

# Carbon allocation and partitioning

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NREM680

Ecosystem Ecology

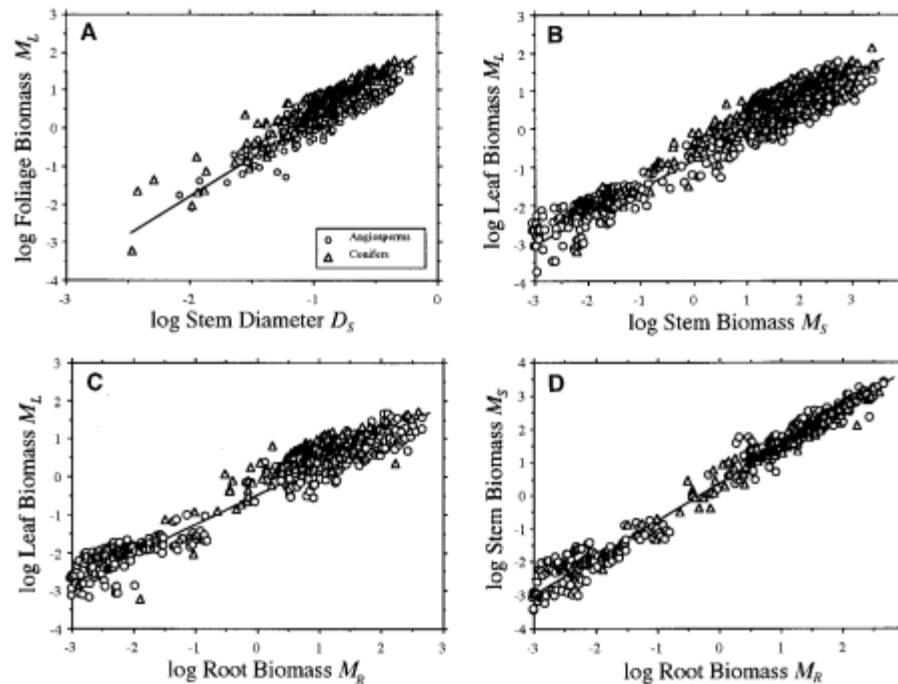
2014

# Confusion

- Carbon allocation from Dickson & Isenbrands (1993):
  - “Biomass not allocated,” but “accumulated the end result of the allocation process.”
  - Translocation and transport should be limited to metabolic process description
  - Carbon allocation: “distribution of carbon within the plant to different plant parts” where allocation is an adaptive response to resource stress
  - Carbon partitioning: division of carbon into metabolic, structural or storage pools

# More confusion:

- Carbon allocation (review by Litton et al 2007):
  - Patterns in live biomass (Enquist & Niklas 2002)



**Fig. 1.**  $D_S$  and  $M_L$ ,  $M_S$ , and  $M_R$  relations for average plants from worldwide data sets. Solid lines are reduced major axis regression curves of log-transformed data. Angiosperm and conifer species are denoted by circles and triangles, respectively. (A)  $M_L$  versus  $D_S$  (trunk diameter at breast height). (B)  $M_L$  versus  $M_S$ . (C)  $M_L$  versus  $M_R$  ( $r^2 = 0.861$ ,  $n = 338$ ,  $F = 2439$ ,  $P < 0.0001$ ). (D)  $M_S$  versus  $M_R$ . See Table 1 for additional statistics. Note, the relatively larger spread in (B) and (C) is due to differences between Angiosperms and Gymnosperms.

# More confusion:

- Carbon allocation (review by Litton (2007)):
  - Patterns in live biomass (Enquist & Niklas (2002))
  - Flux (Keith et al (1997)): Both pools and fluxes

Table 4. Components of annual belowground carbon allocation (tC ha<sup>-1</sup>)

|   | Unfertilized | P-fertilized | SED*  | P      |
|---|--------------|--------------|-------|--------|
| 1. Soil CO <sub>2</sub> efflux                        | 7.11         | 6.55         | 0.137 | <0.001 |
| 2. Litterfall   | 2.46         | 2.77         | 0.294 | n.s.   |
| 3. Coarse root production                             | 0.45         | 0.60         | 0.086 | n.s.   |
| 4. Belowground carbon allocation<br>4 = [(1 - 2) + 3] | 5.10         | 4.38         | 0.336 | <0.01  |

\* Standard Error of the Difference of the means.

# More confusion:

- Carbon allocation (review by Litton et al 2007):
  - Patterns in live biomass (Enquist & Niklas 2002)
  - Flux (Keith et al (1997)): Both pools and fluxes
  - Distribution of flux (Giardina et al 2003):

$$\text{TBCA} = F_S + F_E - F_A + \Delta C_S + \Delta C_R + C_L$$

where:

$F_S$  = soil surface CO<sub>2</sub> efflux

$F_E$  = leached C

$F_A$  = litterfall

$\Delta C_S$  = change in C in mineral soil

$\Delta C_R$  = increment of C in root biomass

$C_L$  = Litter layer mass

# Terminology

- Biomass: amount of material present (eg. g, kg, etc.)
- Flux: Movement of carbon to specific component of the ecosystem per unit time (eg.  $\text{g yr}^{-1}$ )
- Pools: amount of material in a component
- Partitioning: GPP/amount used by component (proportion or percentage)
- Allocation: general term for where and how much carbon is throughout the ecosystem (biomass) and where it is moving to/from (flux and partitioning)

# Estimation of components

- Mass Balance Approach
- Gross Primary Production (GPP)
  - $GPP = \text{total assimilated } CO_2 - (R_{\text{leaf}(\text{day})} + \text{photorespiration})$
  - $GPP = ANPP + APR + TBCF$
- Annual Net Primary Production (ANPP)
- Above Ground Respiration (APR)
- Total Below Ground Carbon Flux (TBCF)

# ANPP

- $ANPP = F_A + F_W + \Delta C_C + \Delta C_W$ 
  - where:
  - $F_A$  = flux of C associated with litterfall
  - $F_W$  = flux of C associated with mortality
  - $\Delta C_C$  = increment of C associated with C content in live leaves
  - $\Delta C_W$  = increment of C associated with aboveground biomass

Simplified as:

$$ANPP_{total} = ANPP_{foliage} + ANPP_{wood}$$

- Where:
  - $ANPP_{foliage} = F_A + \Delta C_C$
  - $ANPP_{wood} = F_W + \Delta C_W$



# Litterfall



<http://www.crestmonsoon.org/maemoh/Photo/Litter.JPG>

# Litterfall

- Annual (or other time scale) C inputs to forest floor
- Estimate  $LAI_{max}$  (corrected for herbivory losses)
- Can be broken up into components
- Rule of thumb: detect 20% difference in litterfall at a site
  - For example, 15-20 for deciduous forest type

# Litterfall

- Processing
  - Subsample for LA if desired (Leaf Mass per Area)
  - Dried 24-48 hours at 70°C
  - Sort (plant part, species, etc.)

$$P_c = (M_c (1-H) C_c (P_{L,f}/P_{L,I})/A)$$

where:

- $P_c$  = Annual production of canopy components
- $M_c$  = annual dry mass of litter
- $H$  = fraction of leaf area lost to herbivory
- $C_c$  = Carbon fraction (typically 50%)
- $P_{L,f}$  = average leaf mass per area of fresh leaves
- $P_{L,I}$  = average leaf mass per area of leaves in the litter
- $A$  = total basket area

# Litterfall

- Complications:
  - System (e.g. deciduous broadleaf vs. coniferous)
  - No measurement of pollen or VOCs
  - Timing (Northern vs. Southern Hemisphere)
  - Decomposition in basket
  - Climate
  - Diameter of twigs (<1 cm typical)
  - Labor

# ANPP

- $ANPP = F_A + F_W + \Delta C_C + \Delta C_W$ 
  - where:
    - $F_A$  = flux of C associated with litterfall
    - $F_W$  = flux of C associated with mortality
      - Added back into estimates
      - Can account for 1-2% per year (Kloeppel et al 2007)
      - Think about length of study

# ANPP

- $ANPP = F_A + F_W + \Delta C_C + \Delta C_W$ 
  - where:
    - $F_A$  = flux of C associated with litterfall
    - $F_W$  = flux of C associated with mortality
    - $\Delta C_C$  = increment of C associated with C content in live leaves
      - Monthly measurements of LAI with LAI-2000 Plant Canopy Analyzers (Li-COR)
      - During overcast, calm conditions
      - Linear interpolation for months that were missed because of climate conditions
      - Overlap and clumping corrected using allometric relationship between DBH and LAI

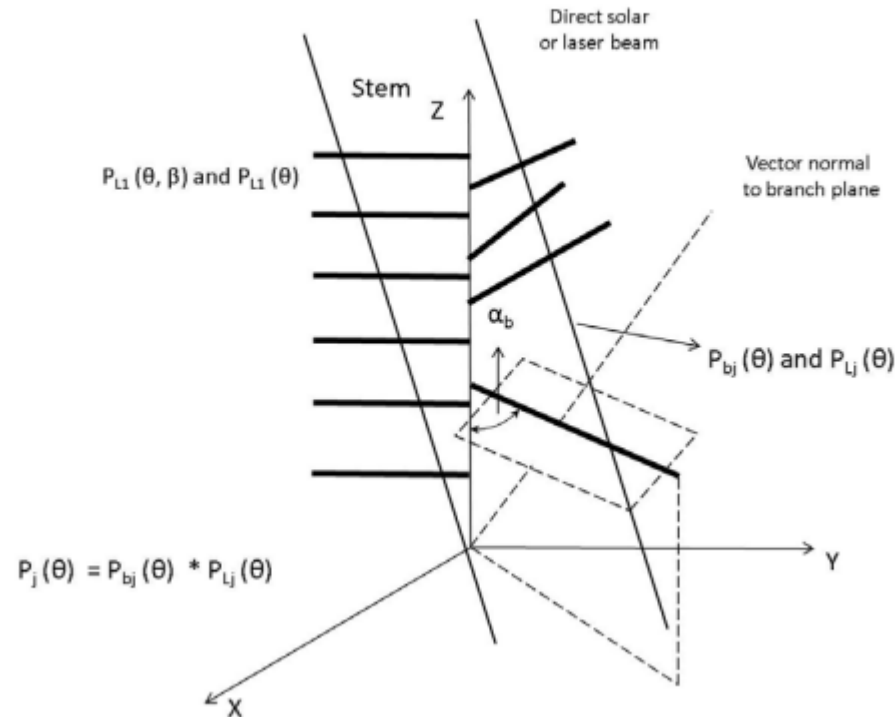
# Leaf Area Direct Measure

- Direct Measure (Litterfall and destructive harvest)
- Used for development of indirect measures
- Most accurate
- Total mass/area = LAI x LMA (for each species)???
- Allometric relationships, such as LAI and DBH
- Complications:
  - Species
  - Forest composition
  - Canopy position
  - Climate
  - Weather

# Leaf Area Indirect Measure

- Effective LAI ( $L_e$ ) – assume random distribution of foliage

**Figure 3.** Schematic diagram illustrating the multi-layer theoretical model to calculate the gap fraction.





# Leaf Area Indirect Measure

- Effective LAI ( $L_e$ ) – assume random distribution of foliage
  - Canopy gap fraction
  - Includes woody components
  - Can convert for non-random distributions (see Kucharik et al (1999) and Gower et al (1999))
  - Often 30-70% of true LAI
  - Without conversion, Plant Area Index (PAI)
  - Can subtract Wood Area Index from PAI to get LAI
- Complications:
  - Forest type (boreal forests have high proportions of wood area to total plant area)
  - Overcompensation ( $LAI \neq PAI - WAI$ )
  - Weather
  - Upper limit (about 5-6)

# LA Indirect Measure

- Digital Camera – Hemispherical
  - Assumes random distribution
  - Diffuse sky conditions
  - Correction factors ( $L_e \rightarrow PAI$ ) unless light environment is only goal
  - Software (eg. CIMES: <http://jmnw.free.fr/>)
  - Key concepts:
    - Consistent exposure
    - Correct for camera and lens
    - Correct for clumping
- LAI 2000 plant canopy gap analyzer (Li-COR)
  - Instantaneous processing
  - Above canopy reference required
  - Underestimation in heterogeneous canopies

# LAI 2000 Plant Canopy Analyzer



[http://envsupport.licor.com/images/env/product\\_list\\_photos/LAI-2000\\_lg.jpg](http://envsupport.licor.com/images/env/product_list_photos/LAI-2000_lg.jpg)

# ANPP

- $ANPP = F_A + F_W + \Delta C_C + \Delta C_W$ 
  - where:
  - $F_A$  = flux of C associated with litterfall
  - $F_W$  = flux of C associated with mortality
  - $\Delta C_C$  = increment of C associated with C content in live leaves
  - $\Delta C_W$  = increment of C associated with aboveground biomass
    - Monthly measurement of DBH, input into site specific allometric equation for DBH and woody biomass

# APR

- $APR = L_{RC} + L_{RM} + W_R$ 
  - where:
    - $L_{RC}$  = sum of construction
    - $L_{RM}$  = sum maintenance respiration
    - $W_R$  = respiration of aboveground wood

# APR

- $APR = L_{RC} + L_{RM} + W_R$ 
  - where:
  - $L_{RC}$  = sum of construction
    - How much energy is expelled in the formation of structural and metabolic compounds (Baruch & Goldstein 1999)
    - Assumed cost to be 25% of leaf NPP, from other research.  
Leaf NPP =  $F_A + \Delta C_C$  (Giardina et al 2003)

# APR

- $APR = L_{RC} + L_{RM} + W_R$ 
  - where:
  - $L_{RC}$  = sum of construction
  - $L_{RM}$  = sum maintenance respiration
    - Estimated by 'periodically' (4 times) measuring  $CO_2$  efflux at night from intact leaves
    - Used towers
    - Plexiglass chambers with PPSystems CIRAS-1 in open system mode
    - Between 21:00 and 02:00
    - Four positions in the canopy
    - $L_{RM} = N_C \times a \times$  (seconds of darkness in 1 year) where  $N_C$  is annual average N content of forest canopy ( $\text{mol N m}^{-2}$ ) and  $a$  is a dark respiration coefficient produced from CIRAS-1 measurements
    - $N_C$  estimated from LAI and from measurement of SLA and Leaf N from harvested leaves

# APR

- $APR = L_{RC} + L_{RM} + W_R$ 
  - where:
  - $L_{RC}$  = sum of construction
  - $L_{RM}$  = sum maintenance respiration

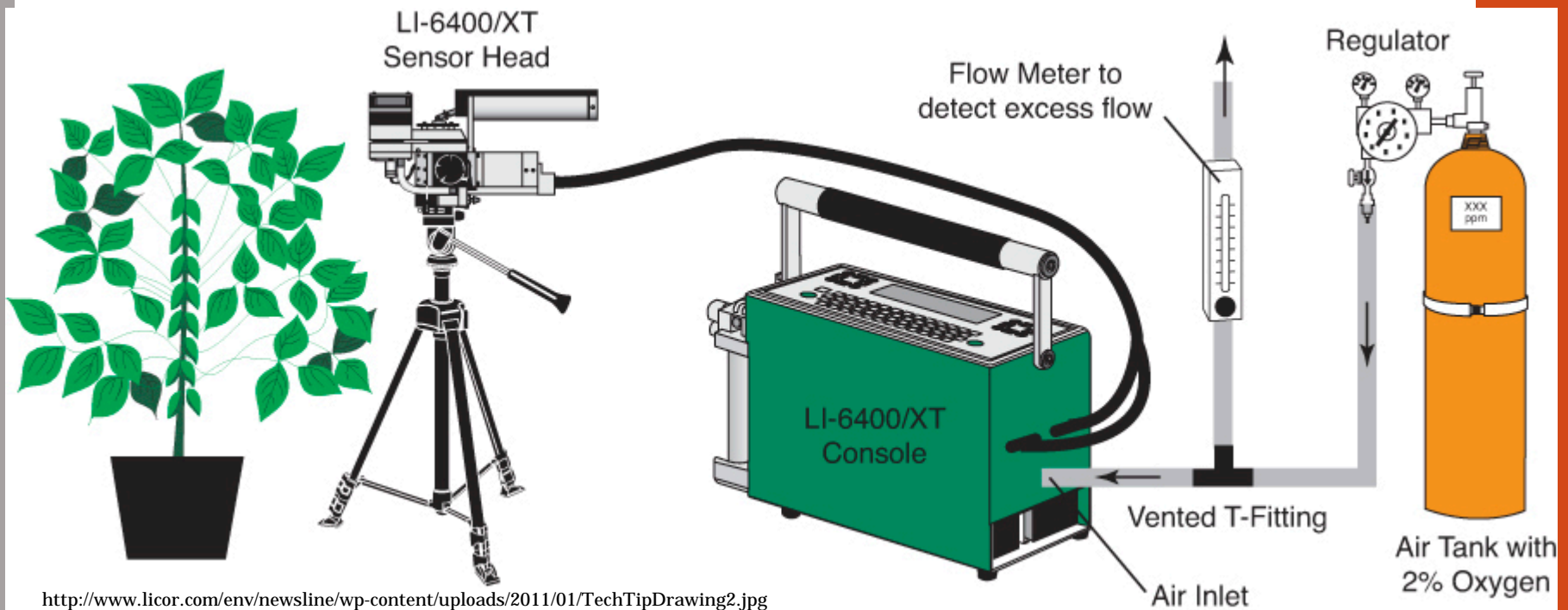


[http://www.ppsystems.com/images/products/EGM-4\\_CPY-4\\_web.jpg](http://www.ppsystems.com/images/products/EGM-4_CPY-4_web.jpg)



# APR

- $APR = L_{RC} + L_{RM} + W_R$ 
  - where:
  - $L_{RC}$  = sum of construction
  - $L_{RM}$  = sum maintenance respiration



# APR

- $APR = L_{RC} + L_{RM} + W_R$ 
  - where:
    - $L_{RC}$  = sum of construction
    - $L_{RM}$  = sum maintenance respiration
    - $W_R$  = respiration of aboveground wood
      - Same PPSystems CIRAS-1 system
      - Applied allometrically derived equation for woody biomass and multiplied by seconds in the year to get flux

# APR

- $APR = L_{RC} + L_{RM} + W_R$ 
  - where:
  - $L_{RC}$  = sum of construction
  - $L_{RM}$  = sum maintenance respiration
  - $W_R$  = respiration of aboveground wood



[http://www.es.e.u-psud.fr/IMG/jpg/Chambre-resp\\_site-4.jpg](http://www.es.e.u-psud.fr/IMG/jpg/Chambre-resp_site-4.jpg)

# APR

- **APR** =  $L_{RC} + L_{RM} + W_R$ 
  - where:
  - $L_{RC}$  = sum of construction
  - $L_{RM}$  = sum maintenance respiration
  - $W_R$  = respiration of aboveground wood
- Sources of error:
  - Assumed cost of construction, but differs and can be important (Baruch & Goldstein 1999)
  - Scaling based on allometric equations: importance of site specific equations
  - Operator
  - Planning
  - Leakage

# TBCF

- $TBCF = F_S + F_E - F_A + \Delta C_S + \Delta C_R + C_L$ 
  - where:
  - $F_S$  = soil surface CO<sub>2</sub> efflux
    - CIRAS-1 Soil Respiration Chamber
    - measured rate x seconds in a month

# TBCF

- $\text{TBCF} = F_S + F_E - F_A + \Delta C_S + \Delta C_R + C_L$ 
  - where:
    - $F_S$  = soil surface  $\text{CO}_2$  efflux
    - $F_E$  = leached C
      - Assumed to be less than 1% of TBCF (per year) in closed canopy forest (Giardina & Ryan 2002)

# TBCF

- $\text{TBCF} = F_S + F_E - F_A + \Delta C_S + \Delta C_R + C_L$ 
  - where:
  - $F_S$  = soil surface CO<sub>2</sub> efflux
  - $F_E$  = leached C
  - $F_A$  = litterfall

# TBCF

- $TBCF = F_S + F_E - F_A + \Delta C_S + \Delta C_R + C_L$ 
  - where:
    - $F_S$  = soil surface CO<sub>2</sub> efflux
    - $F_E$  = leached C
    - $F_A$  = litterfall
    - $\Delta C_S$  = change in C in mineral soil (see Burton & Pregitzer 2008)
      - Site specific
      - Volumetric pits
      - Combustion at high temperature (1000°C) with elemental analyzer
      - Problems: removal of inorganic C, stone%, organic soils, forest heterogeneity
      - Some assume no change below a certain depth (Giardina & Ryan 2002)



# TBCF

- **$TBCF = F_S + F_E - F_A + \Delta C_S + \Delta C_R + C_L$** 
  - where:
    - $F_S$  = soil surface CO<sub>2</sub> efflux
    - $F_E$  = leached C
    - $F_A$  = litterfall
    - $\Delta C_S$  = change in C in mineral soil
    - $\Delta C_R$  = increment of C in root biomass
      - Coarse roots (>10 mm diameter): relationship between coarse root biomass and aboveground biomass
        - 20-30% of aboveground woody biomass (Burton and Pregitzer 2008)
        - Dead roots important
      - Fine roots
        - Some assume no net change during course of study and overall C stock can be low compared to other components (Burton and Pregitzer 2008; Giardina et al 2003)
        - Some argue that models must take this into account (Wolf et al 2011)
        - Sorting, labor intensive

# TBCF

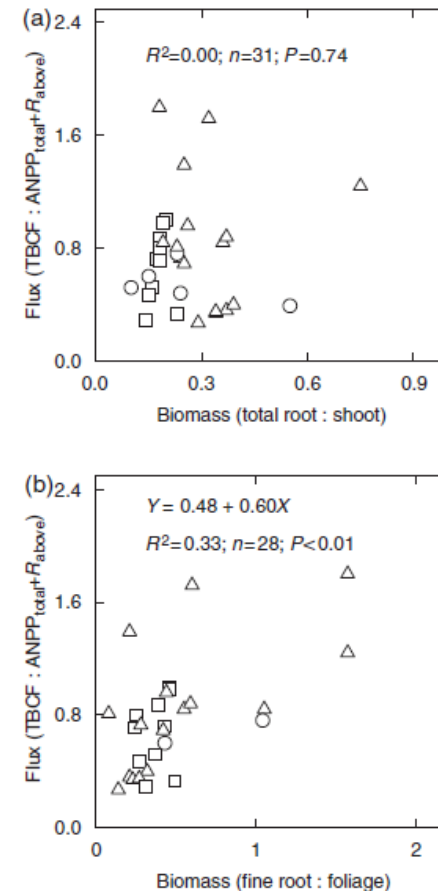
- $\text{TBCF} = F_S + F_E - F_A + \Delta C_S + \Delta C_R + C_L$ 
  - where:
    - $F_S$  = soil surface  $\text{CO}_2$  efflux
    - $F_E$  = leached C
    - $F_A$  = litterfall
    - $\Delta C_S$  = change in C in mineral soil
    - $\Delta C_R$  = increment of C in root biomass
    - $C_L$  = Litter layer mass
      - Litter traps, dried samples, assume 50% C

# Allocation and Partitioning

- Individual level:
  - Above-ground:below-ground
  - DBH/Height
  - Fine Root:LA
- Individual as part of NPP (from Wolf et al 2011)
  - Importance of ontogeny
  - Gfol (NPPfol/density of stand)
  - Gfroot (NPPfroot/density of stand)
  - Gcroot (NPPcroot/density of stand)
  - Gstem (NPPstem/density of stand)
- Stand level (from Nouvellon et al 2012)
  - TBCF/GPP
  - ANPP/TBCF
  - $\Delta B_w$ /ANPP
  - $\Delta B_w$ /GPP

# “Carbon allocation in forest ecosystems” by Litton et al 2007

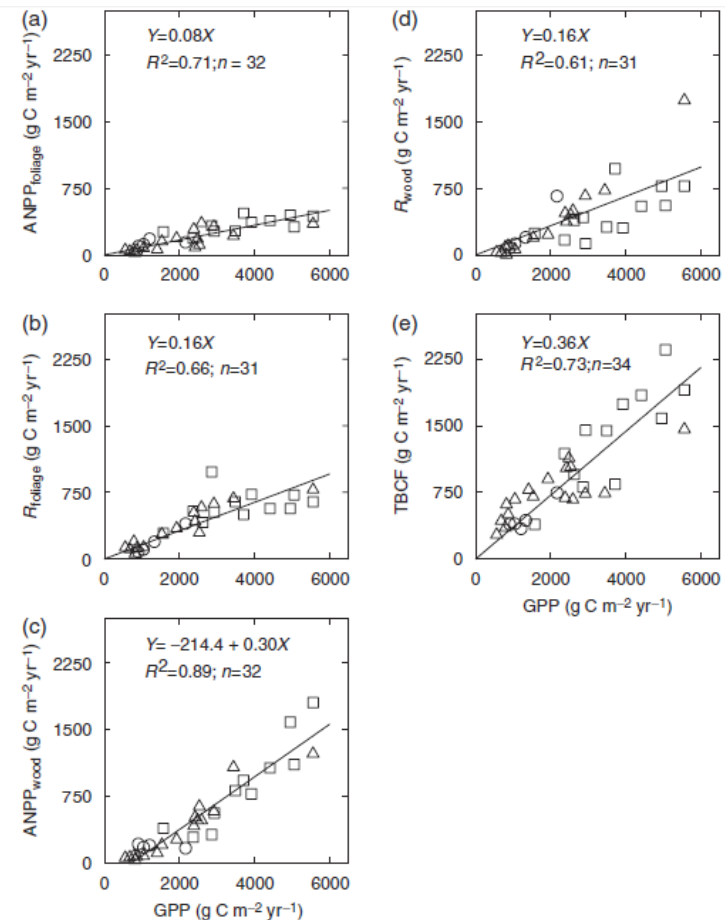
- Annual carbon flux and partitioning cannot be inferred by biomass ratios.
  - Multiyear accumulated wood
  - Storage in roots
  - Short lived leaves and fine roots
  - Annual plants could be an exception



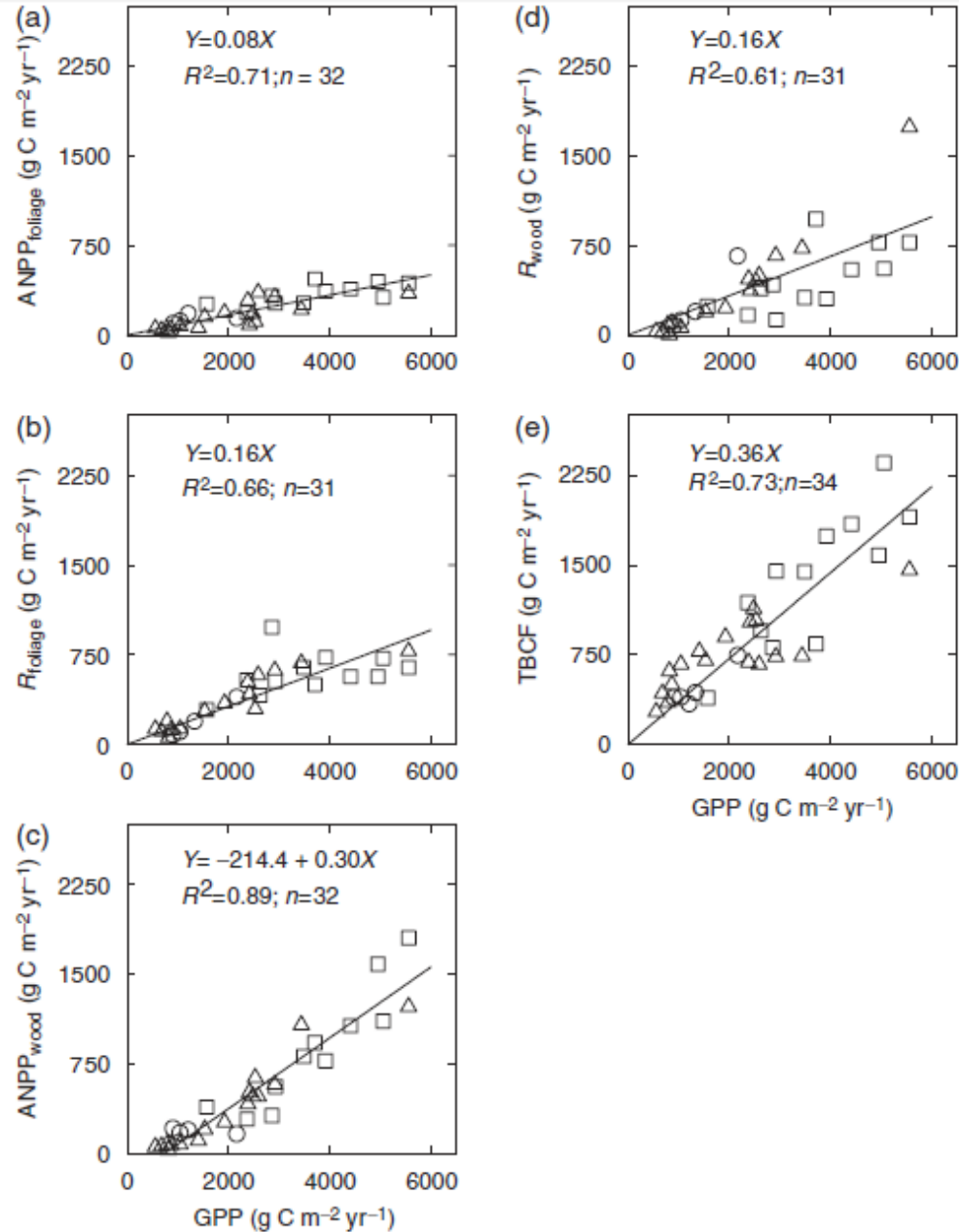
**Fig. 2** Carbon flux is poorly related to biomass in forest ecosystems. Biomass ratios and flux (TBCF : ANPP<sub>total</sub> + R<sub>above</sub>, an ecosystem carbon flux analog to root : shoot biomass) were not related for (a) total root : shoot across diverse forest ecosystems that represent gradients in resource availability, stand age and competition. A somewhat better relationship existed between (b) flux and fine root : foliage biomass. Triangles are needleleaf evergreen forests, circles are temperate deciduous forests, and squares are broadleaf evergreen forests. TBCF, total below-ground carbon flux.

# “Carbon allocation in forest ecosystems” by Litton et al 2007

- There is a correlation between different component fluxes and GPP:
  - foliage production
  - foliage respiration
  - wood production
  - wood respiration
  - total belowground carbon flux



**Fig. 4** (a) Foliage production (ANPP<sub>foliage</sub>), (b) foliage respiration ( $R_{\text{foliage}}$ ), (c) wood production (ANPP<sub>wood</sub>), (d) wood respiration ( $R_{\text{wood}}$ ), and (e) total belowground carbon flux (TBCF) all exhibited strong linear relationships with GPP across diverse forest ecosystems ( $P < 0.01$ ). Zero-intercept regressions were used where the constant was not significant at  $\alpha = 0.05$ . Triangles are needleleaf evergreen forests, circles are temperate deciduous forests, and squares are broadleaf evergreen forests. GPP, gross primary productivity.



**Fig. 4** (a) Foliage production (ANPP<sub>foliage</sub>), (b) foliage respiration ( $R_{\text{foliage}}$ ), (c) wood production (ANPP<sub>wood</sub>), (d) wood respiration ( $R_{\text{wood}}$ ), and (e) total belowground carbon flux (TBCF) all exhibited strong linear relationships with GPP across diverse forest ecosystems ( $P < 0.01$ ). Zero-intercept regressions were used where the constant was not significant at  $\alpha = 0.05$ . Triangles are needleleaf evergreen forests, circles are temperate deciduous forests, and squares are broadleaf evergreen forests. GPP, gross primary productivity.

# “Carbon allocation in forest ecosystems” by Litton et al 2007

- Total belowground carbon flux increases with aboveground net primary productivity
  - ANPP may not accurately predict TBCF

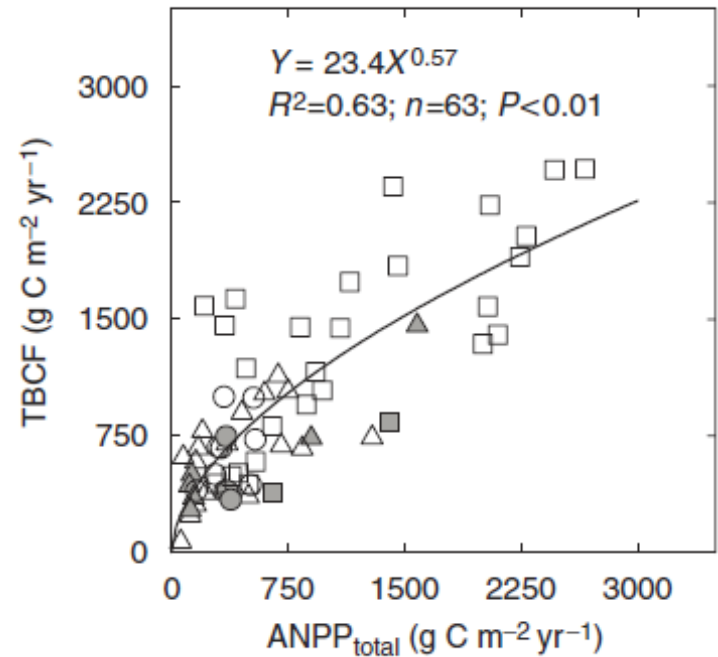


Fig. 5 Across forests, carbon flux to belowground (TBCF) increased with total aboveground net primary production (ANPP<sub>total</sub>). TBCF was estimated as soil-surface CO<sub>2</sub> efflux minus aboveground litterfall plus any measured changes in soil carbon pools for all studies except those indicated with gray fill, where TBCF was estimated as BNPP<sub>root</sub> + R<sub>root</sub>. Triangles are needleleaf evergreen forests, circles are temperate deciduous forests, and squares are broadleaf evergreen forests. TBCF, total belowground carbon flux.

# “Carbon allocation in forest ecosystems” by Litton et al 2007

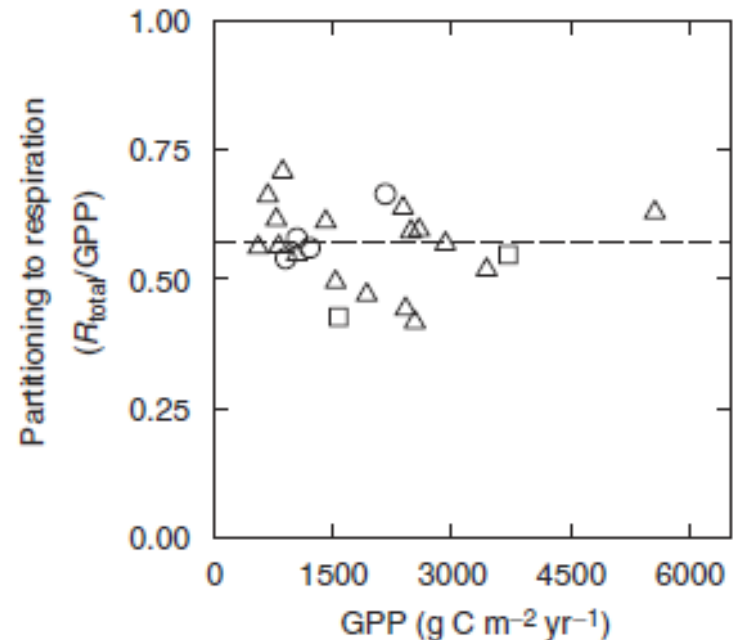
- Autotrophic respiration is strongly and positively related to GPP
- Again, the relationship differs between components
  - Less increase in wood respiration than foliage respiration per increase in GPP
    - Wood has less metabolic activity





# “Carbon allocation in forest ecosystems” by Litton et al 2007

- GPP partitioning to respiration is constant across a wide range of GPP in forest ecosystems
  - Average 57% of GPP
- Does not vary with resource availability, competition or stand age



**Fig. 7** There was a strong central tendency in partitioning to respiration ( $R_{\text{total}}$ ) across diverse forest ecosystems that represent gradients in resource availability, stand age and competition [ $0.57 \pm 0.02$  (Mean  $\pm$  1 SE)]. The dashed line is the slope of the relationship between GPP and  $R_{\text{total}}$  ( $R_{\text{total}} = 0.57 \times \text{GPP}$ ;  $R^2 = 0.95$ ;  $n = 23$ ;  $P < 0.01$ ). However, partitioning to  $R_{\text{total}}$  did vary across sites – the range for studies analyzed was 42–71%. Triangles are needleleaf evergreen forests, circles are temperate deciduous forests, and squares are broadleaf evergreen forests.

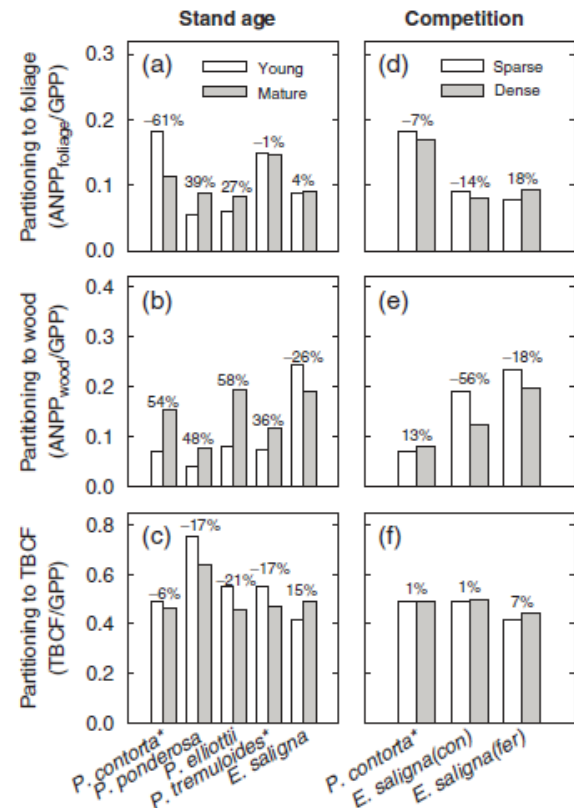
# “Carbon allocation in forest ecosystems” by Litton et al 2007

- There were variations across different sites- 42%-71% of GPP
  - 71% boreal spruce
  - 66% boreal pine
  - 68% tropical forest



# “Carbon allocation in forest ecosystems” by Litton et al 2007

- GPP partitioning to ANPP increases and to total belowground flux decreases with increasing stand age
  - Exceptions:
    - *Eucalyptus saligna* in Hawaii
    - Lodgepole pine in Wyoming



**Fig. 8** Carbon partitioning varied with stand age (a–c), but not competition (i.e. tree density; d–f). Variation with age was a result of increased partitioning to (a) ANPP<sub>foliage</sub> and (b) ANPP<sub>wood</sub>, (c) and decreased partitioning to TBCF in mature stands for all sites but *Eucalyptus saligna*. Data are from Litton et al. (2004) for *Pinus contorta*, Law et al. (2001) for *Pinus ponderosa*, Ewel et al. (1987) and Gholz & Fisher (1982) for *Pinus elliotii*, Fornwalt (1999) for *Populus tremuloides*, and Ryan et al. (2004) for *E. saligna*. For studies denoted with an \*,  $R_{\text{foliage}}$  and  $R_{\text{wood}}$  were estimated using relationships with ANPP<sub>foliage</sub> and ANPP<sub>wood</sub> (Fig. 6a and b). TBCF, total belowground carbon flux.

# “Carbon allocation in forest ecosystems” by Litton et al 2007

- Intraspecific competition (tree density) had no consistent effect on GPP partitioning between ANPP and TBCF
- Increased nutrient and water availability increased partitioning to ANPP and decreased partitioning to TBCF
  - Except P
  - Response to water had more variability



# Carbon allocation in forest ecosystems” by Litton et al

- Priorities do NOT exist for the products of photosynthesis.
  - such that carbon is used first by higher priority tissues and only released to other tissues when those needs are satisfied
  - Because with increased GPP, all pools and fluxes increased.





# Partitioning and Climate

**Table 6.** Annual C fluxes ( $\text{g m}^{-2} \text{ year}^{-1}$ ) at the three forest sites

|  | Tropical          | Temperate        | Boreal           |
|--|-------------------|------------------|------------------|
| Component fluxes:  |                   |                  |                  |
| Above ground vegetation:                                     |                   |                  |                  |
| (1) Gross photosynthesis of tree foliage ( $G_p$ )           | 3040 <sup>1</sup> | 1725             | 963              |
| (2) Respiration of tree foliage                              | 410 <sup>2</sup>  | 191              | 216 <sup>7</sup> |
| (3) Respiration of tree wood                                 | 390 <sup>2</sup>  | 196              | 87 <sup>8</sup>  |
| (4) Leaf and wood detritus                                   | 700 <sup>3</sup>  | 360 <sup>4</sup> | 51 <sup>5</sup>  |
| (5) Net biomass increment                                    | 170 <sup>3</sup>  | 150 <sup>4</sup> | 110 <sup>5</sup> |
| (6) Transport to roots (1) – (2) – (3) – (4) – (5)           | 1370              | 828              | 499              |
| Below ground vegetation:                                     |                   |                  |                  |
| (7) Respiration of roots                                     | 680 <sup>1</sup>  | 395              | 143 <sup>6</sup> |
| (8) Net root biomass increment                               | 60 <sup>1</sup>   | 39               | 30 <sup>6</sup>  |
| (9) Root detritus production                                 | 630 <sup>1</sup>  | 395              | 326              |
| (10) Total ground respiration                                | 1650 <sup>2</sup> | 753              | 592              |
| (11) Heterotrophic Respiration (10) – (2) – (3)              | 970               | 359              | 449              |
| (12) Autotrophic Respiration (15) – (11)                     | 1480              | 782              | 446              |
| Soil:  |                   |                  |                  |
| (13) Change in SOM (4) + (9) – (11)                          | +360              | +396             | –72              |
| (14) Total C influx (1)                                      | 3040              | 1725             | 963              |
| (15) Total C efflux (14) – (16)                              | 2450              | 1140             | 895              |
| (16) Net ecosystem exchange (NEE)                            | 590               | 585              | 68               |
| (17) $N_p$ (1) – (2) – (3) – (7)<br>or (4) + (5) + (8) + (9) | 1560              | 944              | 517              |
| (18) $N_p/G_p$ (17)/(1)                                      | 51%               | 55%              | 54%              |
| Mean carbon residence times (years):                         |                   |                  |                  |
| (19) Biomass   | 16                | 10               | 12               |
| (20) Soil and litter   | 15                | 10               | 106              |
| (21) Total ecosystem   | 29                | 18               | 89               |

<sup>1</sup> from Malhi *et al.* 1998, Malhi *et al.* unpublished data; <sup>2</sup> from Meir *et al.* 1996, for another site in Rondonia; <sup>3</sup> from Higuchi *et al.* (1997); <sup>4</sup> from Edwards *et al.* 1989; <sup>5</sup> from Gower *et al.* 1997; <sup>6</sup> from Steele *et al.* 1997; <sup>7</sup> from Rayment 1998; <sup>8</sup> from Lavigne & Ryan 1997

# Partitioning and Nutrient Availability

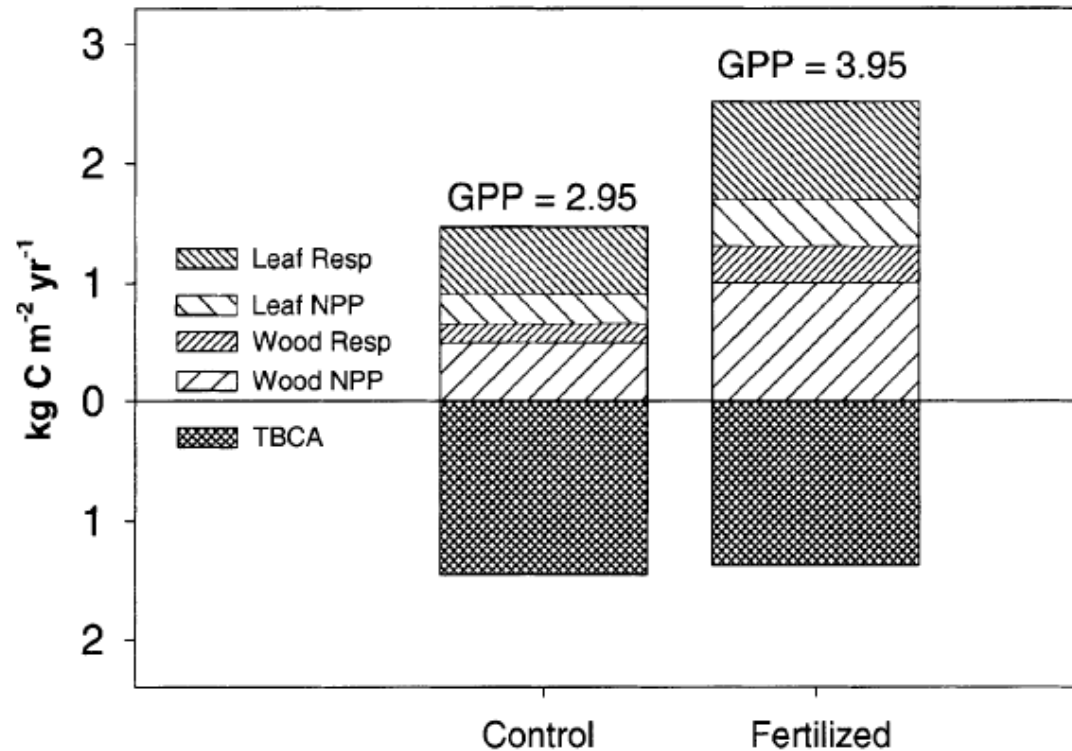
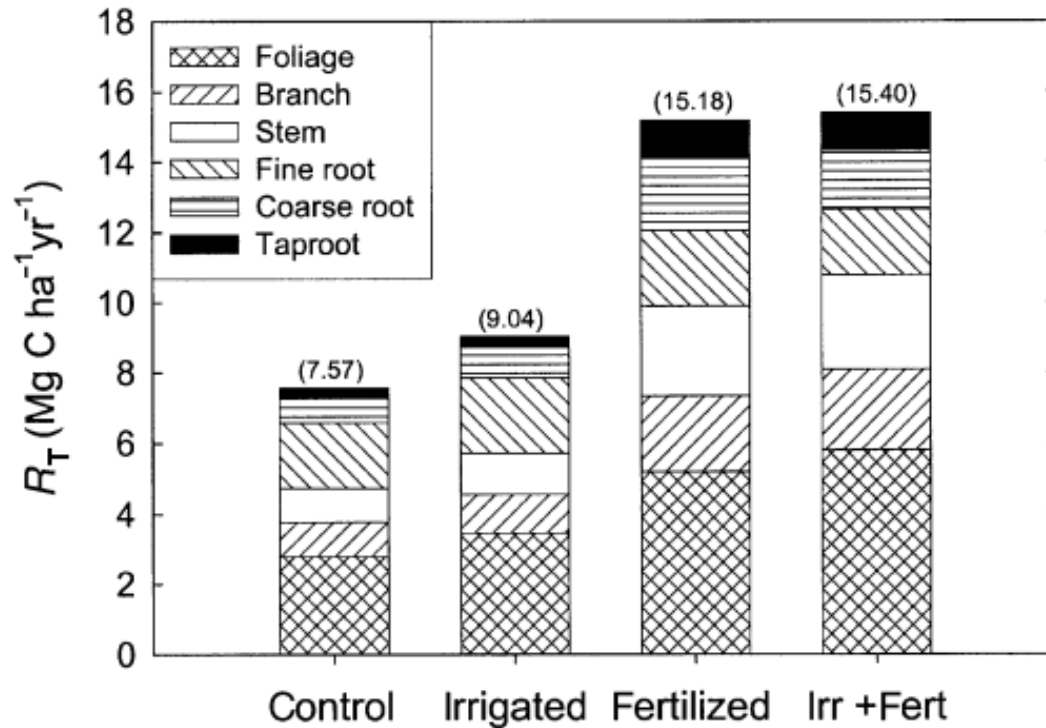


Fig. 1 Gross primary production (mean of three years of postfertilization data) in unfertilized and adjacent fertilized stands of *E. saligna* in Pepe'ekeo, Hawai'i, and the constituent above and belowground components (see the Appendix for term definitions).

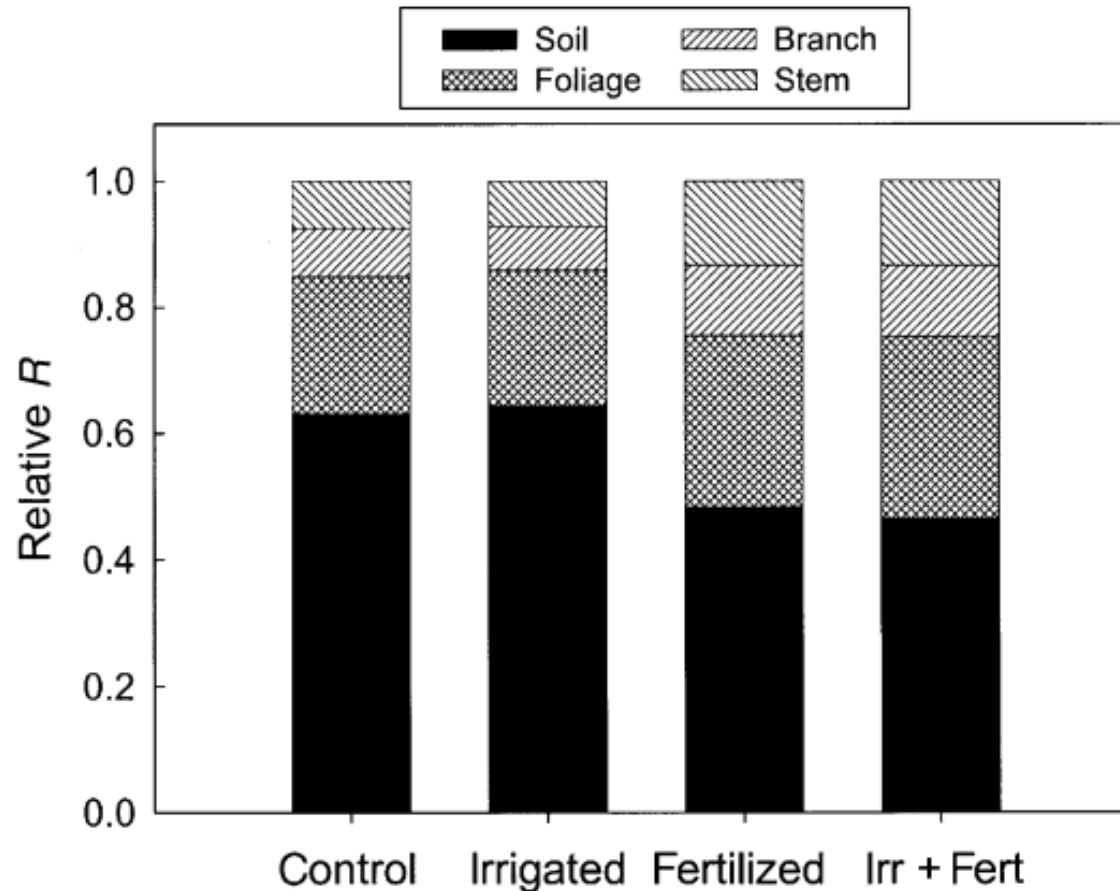
# Partitioning, Water, and Nutrients



**Fig. 2** Mean annual carbon flux from total respiration ( $R_T$ ) (maintenance plus growth respiration) by tissue component in 12-year-old loblolly pine plantations. Values were generated using Eqns (2) and (3).



# Partitioning, Water, and Nutrients



**Fig. 6** Fraction of ecosystem respiration ( $R_E$ ) generated from soil and aboveground components.

# “...Carbon Allocation in Monocultures and Mixed Species Plantations... in Brazil” by Nouvellon et al 2012

- **Jean-Pierre Bouillet**

- Cirad scientist
- Currently visiting professor at the **University of Sao-Paulo** (USP-Esalq) in Brazil
- Silviculture of mixed-species Eucalyptus plantations
- Diploma (1984) and PhD (1993) in Forest Sciences from Engref, Nancy (France)
- Experience in French Guyana (tree breeding), Madagascar (pine and eucalyptus), Congo (productivity of eucalyptus), and France (management of tropical forest ecosystems)
- Published more than 35 peer-reviewed journal articles

# “...Carbon Allocation in Monocultures and Mixed Species Plantations... in Brazil” by Nouvellon et al 2012

**Jean-Pierre Bouillet**



[http://intens-fix.cirad.fr/var/intens\\_fix/storage/images/intens-fix/faits-marquants/visite-de-j.p.-bouillet-a-orleans-le-30-mai-2011/31152-2-fre-FR/visite-de-j.p.-bouillet-a-orleans-le-30-mai-2011.jpg](http://intens-fix.cirad.fr/var/intens_fix/storage/images/intens-fix/faits-marquants/visite-de-j.p.-bouillet-a-orleans-le-30-mai-2011/31152-2-fre-FR/visite-de-j.p.-bouillet-a-orleans-le-30-mai-2011.jpg)

# **“...Carbon Allocation in Monocultures and Mixed Species Plantations... in Brazil” by Nouvellon et al 2012**

- **Yann Nouvellon**
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  - **Has 158.79 Impact Points and 74 followers on Research Gate**



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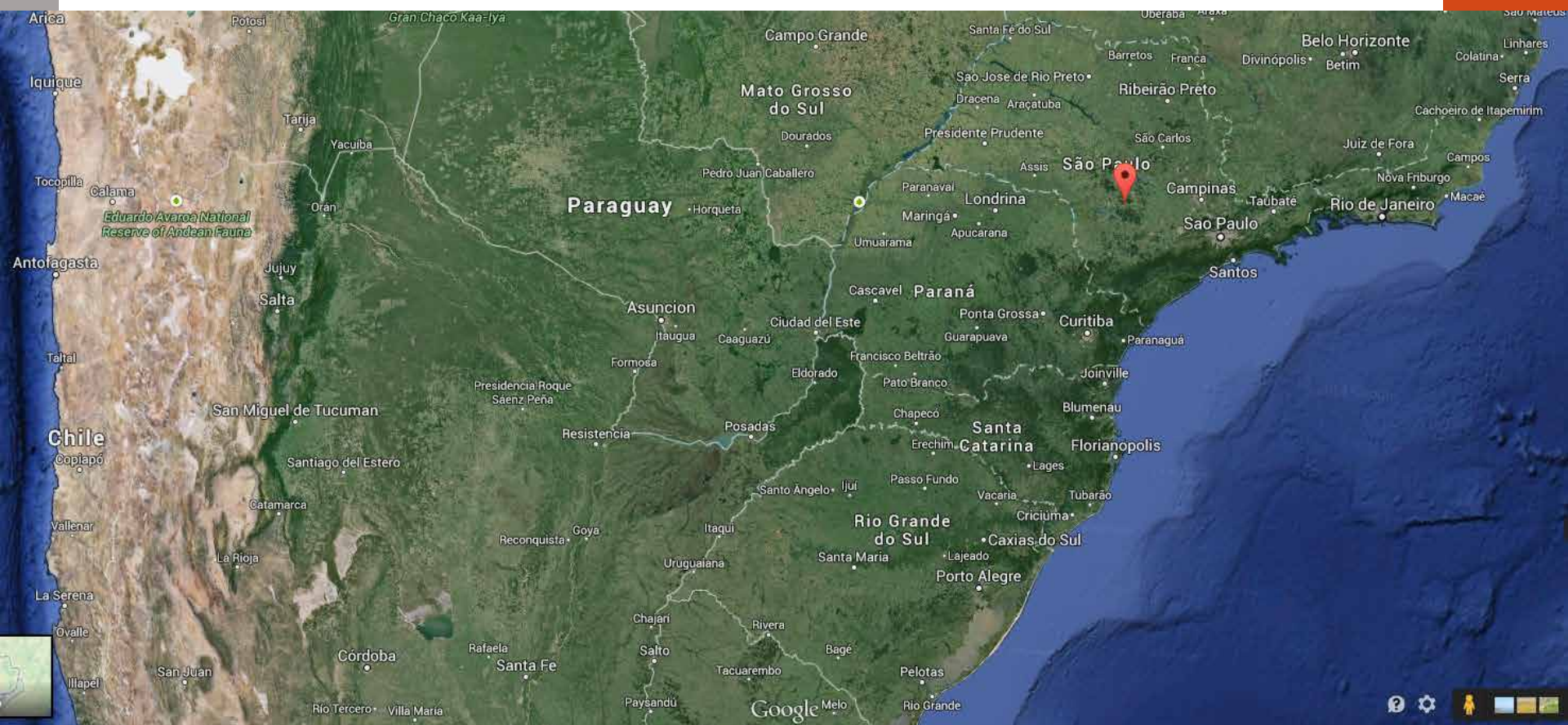


# “...Carbon Allocation in Monocultures and Mixed Species Plantations... in Brazil” by Nouvellon et al 2012





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# “...Carbon Allocation in Monocultures and Mixed Species Plantations... in Brazil” by Nouvellon et al 2012

- *Eucalyptus grandis* summary
  - Height: 43-55m
  - Diameter: 122-183cm
  - Growth: 2 m year<sup>-1</sup>
  - Characteristics: shade intolerant
  - Plantations: >500,000 ha worldwide
  - Uses: pulpwood, poles, pallets, veneer, landscaping
  - Natural distribution
    - Soils: alluvial and volcanic loams
    - 26-33 degrees S
    - Mean minimum temperature from 2-10°C and maximum up to 29°C
    - Rainfall: 1020-1780mm with distinct dry season





# “...Carbon Allocation in Monocultures and Mixed Species Plantations... in Brazil” by Nouvellon et al 2012

- *Acacia mangium* summary

- Height: up to 30 m
- Growth: ~1 m year<sup>-1</sup>
- Characteristics: shade intolerant
- Plantations: extensive worldwide (eg. 1.5 Mha in Asia in 2006)
- Uses: pulpwood, pallet, timber
- Natural distribution
  - Soils: alluvial and volcanic, sandy or loamy; tolerates acid (< 4 pH) and low nutrient soils well
  - At the edges of rainforests or coastal plain
  - Mean minimum month from 15-22°C and maximum up to 31-34°C
  - Rainfall: 1500-3000 mm with distinct dry season





# “...Carbon Allocation in Monocultures and Mixed Species Plantations... in Brazil” by Nouvellon et al 2012

**Questions:** Is lower production in mixed plantations due to a shift in partitioning to TBCF?

**Hypotheses:**

1. Species differences for wood production were partly explained by different C partitioning strategies
2. Lower partitioning to aboveground biomass mostly explains lower wood production in the mixture in comparison to the eucalypt monoculture

# “...Carbon Allocation in Monocultures and Mixed Species Plantations... in Brazil” by Nouvellon et al 2012

- Tree Growth
  - Mixed plot
    - *Eucalyptus grandis* dominated
      - Higher growth rate
  - Mean tree height was intermediate
  - Stand basal areas
    - Not different between the 3 treatments
    - Mixed plot
      - Individual basal area
        - *Eucalyptus grandis* greater than in monoculture
        - *Acacia mangium* less than monoculture
          - Interspecific competition

# “...Carbon Allocation in Monocultures and Mixed Species Plantations... in Brazil” by Nouvellon et al 2012

- Mixed Plot
  - *Acacia mangium*
    - Higher height/basal area than monoculture
      - Less number of stems
  - *Eucalyptus grandis*
    - Opposite case
- Total Above Ground Biomass Wood Biomass
  - Affected by stand height
    - *Eucalyptus grandis* monoculture -highest
    - Mixed Plot- intermediate
    - *Acacia mangium* monoculture-shortest

# “...Carbon Allocation in Monocultures and Mixed Species Plantations... in Brazil” by Nouvellon et al 2012

- Above Ground Biomass
  - Mixed plot
    - Greatest leaf biomass
      - leaf biomass/Total aboveground biomass
    - *Eucalyptus grandis*
      - 43% more wood biomass per tree
      - 74% more leaf biomass per tree
    - *Acacia mangium*
      - 53% less wood biomass
      - 24% less leaf biomass
- No differences in leaf litterfall
- Litterfall accounted for:
  - 24% ANPP *Eucalyptus grandis* monoculture
  - 22% ANPP *Acacia mangium* monoculture

# “...Carbon Allocation in Monocultures and Mixed Species Plantations... in Brazil” by Nouvellon et al 2012

- Total Belowground Carbon Flux (TBCF)
  - Cumulative Soil CO<sub>2</sub> efflux ( $F_{\text{scum}}$ )
    - Lowest in *Acacia mangium* monoculture
    - Highest in the mixed plot
      - 54% more near *Eucalyptus grandis* monoculture
  - Annual litterfall ( $L_{\text{cum}}$ )
    - Lowest in *Acacia mangium* monoculture
      - Less woody litterfal

# “...Carbon Allocation in Monocultures and Mixed Species Plantations... in Brazil” by Nouvellon et al 2012

- Total Belowground Carbon Flux
  - Significantly lower in *Acacia mangium* monoculture than other monoculture
  - Forest Floor Carbon ( $C_L$ )
    - Decreased in *Acacia mangium* monoculture
    - Increased in the mixed plot and *Eucalyptus grandis* monoculture
  - No differences in C efflux from coarse roots and stumps from previous rotations ( $\Delta C_L / \Delta t$ )
  - Coarse and medium root biomass increment ( $\Delta B_R$ )
    - Lowest in *Acacia mangium* monoculture
    - Highest in *Eucalyptus grandis* monoculture

# “...Carbon Allocation in Monocultures and Mixed Species Plantations... in Brazil” by Nouvellon et al 2012

| Ratio              | <i>Eucalyptus grandis</i> monoculture (Kg C) | Mixed Plot (Kg C) | <i>Acacia mangium</i> monoculture (Kg C) |
|--------------------|--|-------------------|--|
| ANPP/TBCF          | Higher<br>1.6                                | Lower<br>1.1      | Higher<br>1.5                            |
| $\Delta B_w$ /ANPP | Higher<br>0.76                               | Lower<br>0.70     | Higher<br>0.76                           |
| $\Delta B_w$ /TBCF | Higher<br>1.3                                | Lower<br>0.79     | Higher<br>1.1                            |

# “...Carbon Allocation in Monocultures and Mixed Species Plantations... in Brazil” by Nouvellon et al 2012

- GPP was 30% higher in *Eucalyptus grandis* monoculture than the other monoculture
  - *Acacia mangium* monoculture was the lowest
- GPP in the mixed plot was intermediate
  - 15% lower than *Eucalyptus grandis* monoculture
  - 10% higher than *Acacia mangium* monoculture



# “...Carbon Allocation in Monocultures and Mixed Species Plantations... in Brazil” by Nouvellon et al 2012

- TBCF/GPP
  - Around 25% for both monocultures.
  - 32% for the mixed plot
- The fraction allocated to above ground wood production ( $\Delta B_w$  /GPP) was higher than TBCF/GPP in monocultures.
  - Opposite effect in mixed plot

# “...Carbon Allocation in Monocultures and Mixed Species Plantations... in Brazil” by Nouvellon et al 2012

- Leaf Area Index (LAI) and Photosynthetically active radiation absorbed by the canopy (APAR)
  - About 35% higher in mixed plot than monocultures
  - No increases in production
    - Lowest light use efficiencies in mixed plot
- Light use efficiencies
  - Higher in *Eucalyptus grandis* monoculture than *Acacia mangium* monoculture

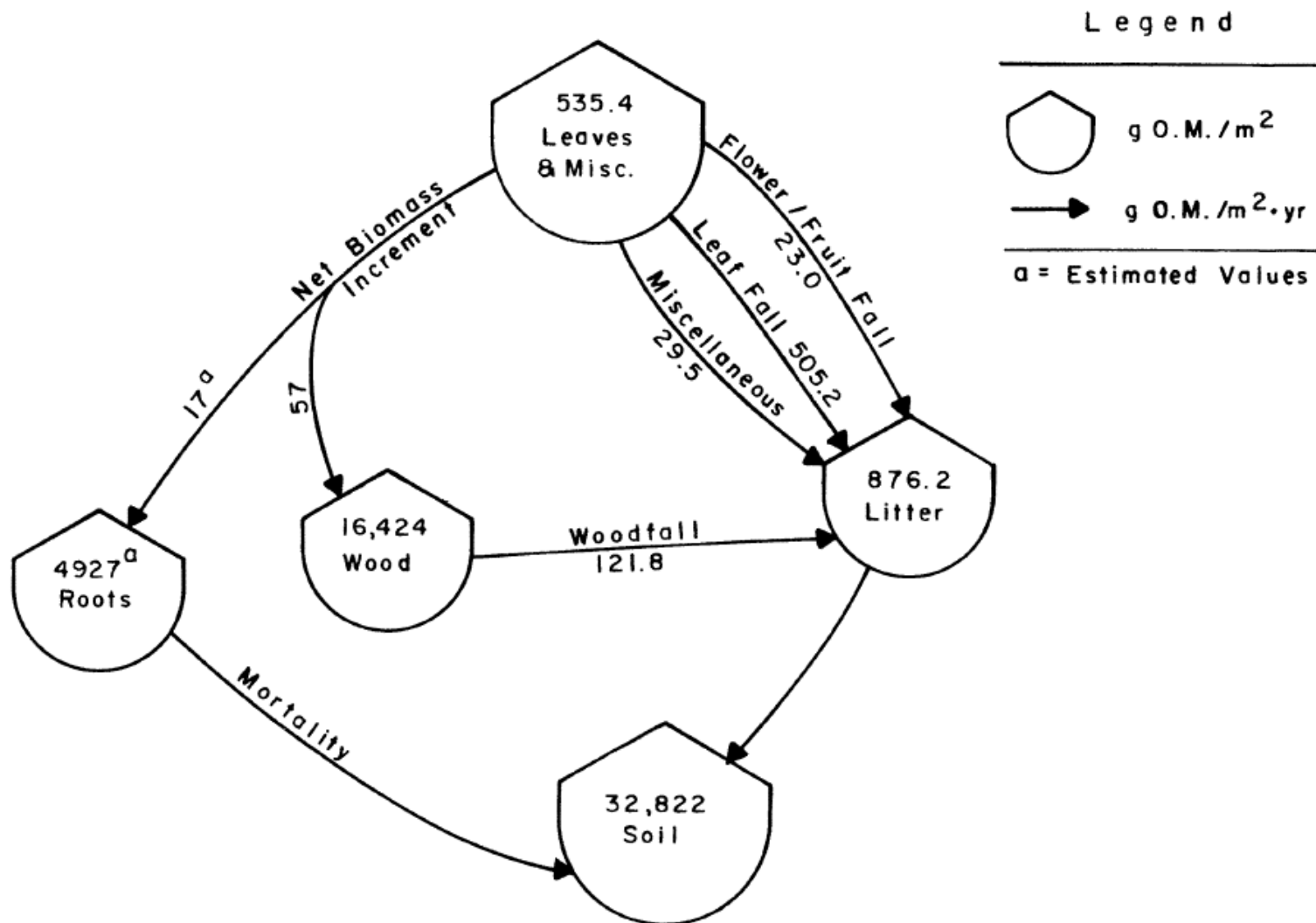


FIGURE 6. Mean annual organic matter (O.M.) budget for two 0.40-ha plots in the Colorado forest.

Peter L. Weaver, Peter G. Murphy. 1990. Forest Structure and Productivity in Puerto Rico's Luquillo Mountain. *BIOTROPICA* 22(1): 69-82

# Allocation and Partitioning

- Plasticity/adaptability of ecosystems
- Small vs. large scale lessons
- Biome variation
- Modeling

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| $\Delta B_w$ /ANPP | 0.76   | 0.70                 | 0.76   |
| $\Delta B_w$ /TBCF | 1.3  | 0.79                 | 1.1  |