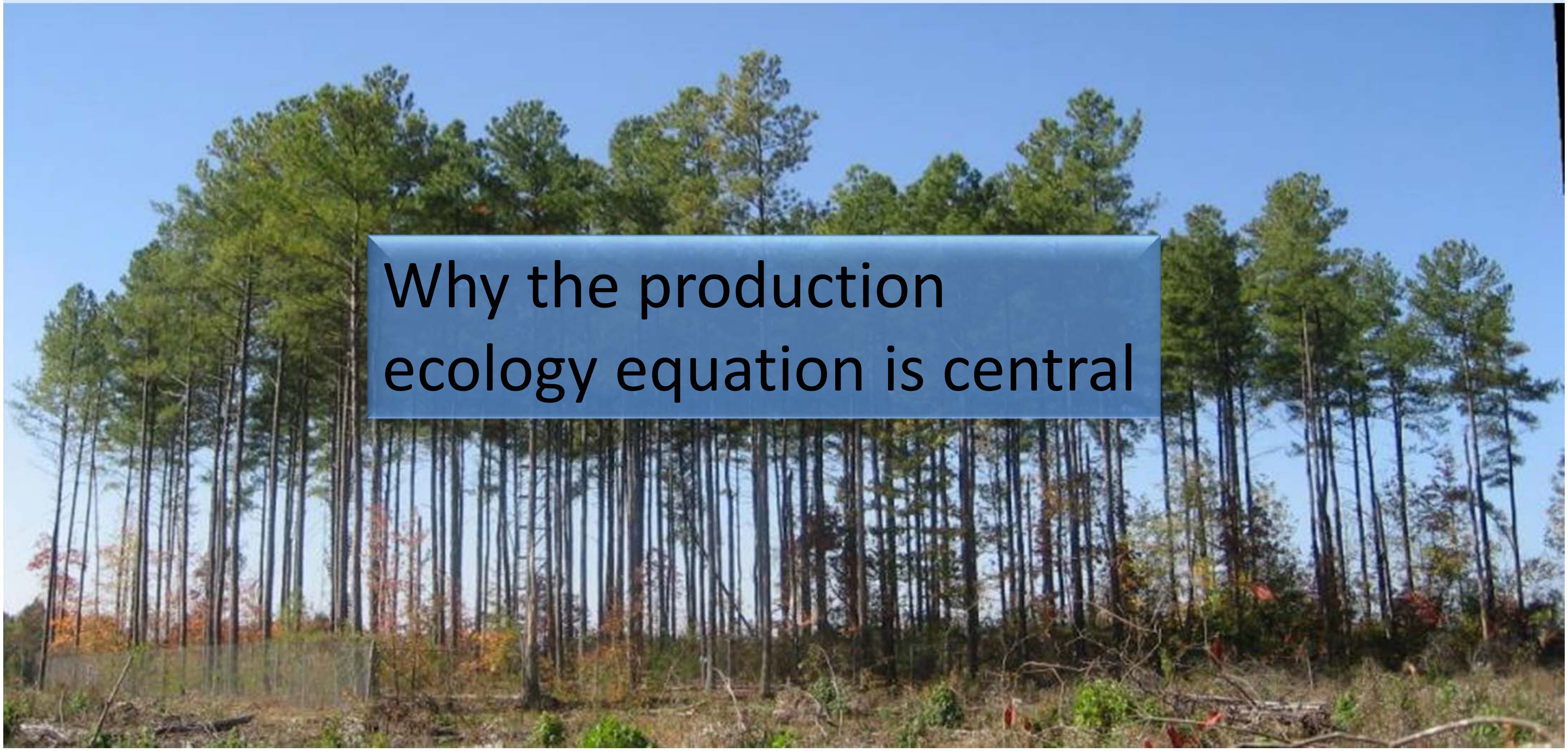

Stape, Binkley, Ryan 2008


Does this pattern result from water supply, or nutrient supply?
25 m
Fertilize: small response
Irrigate: large response

These are classic approaches in forestry (and Science):

1. Measure a pattern
2. Hypothesize a factor driving the pattern
3. Experiment with factor levels

*= powerful, process-based understanding*



Understanding the "species" factor requires a different approach than irrigation or fertilization

Why is the wood production in this spruce stand 30% greater than in the adjacent beech?

## The basic way to explain forest growth patterns:

1. What are the resource supplies available in the environment?
2. What proportion of the available supplies do trees obtain?
3. How efficiently do trees utilize these resources to fix carbon?
4. How do the trees allocate the fixed carbon among leaves, stems, roots?

## *The Production Ecology Equation*

(from Montieth 1977, Linder 1985 and others…)

Production = Resource supply
X Proportion of supply captured
X Efficiency of using captured resource

Wood Production = Resource supply
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X Efficiency of using captured resource
- Respiration and allocation to other tissues

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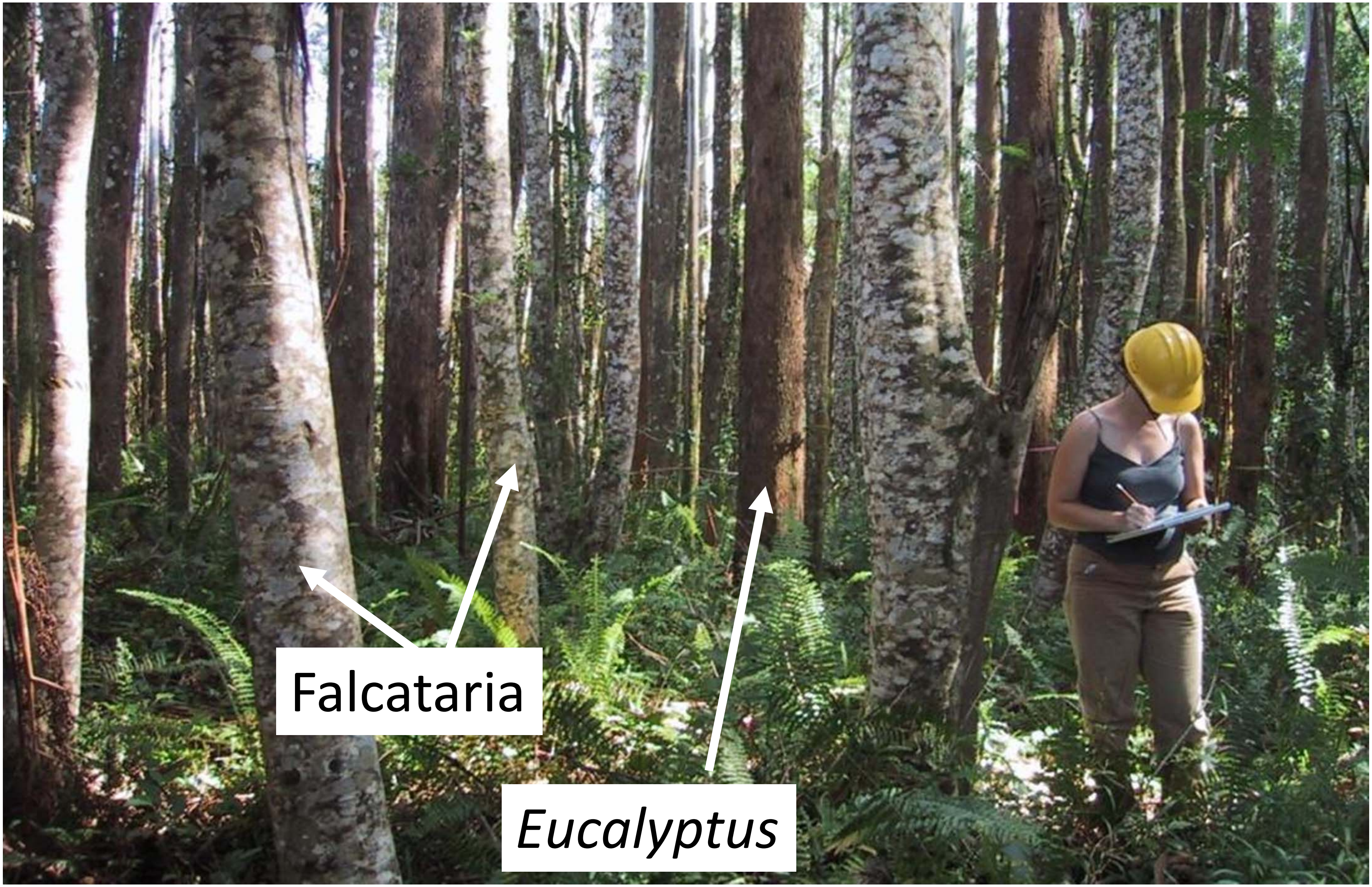
Wood production = 5000 MJ/$m^2$ light supply (5000 MJ/$m^2$)
X 90% capture (4500 MJ/$m^2$)
X 1 g C/MJ light captured (4500 gC/$m^2$)
- 70% allocation to other tissues (-2150 gC/$m^2$)

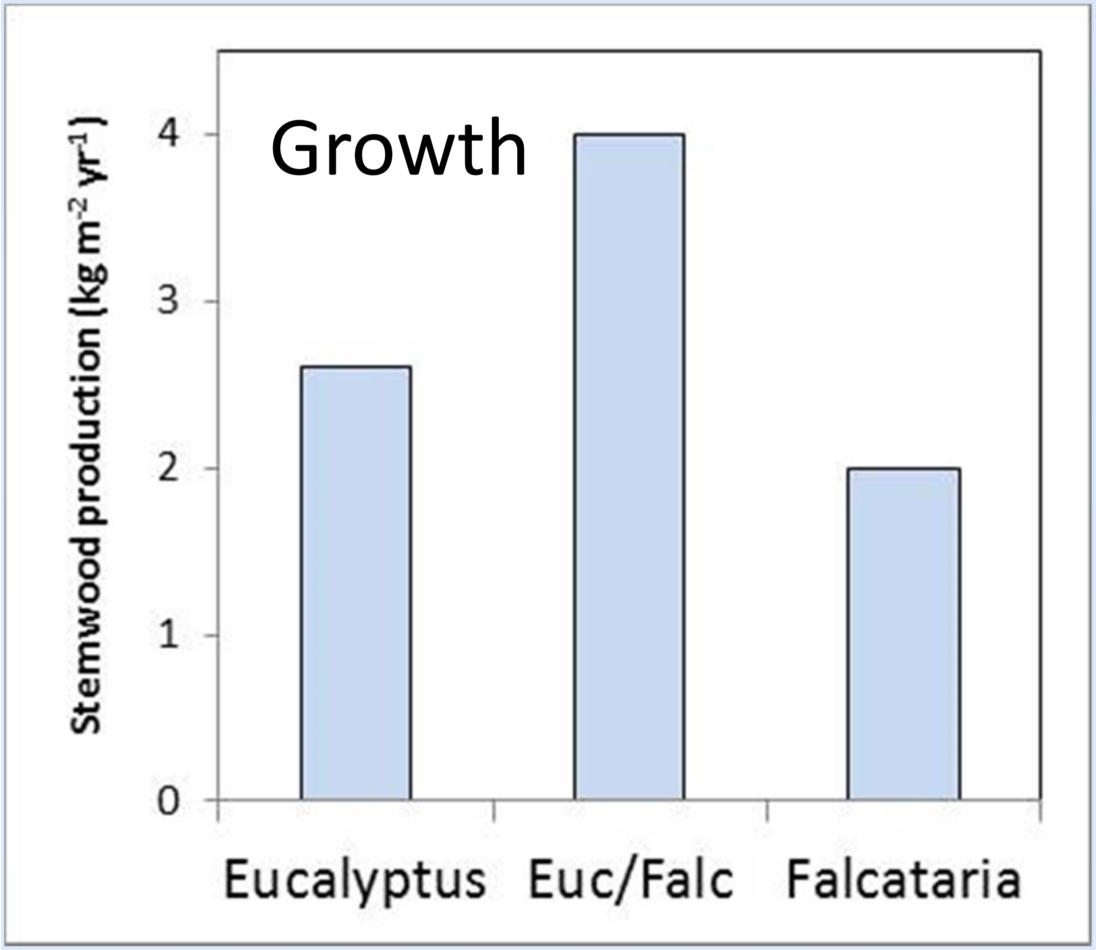
**= 1350 gC/$m^2$ wood**

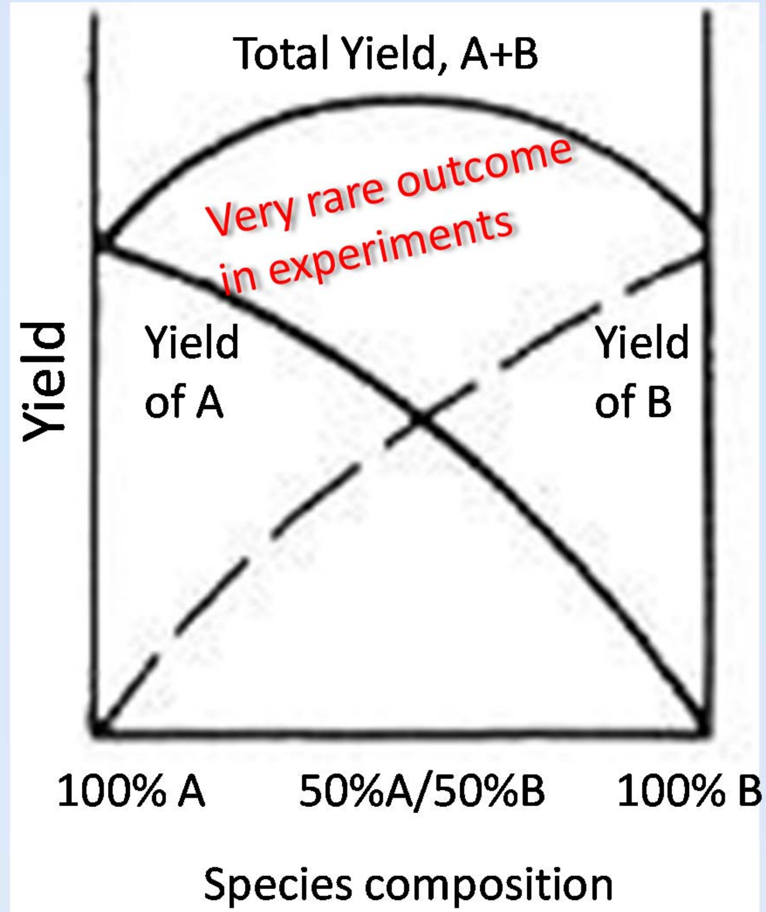
Bottom line: Wood production = 1.35 kg C/$m^2$
(= 2.7 kg wood/$m^2$)

An example with species mixtures: Mixing *Eucalyptus saligna* with N-fixing *Falcataria mollucana* in Hawaii



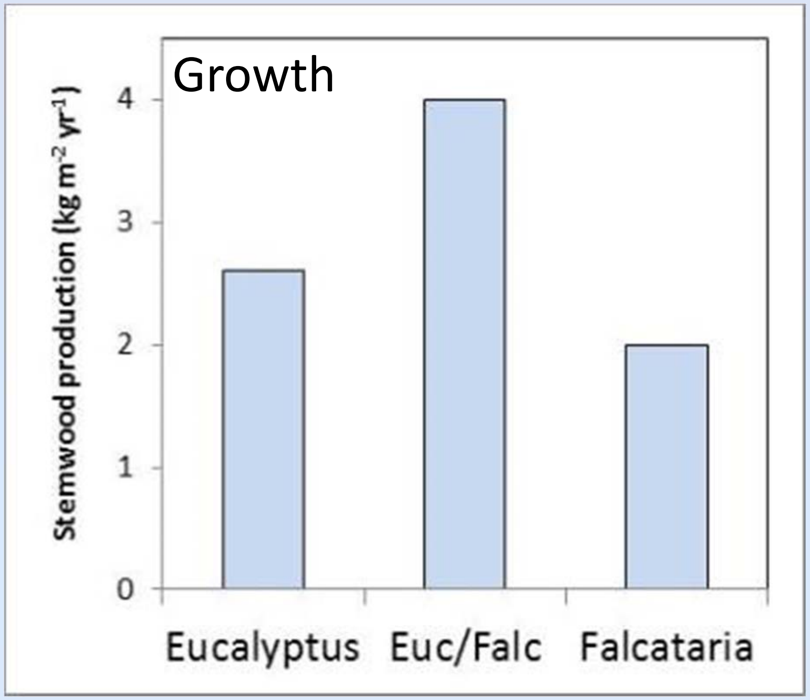
# Yield pattern:

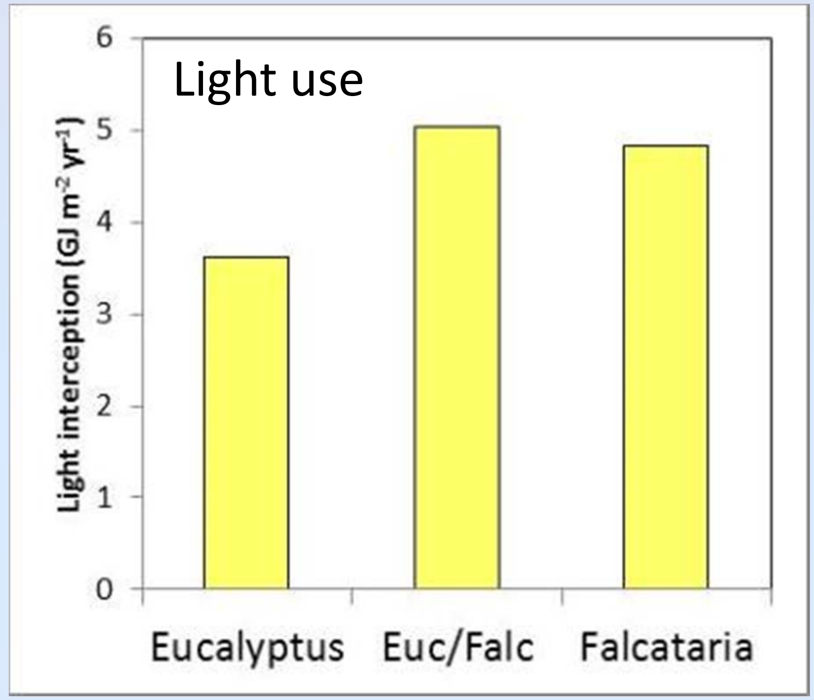


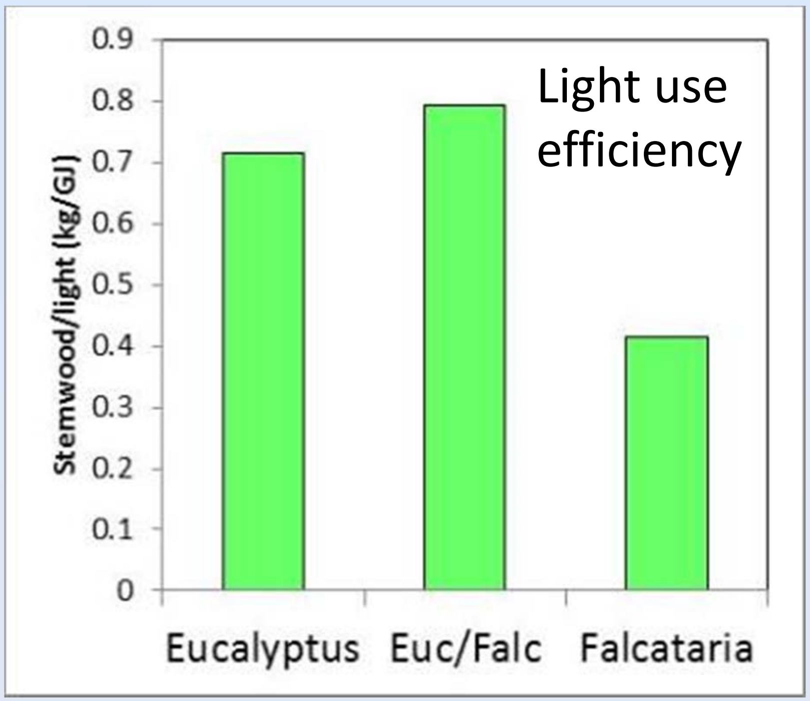




But *why* (how) did this pattern develop?

Binkley, Dunkin, DeBell, and Ryan 1992



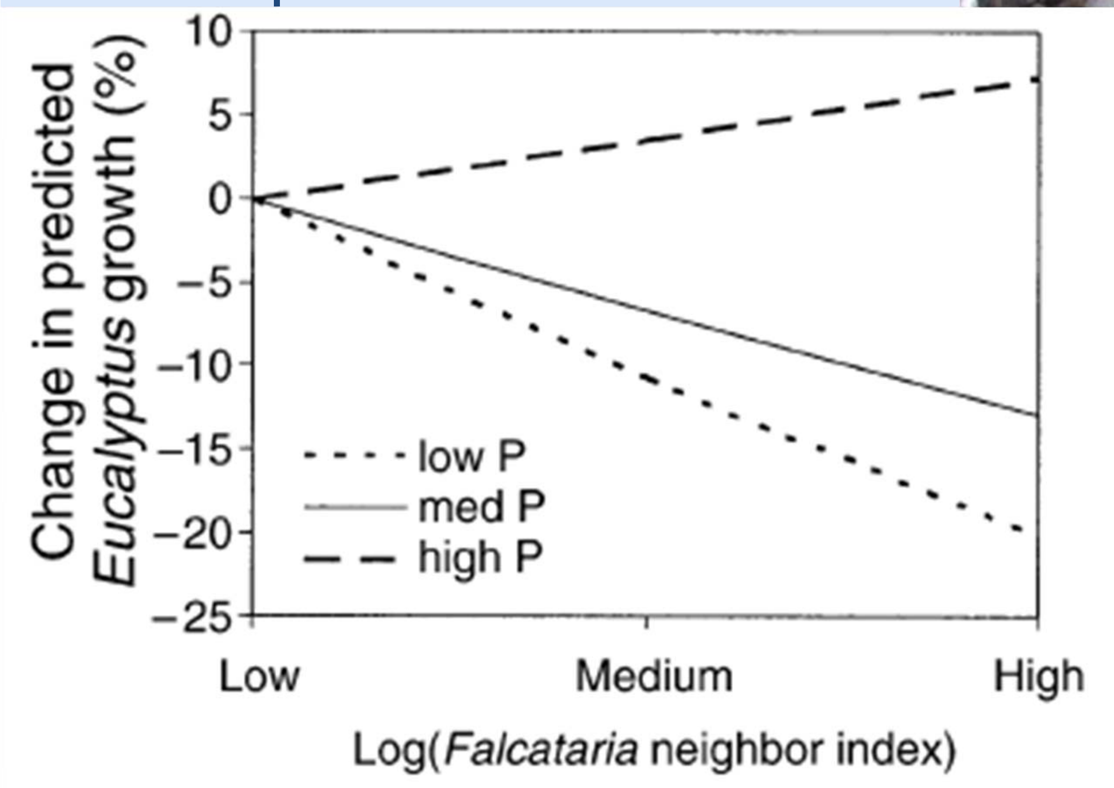



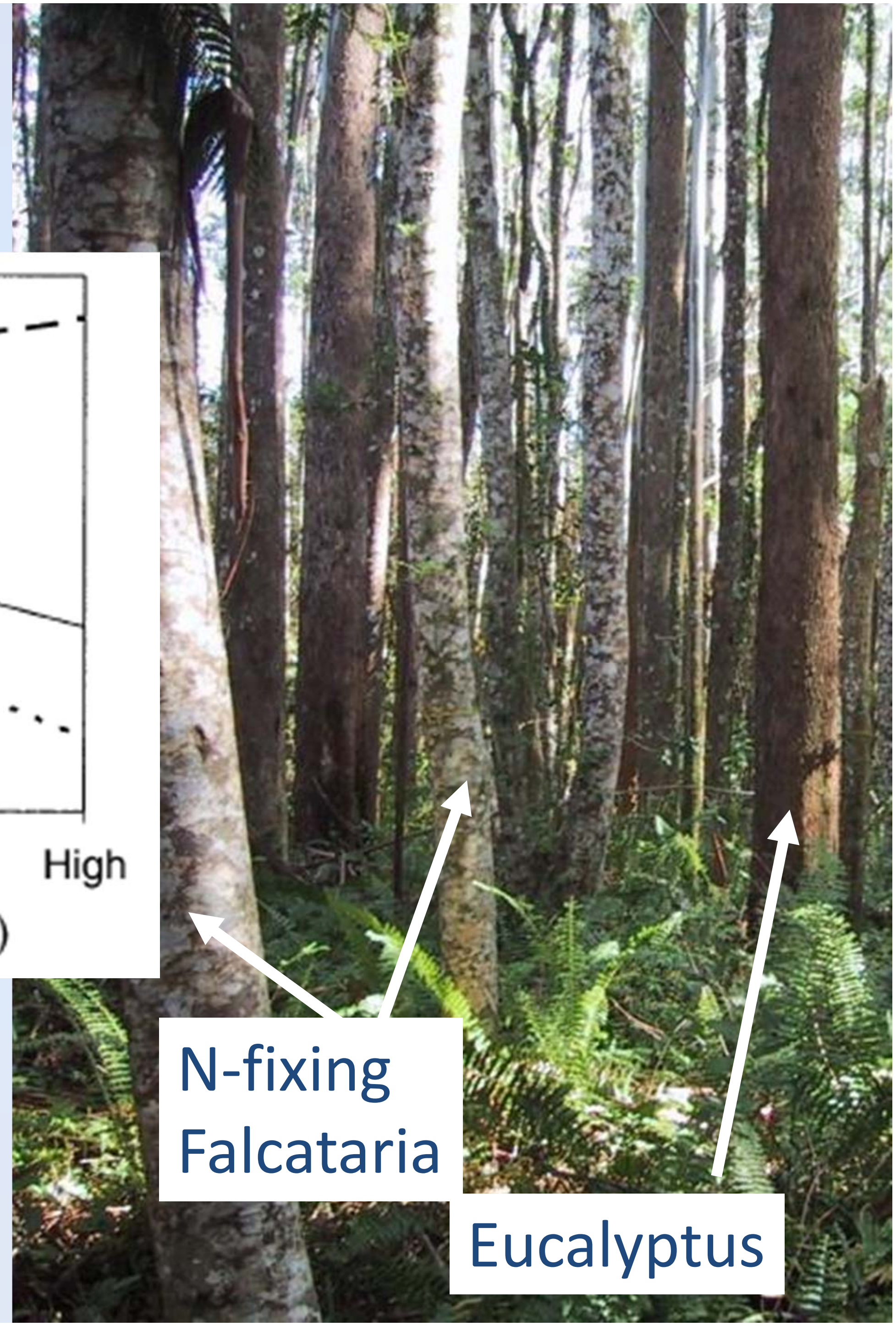




Mixture grew 75% more wood than monocultures; intercepted more light than Euc. monoculture, and used light more efficiently than Falc. monoculture

Binkley, Dunkin, DeBell, and Ryan 1992

“Competition” can get pretty interesting when trees aren’t all one species.



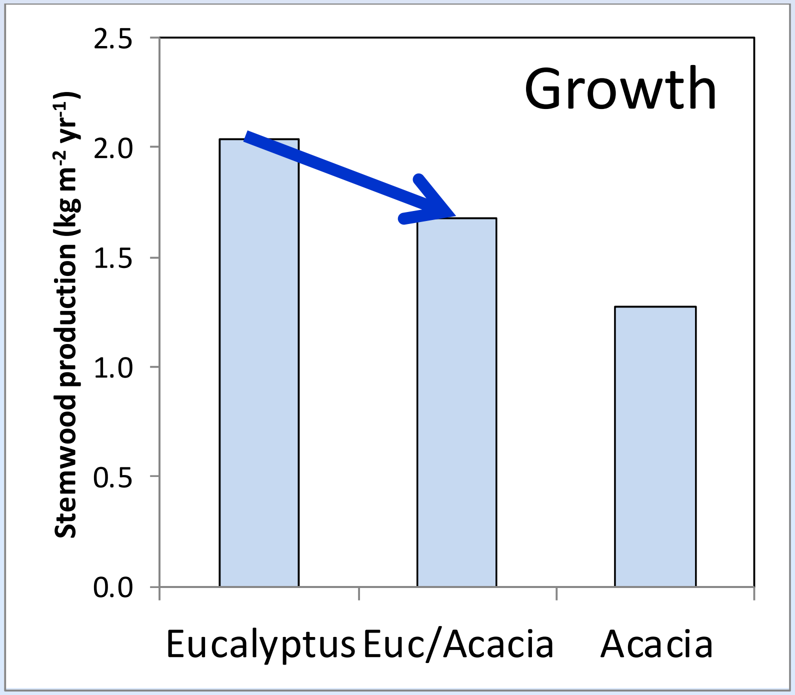

Facaltaria trees can raise or lower growth of Eucalyptus trees, depending on soil phosphorus supply

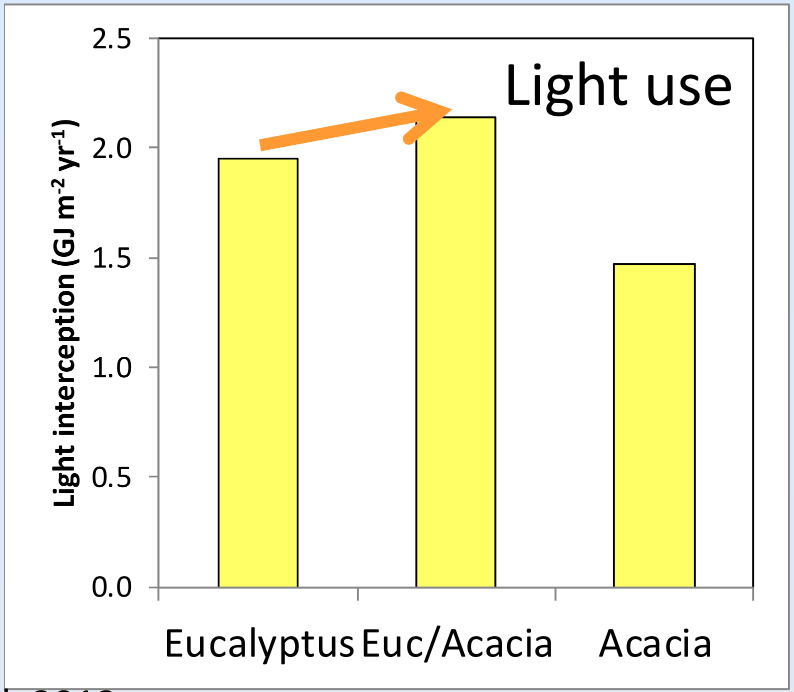
Boyden et al. 2007

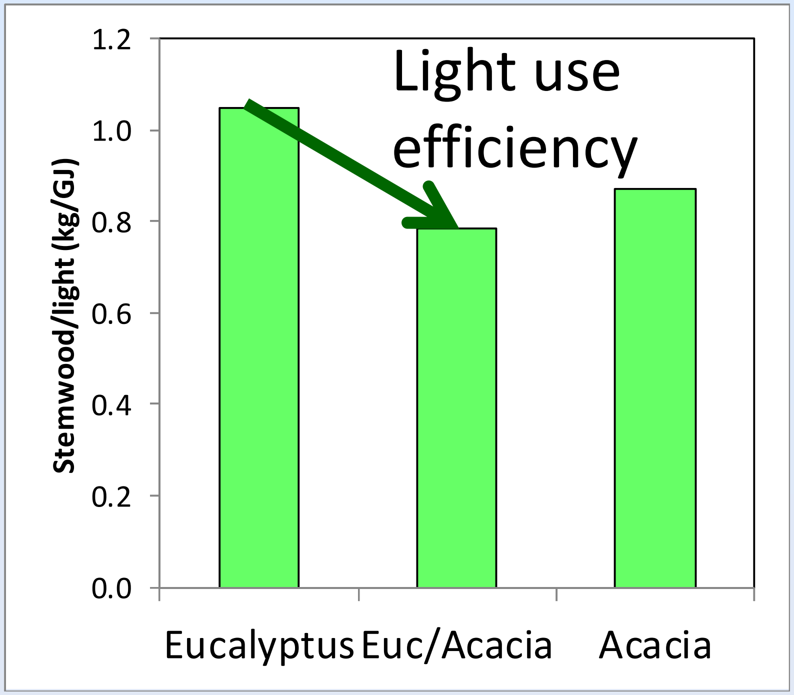
What can one experiment tell us? Well, that's 0 degrees of freedom with respect to forests of the world.

A similar experiment in Brazil, with *Eucalyptus* and N-fixing *Acacia mangium*

Mixture did not match *Eucalyptus* monoculture: efficiency dropped more than light interception increased

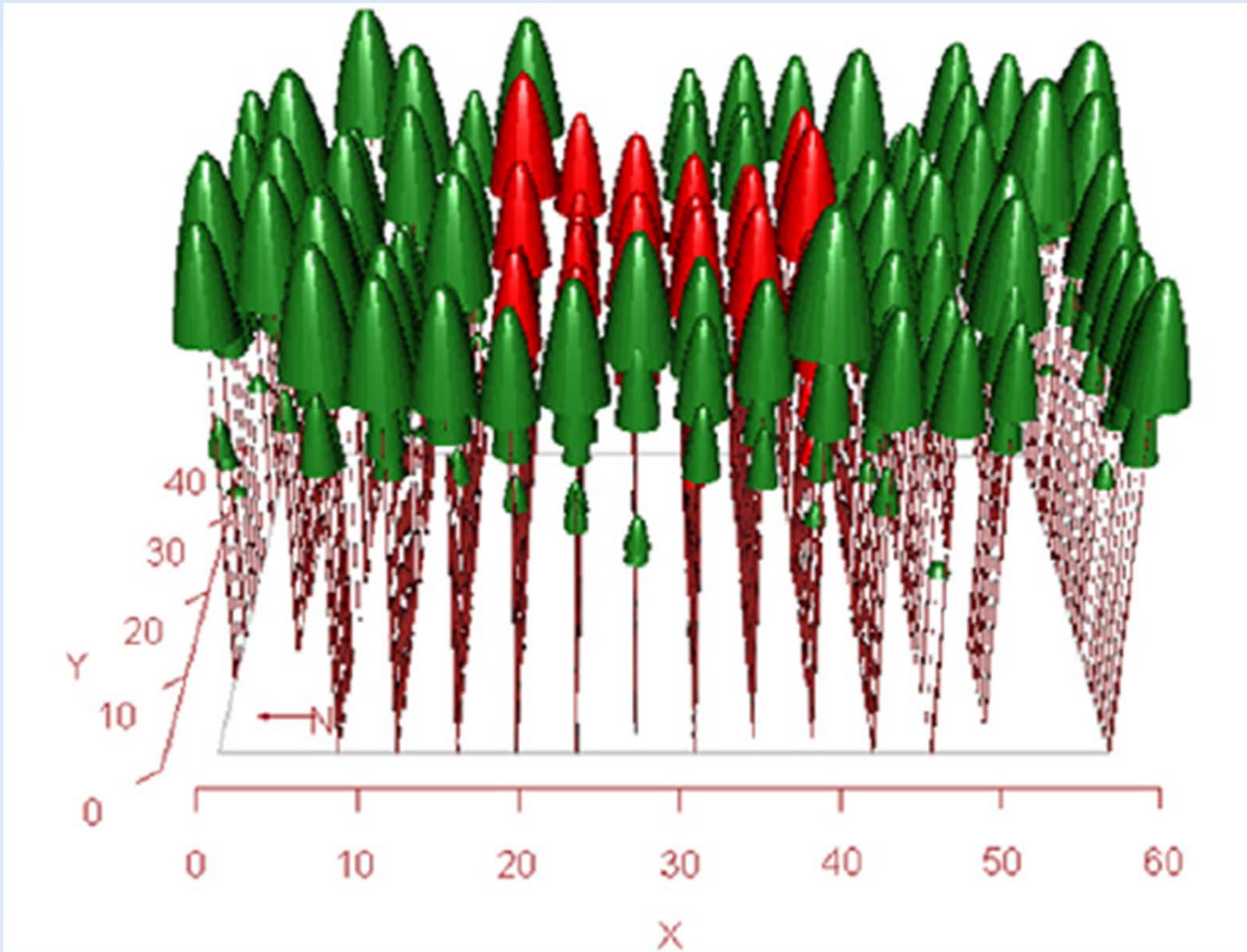



le Maire et al. 2013

The Production Ecology Equation can be used at the scale of individual trees, with light use modeled for each crown:

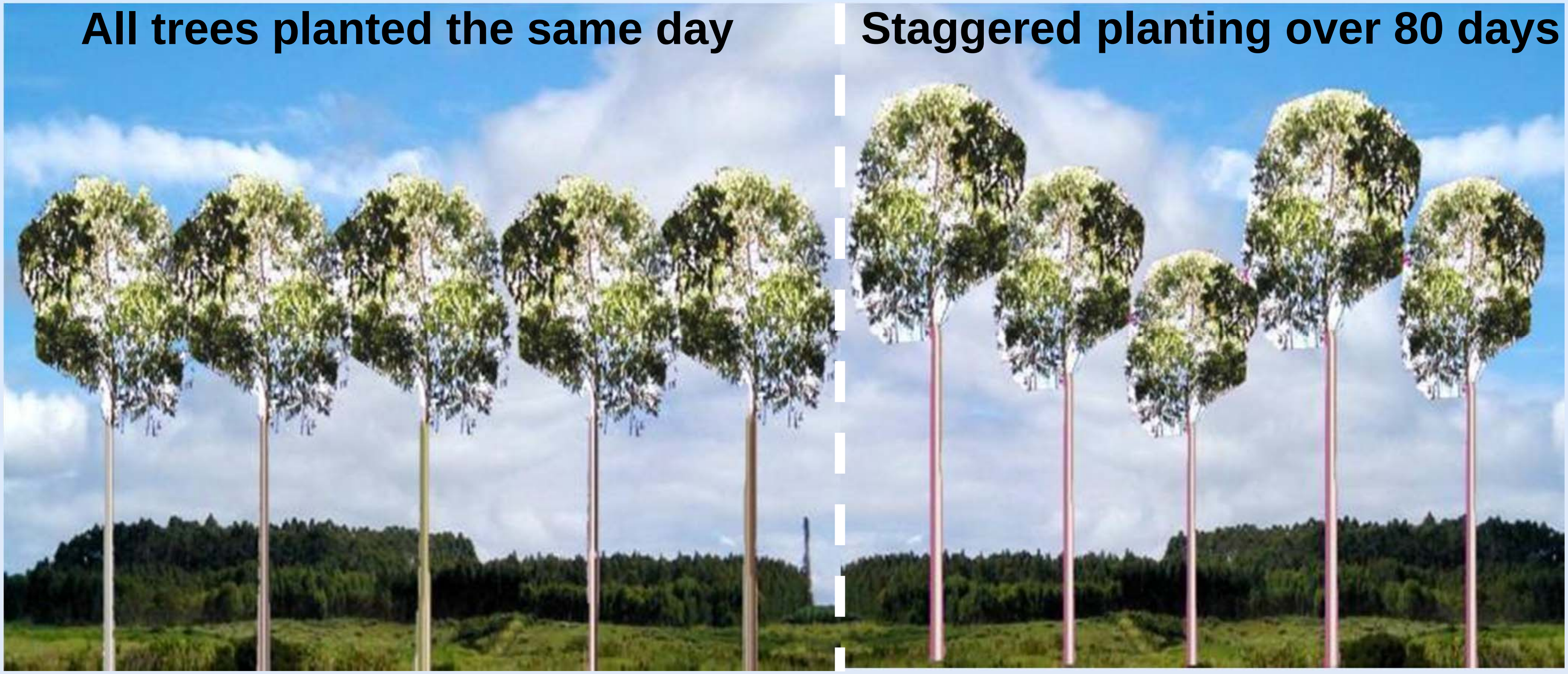



Stem production, light absorption and light use efficiency between dominant and non-dominant trees of *Eucalyptus grandis* across a productivity gradient in Brazil

Otávio Camargo Campoe[a,*], José Luiz Stape[b], Yann Nouvellon[c,d], Jean-Paul Laclau[c,e], William L. Bauerle[f], Dan Binkley[g], Guerric Le Maire[c]

Campoe et al. 2012

Rather than look at the influence of species diversity, let's examine the effect of diversity of tree sizes for monoclonal forests:

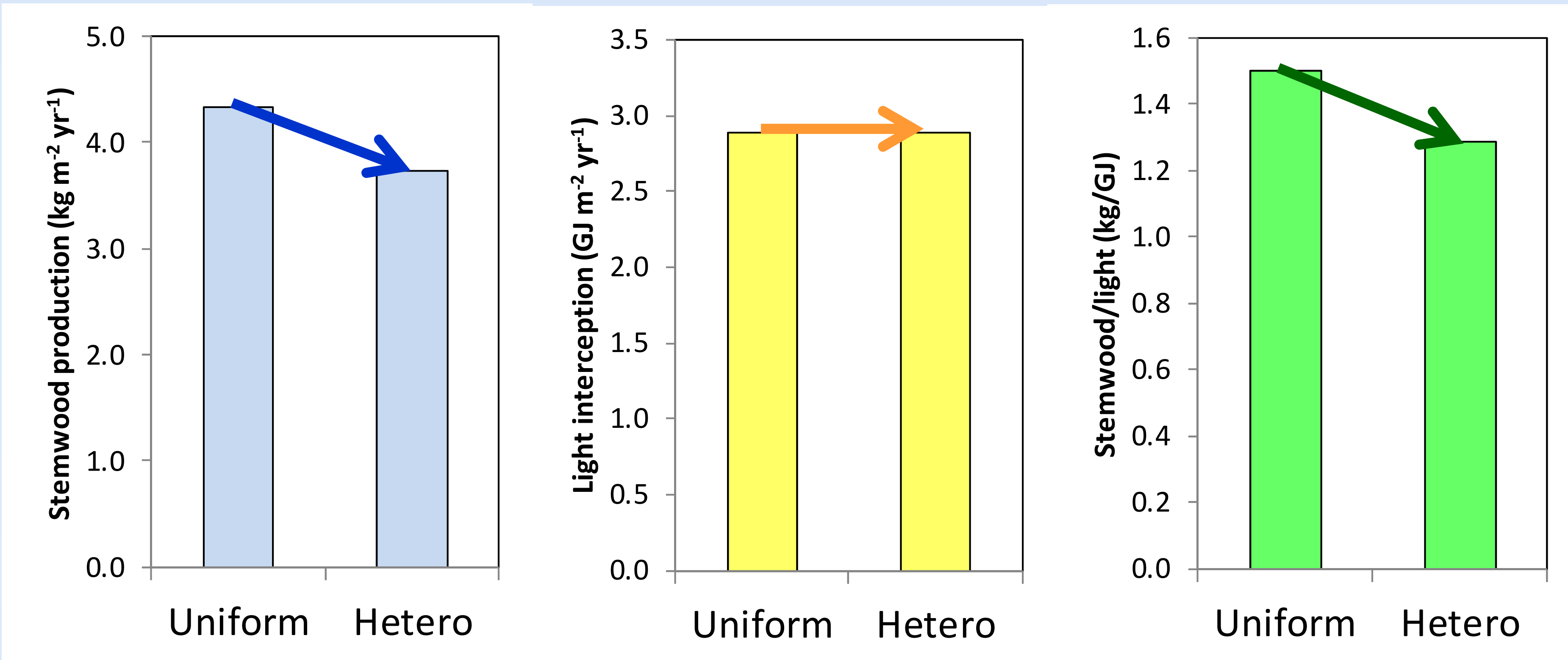


BEPP
BRASIL EUCALYPTUS PRODUTIVIDADE POTENCIAL

[redacted]


10% difference might not be surprising?

Heterogeneity of tree sizes lowered stand growth because of a loss of efficiency of using light:

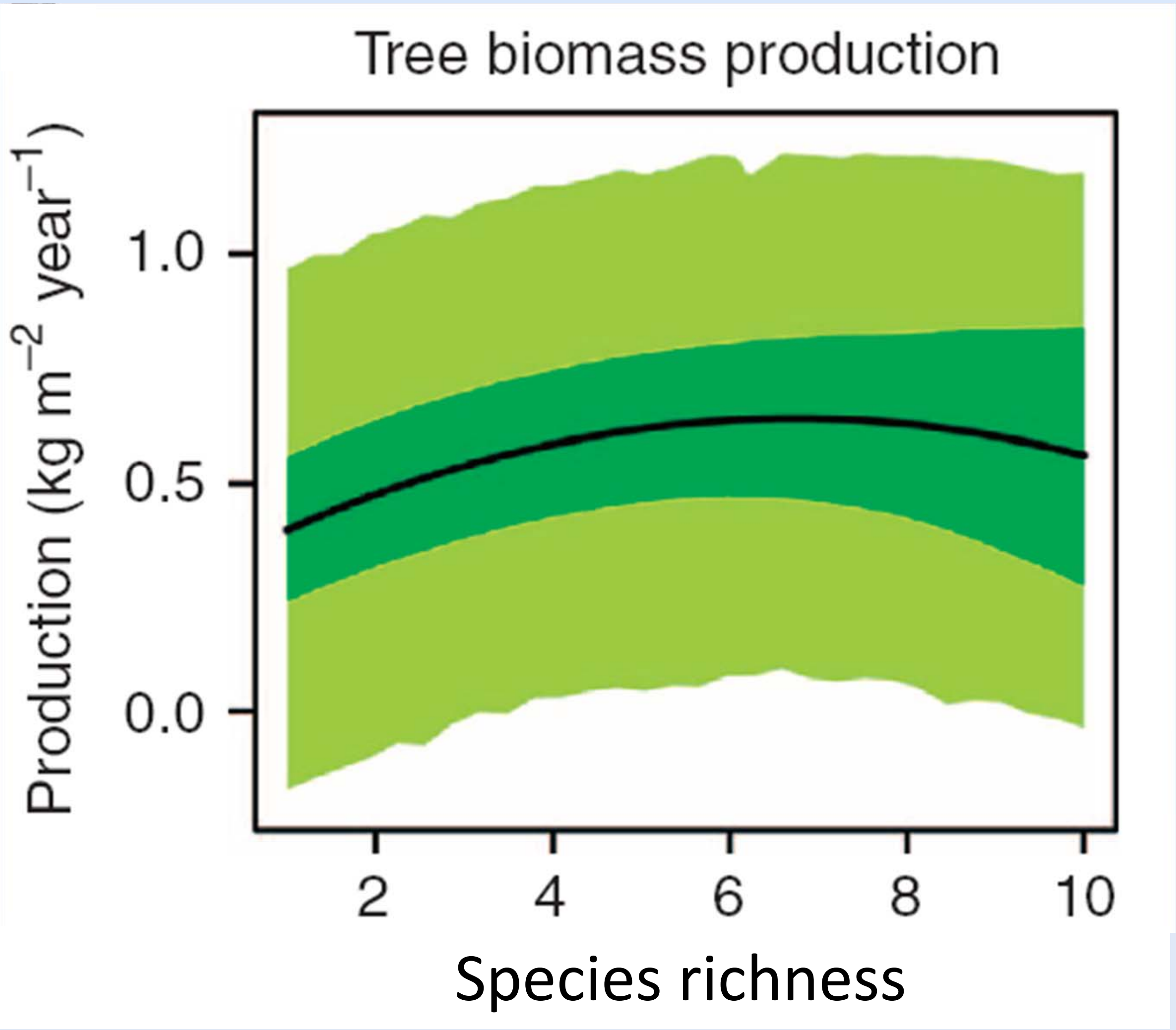


Based on the Production Ecology Equation, how could mixtures of species grow faster than the best-performing monoculture?

Option A: Mixture has higher resource supply in the environment

Option B: Mixture uses higher proportion of available resources

Option C: Mixture uses resources more efficiently



Option A:
Mixture has higher resource supply in the environment

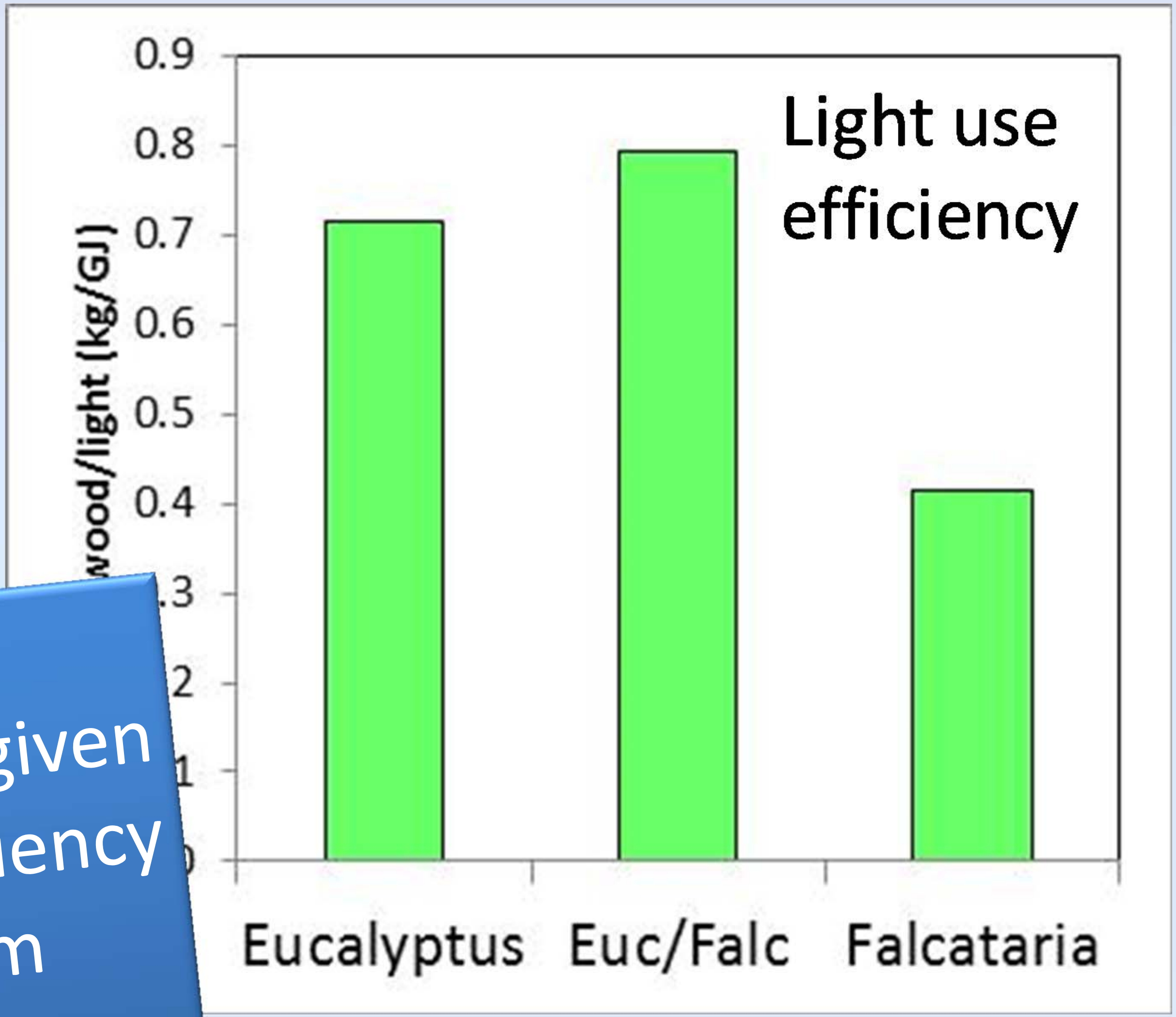
A1: Mixture on a richer site than monoculture

A2: Mixture raises resource supply in the environment

Option B: Mixture uses higher proportion of available resources

10% difference might not be surprising?

Option C: Mixture uses resources more efficiently




I speculate this would be rare, given the loss of efficiency that comes from heterogeneity in tree sizes…

Benediction:

It's time to test (experiment!) on *why* (how) mixtures differ (or not) from monocultures.

How, exactly, do the components of the Production Ecology Equation differ?