Carbon Cycling - Production Processes

- Objectives
  - Net primary production (NPP)
  - Carbon Allocation

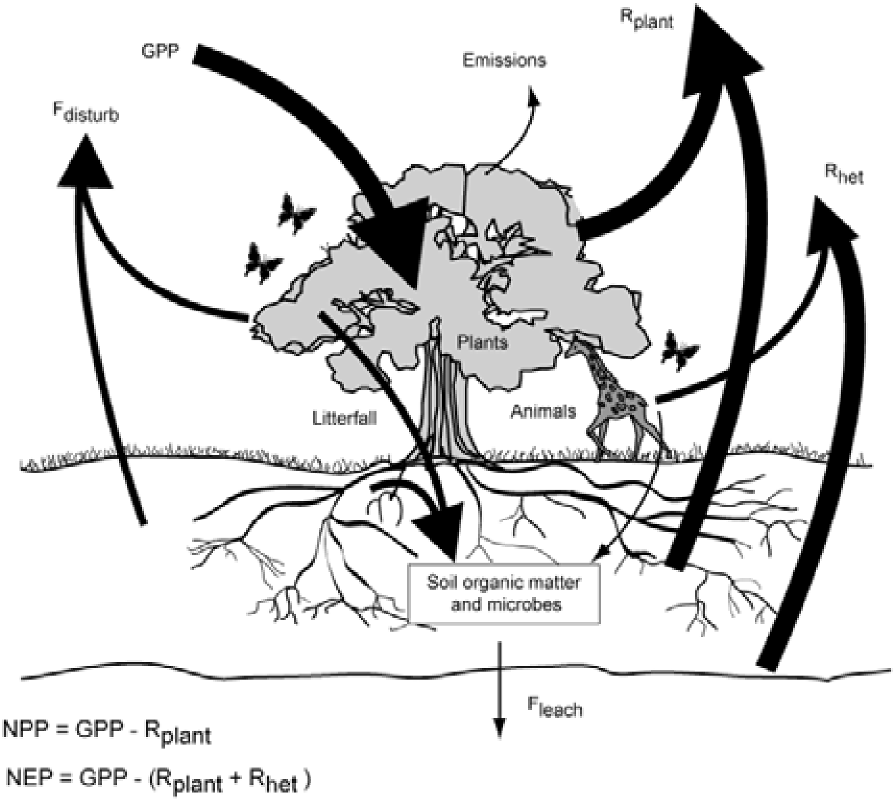
Carbon Cycling - Production Processes

- C is the energy currency of ecosystems
  - Plant (autotrophic) production is the base of food/energy pyramids
    - Ecosystem goods and services
- Plant C cycling to a large extent controls CO_2 concentrations in the atmosphere
  - CO_2 removed via photosynthesis and returned via respiration (plants & animals) & disturbances
- Plant-derived C fundamental to belowground (i.e., soil) processes

Carbon Cycling - Production Processes

- C enters via photosynthesis
  - Gross Primary Production (GPP)
    - Net photosynthesis (Gross photo - foliage *R* during the day)

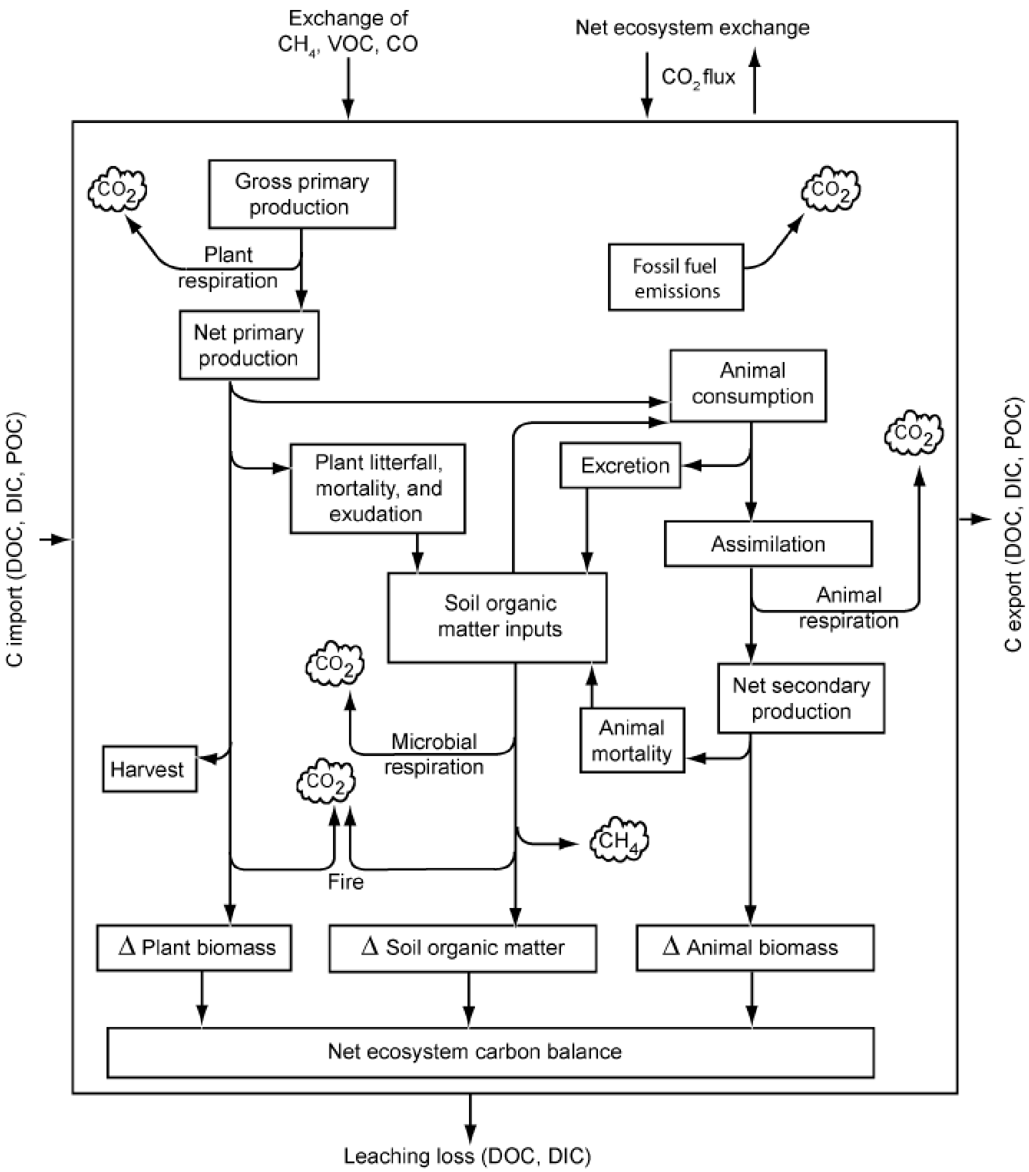
  1. Accumulates in ecosystems (C sequestration) as: (a) plant biomass; (b) Microbial biomass &/or SOM; or (c) animal biomass
     - NPP is base of this C
  2. Returned to the atmosphere via (a) respiration (*R*; autotrophic or heterotrophic); (b) VOC emissions; or (c) disturbance
  3. Leached from or transferred laterally to another ecosystem



Carbon Cycling - Production Processes

- Net primary production = Net C gain (or loss) by primary producers (i.e., plants)
  - NPP is the energy that sustains all organisms
  - NPP = GPP – R_{plant}
    - Includes **new plant biomass**, soluble organic compounds, C transfer to symbionts, C loss to herbivory, VOC emissions, etc.
    - C available to heterotrophs
    - C available to be sequestered (or stored) in ecosystems
      - Live biomass
      - Detrital biomass
    - Eventually, C from NPP will be lost via heterotrophic respiration and/or disturbance, or stored in soils as SOM

Carbon Cycling - Production Processes



Carbon Cycling - Production Processes

- NPP = GPP - R_{plant}
  - Typically measured on annual time scales
    - Units of biomass or C / unit area / unit time
      - g C m^{-2} yr^{-1}
- Most studies concentrate on aboveground NPP (ANPP)
  - Total NPP = ANPP + BNPP
  - Important to differentiate TNPP vs. ANPP vs. BNPP

Carbon Cycling - Production Processes

Components of NPP	% of NPP
New plant biomass	40-70
Leaves and reproductive parts (fine litterfall)	10-30
Apical stem growth	0-10
Secondary stem growth	0-30
New roots	30-40
Root secretions	20-40
Root exudates	10-30
Root transfers to symbionts	10-30
Losses to herbivores, mortality	1-40
Volatile emissions	0-5

- Most studies ignore herbivory, VOC, & understory NPP
  - Is that a safe assumption???

Carbon Cycling - Production Processes

- Most studies concentrate on new plant biomass
    - NPP ≈ DBiomass
    - Need to account for biomass increment **and** loss
        - NPP = DBiomass + Litterfall

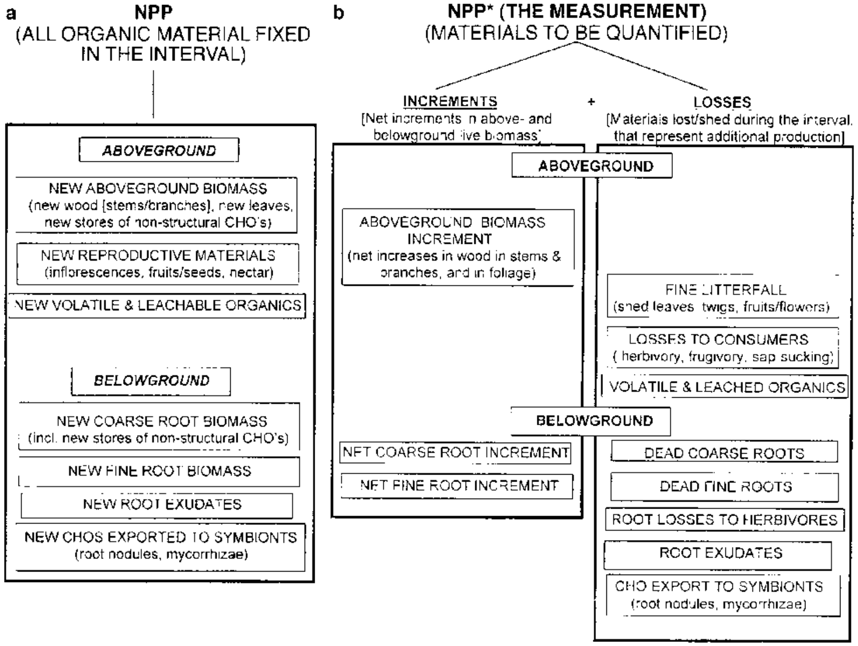
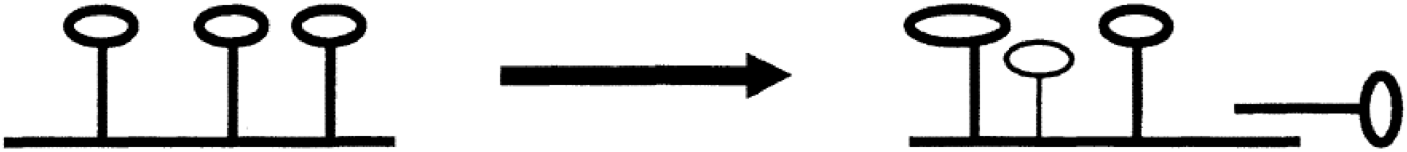


FIG. 1. The components of (a) forest NPP and (b) NPP*, the sum of all materials that together represent: (1) the amount of new organic matter that is retained by live plants at the end of the interval, and (2) the amount of organic matter that was both produced and lost by the plants during the same interval. CHO = carbohydrates.

(Clark et al. 2001)

Carbon Cycling - Production Processes

MEASURING FOREST NPP



Time: t_1 t_2

***AGB:** 5 6 7 5.5 2.5 6.6

Approach 1:

Stand Increment = (Σ Increments of surviving trees) + (Σ Increments(s) of ingrowth)

= ((5.5 – 5.0) + (6.6 – 6.0)) + (2.5 – 2.0)

= (0.5 + 0.6) + (0.5)

Approach 2:

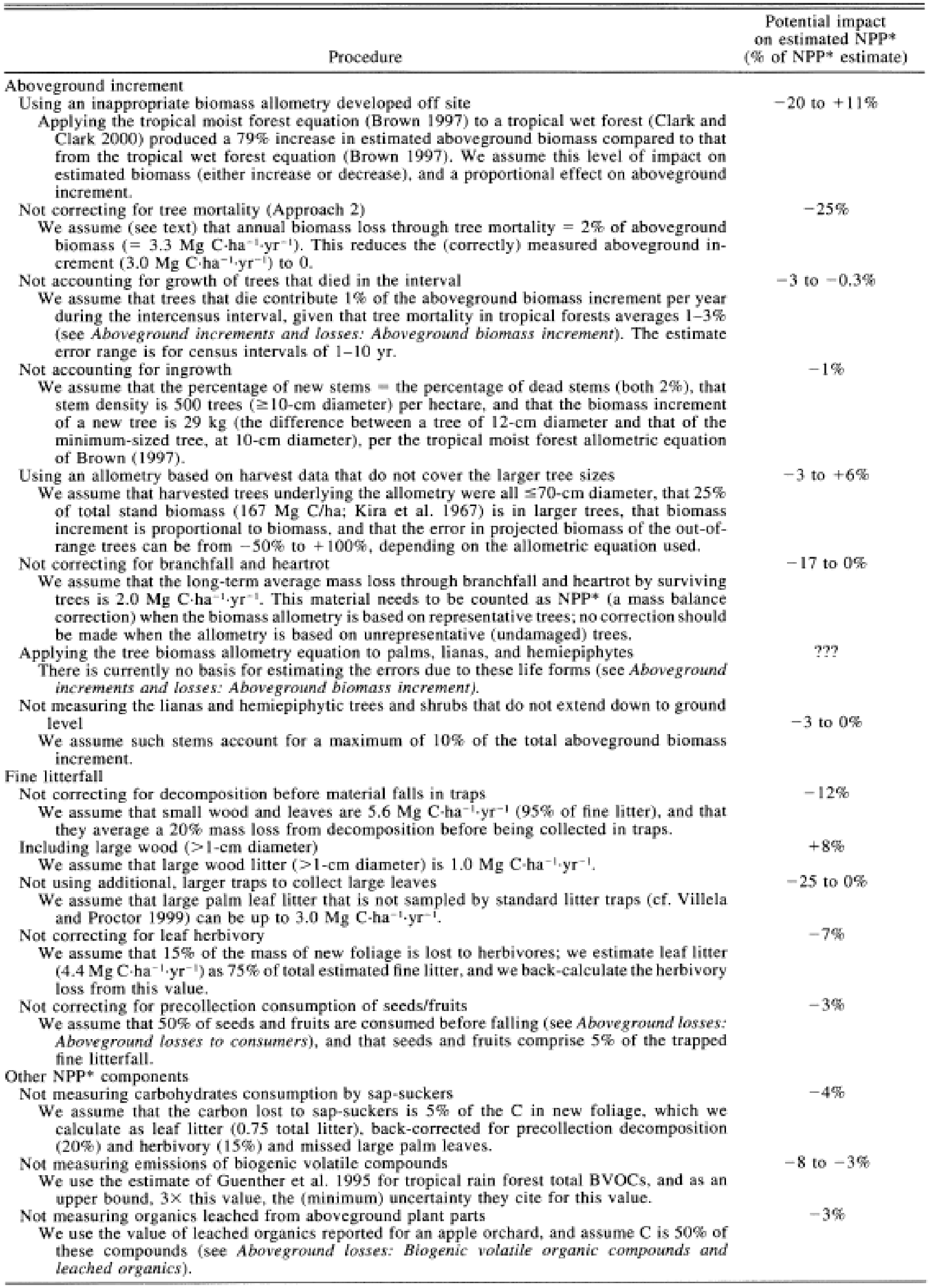
Stand Increment = (ΣAGB at t_2 – ΣAGB at t_1) + (Σ Biomass of trees that died in the interval) – [(Biomass of a minimum size tree) × (number of new trees)]

= ((5.5 + 2.5 + 6.6) – (5 + 6 + 7)) + (7) – (2 × 1)

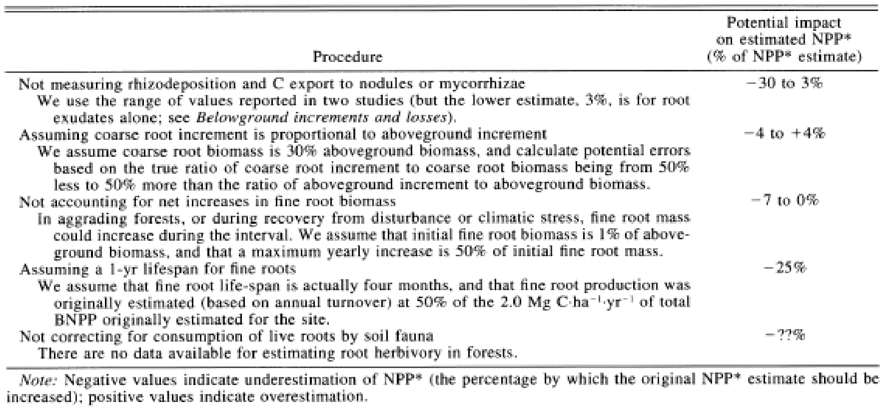
= (14.6 – 18.0) + (7) – (2)

= 1.6

(Clark et al. 2001)



Procedure	Potential impact on estimated NPP* (% of NPP* estimate)
Aboveground increment	
Using an inappropriate biomass allometry developed off site	−20 to +11%
Applying the tropical moist forest equation (Brown 1997) to a tropical wet forest (Clark and Clark 2000) produced a 79% increase in estimated aboveground biomass compared to that from the tropical wet forest equation (Brown 1997). We assume this level of impact on estimated biomass (either increase or decrease), and a proportional effect on aboveground increment.	
Not correcting for tree mortality (Approach 2)	−25%
We assume (see text) that annual biomass loss through tree mortality = 2% of aboveground biomass (= 3.3 Mg C·ha^{-1}·yr^{-1}). This reduces the (correctly) measured aboveground increment (3.0 Mg C·ha^{-1}·yr^{-1}) to 0.	
Not accounting for growth of trees that died in the interval	−3 to −0.3%
We assume that trees that die contribute 1% of the aboveground biomass increment per year during the intercensus interval, given that tree mortality in tropical forests averages 1–3% (see *Aboveground increments and losses: Aboveground biomass increment*). The estimate error range is for census intervals of 1–10 yr.	
Not accounting for ingrowth	−1%
We assume that the percentage of new stems = the percentage of dead stems (both 2%), that stem density is 500 trees (≥10-cm diameter) per hectare, and that the biomass increment of a new tree is 29 kg (the difference between a tree of 12-cm diameter and that of the minimum-sized tree, at 10-cm diameter), per the tropical moist forest allometric equation of Brown (1997).	
Using an allometry based on harvest data that do not cover the larger tree sizes	−3 to +6%
We assume that harvested trees underlying the allometry were all ≤70-cm diameter, that 25% of total stand biomass (167 Mg C/ha; Kira et al. 1967) is in larger trees, that biomass increment is proportional to biomass, and that the error in projected biomass of the out-of-range trees can be from −50% to +100%, depending on the allometric equation used.	
Not correcting for branchfall and heartrot	−17 to 0%
We assume that the long-term average mass loss through branchfall and heartrot by surviving trees is 2.0 Mg C·ha^{-1}·yr^{-1}. This material needs to be counted as NPP* (a mass balance correction) when the biomass allometry is based on representative trees; no correction should be made when the allometry is based on unrepresentative (undamaged) trees.	
Applying the tree biomass allometry equation to palms, lianas, and hemiepiphytes	???
There is currently no basis for estimating the errors due to these life forms (see *Aboveground increments and losses: Aboveground biomass increment).*	
Not measuring the lianas and hemiepiphytic trees and shrubs that do not extend down to ground level	−3 to 0%
We assume such stems account for a maximum of 10% of the total aboveground biomass increment.	
Fine litterfall	
Not correcting for decomposition before material falls in traps	−12%
We assume that small wood and leaves are 5.6 Mg C·ha^{-1}·yr^{-1} (95% of fine litter), and that they average a 20% mass loss from decomposition before being collected in traps.	
Including large wood (>1-cm diameter)	+8%
We assume that large wood litter (>1-cm diameter) is 1.0 Mg C·ha^{-1}·yr^{-1}.	
Not using additional, larger traps to collect large leaves	−25 to 0%
We assume that large palm leaf litter that is not sampled by standard litter traps (cf. Villela and Proctor 1999) can be up to 3.0 Mg C·ha^{-1}·yr^{-1}.	
Not correcting for leaf herbivory	−7%
We assume that 15% of the mass of new foliage is lost to herbivores; we estimate leaf litter (4.4 Mg C·ha^{-1}·yr^{-1}) as 75% of total estimated fine litter, and we back-calculate the herbivory loss from this value.	
Not correcting for precollection consumption of seeds/fruits	−3%
We assume that 50% of seeds and fruits are consumed before falling (see *Aboveground losses: Aboveground losses to consumers*), and that seeds and fruits comprise 5% of the trapped fine litterfall.	
Other NPP* components	
Not measuring carbohydrates consumption by sap-suckers	−4%
We assume that the carbon lost to sap-suckers is 5% of the C in new foliage, which we calculate as leaf litter (0.75 total litter), back-corrected for precollection decomposition (20%) and herbivory (15%) and missed large palm leaves.	
Not measuring emissions of biogenic volatile compounds	−8 to −3%
We use the estimate of Guenther et al. 1995 for tropical rain forest total BVOCs, and as an upper bound, 3× this value, the (minimum) uncertainty they cite for this value.	
Not measuring organics leached from aboveground plant parts	−3%
We use the value of leached organics reported for an apple orchard, and assume C is 50% of these compounds (see *Aboveground losses: Biogenic volatile organic compounds and leached organics*).	



Procedure	Potential impact on estimated NPP* (% of NPP* estimate)
Not measuring rhizodeposition and C export to nodules or mycorrhizae	−30 to 3%
We use the range of values reported in two studies (but the lower estimate, 3%, is for root exudates alone; see *Belowground increments and losses*).	
Assuming coarse root increment is proportional to aboveground increment	−4 to +4%
We assume coarse root biomass is 30% aboveground biomass, and calculate potential errors based on the true ratio of coarse root increment to coarse root biomass being from 50% less to 50% more than the ratio of aboveground increment to aboveground biomass.	
Not accounting for net increases in fine root biomass	−7 to 0%
In aggrading forests, or during recovery from disturbance or climatic stress, fine root mass could increase during the interval. We assume that initial fine root biomass is 1% of aboveground biomass, and that a maximum yearly increase is 50% of initial fine root mass.	
Assuming a 1-yr lifespan for fine roots	−25%
We assume that fine root life-span is actually four months, and that fine root production was originally estimated (based on annual turnover) at 50% of the 2.0 Mg C·ha^{-1}·yr^{-1} of total BNPP originally estimated for the site.	
Not correcting for consumption of live roots by soil fauna	−??%
There are no data available for estimating root herbivory in forests.	

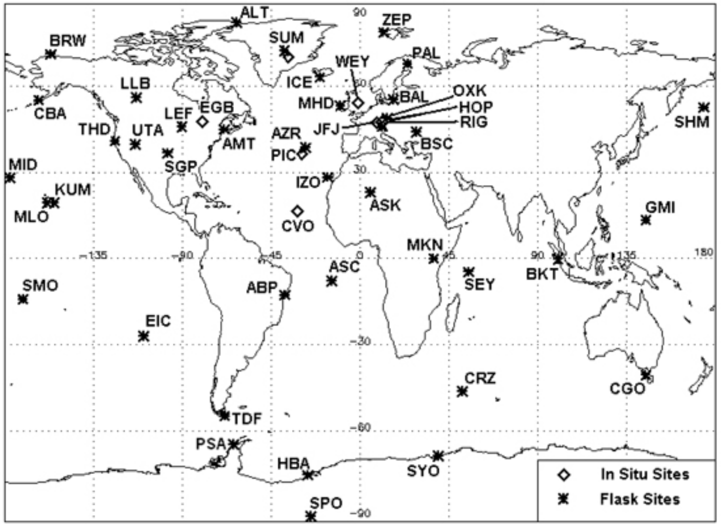
Note: Negative values indicate underestimation of NPP* (the percentage by which the original NPP* estimate should be increased); positive values indicate overestimation.

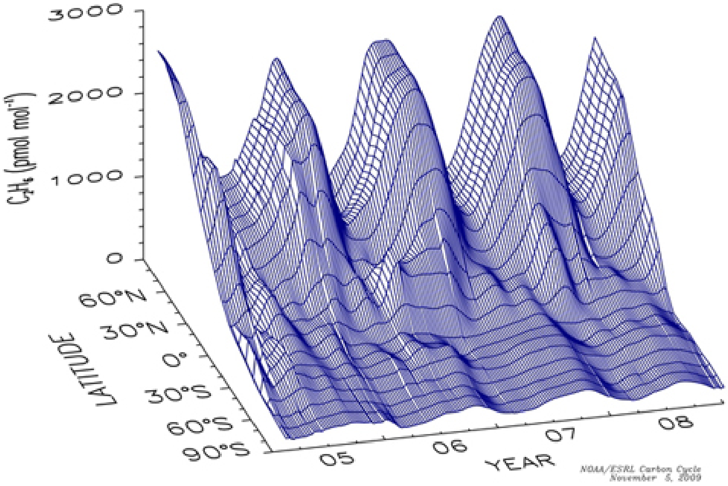
Estimating NPP correctly is time consuming and complicated!

(Clark et al. 2001)

Carbon Cycling - Production Processes

- VOCs produced by plants are an important input of atmospheric gases → tropospheric chemistry
  - Primarily isoprenes
  - VOCs account for only ~0.1 - 4% of GPP (Kesselmeier et al. 2002)
    - Mean = 1.2% of GPP

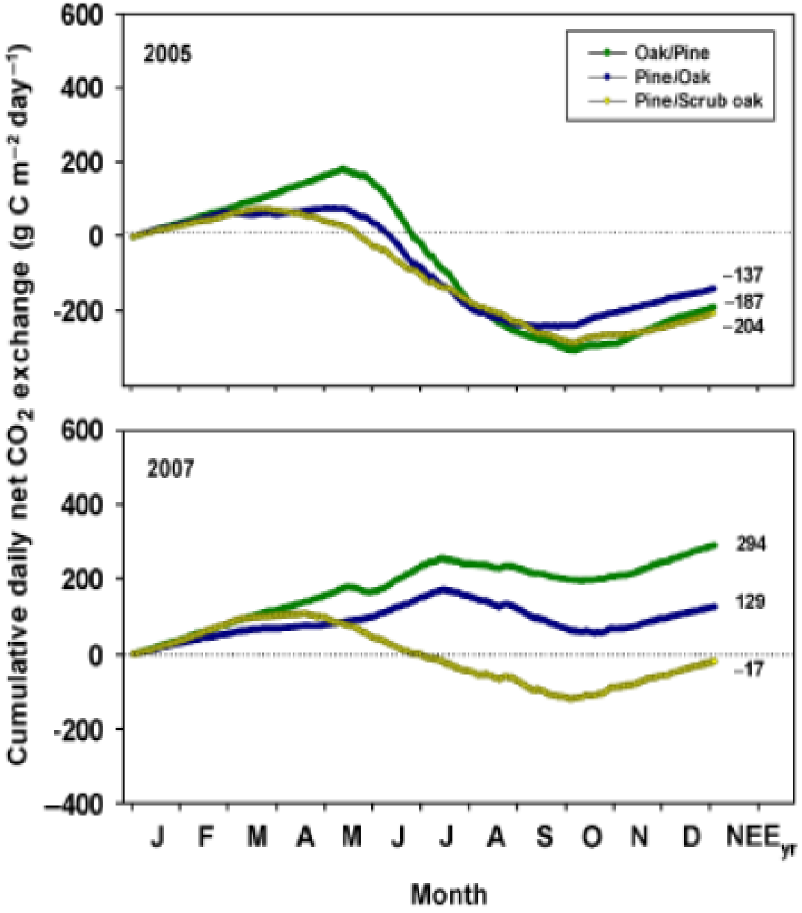




(Helmig *et al*. 2009)

Carbon Cycling - Production Processes

- Herbivory
  - Typically relatively low background rates
    - Exception would be ecosystems with large herbivores (i.e., grazing systems)
  - But periodic large insect outbreaks are the norm for many ecosystems, & can have very large impact on C dynamics



(Clark et al. 2010)

Carbon Cycling - Production Processes

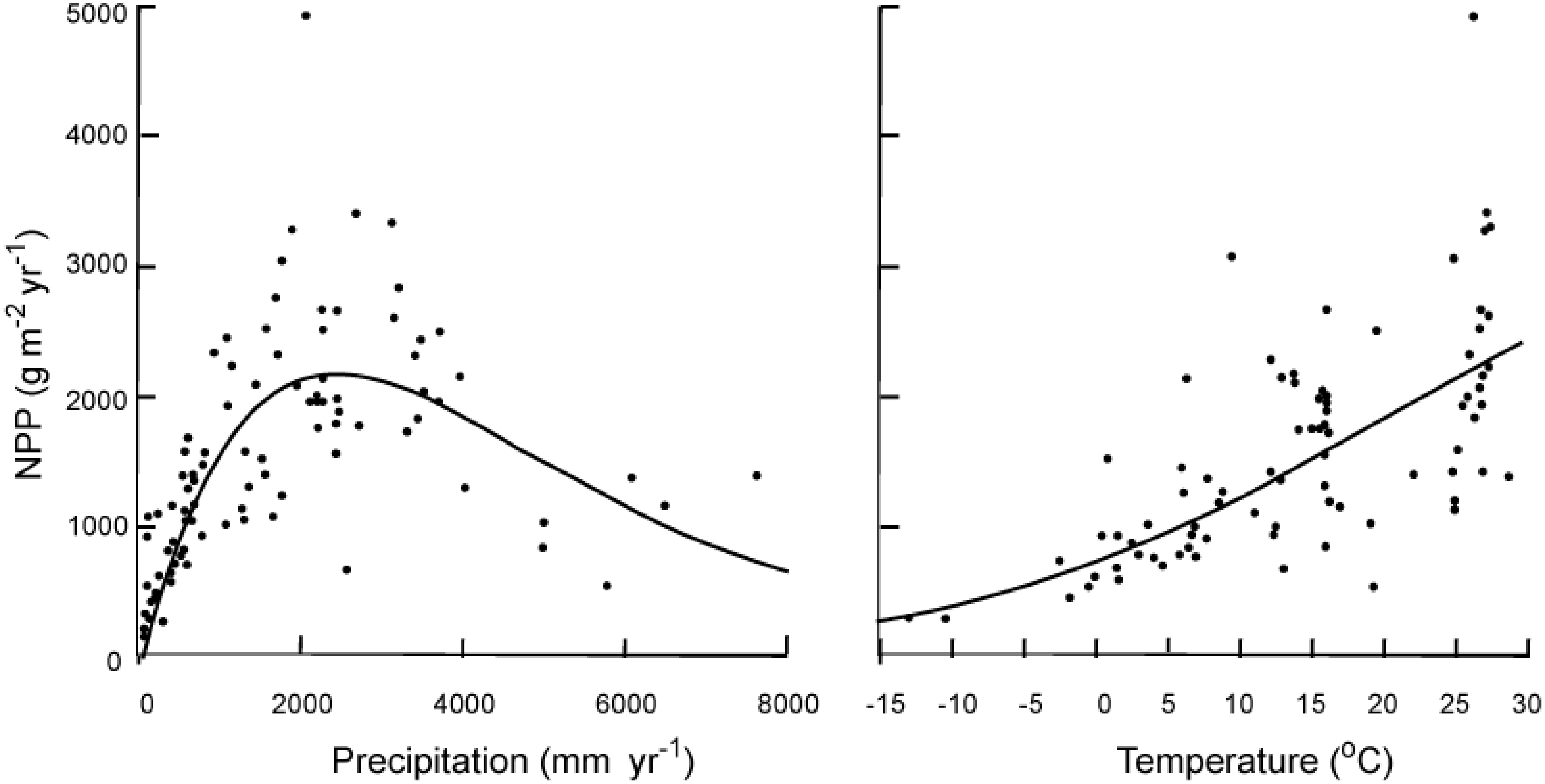
- Measuring NPP
  - NPP ≈ DBiomass
  - Need to account for biomass increment <u>and</u> loss because plant tissue is continually shed
    - TNPP = (DLeaf Bio. + Leaf Litter.) + (DWood Bio. + Wood Litter.) + (DRoot Bio. + Root Litter.)
      - Other losses not being accounted for?
    - ANPP = (DAboveground Bio. + Aboveground litterfall)
    - ANPP = (Aboveground litterfall) if forest is at “steady state”
      - i.e., New Biomass = Loss of Old Biomass

Carbon Cycling - Production Processes

- Physiological controls over NPP driven by plant demand for C (sink strength)
  - Env. controls over photosynthesis on short term (seconds to weeks)
    - Plants adjust components of photosynthesis so physical and biochemical processes co-limit carbon fixation
  - Governed by soil resources on long term (months to annual) via control over leaf area
    - Climate influences NPP by determining availability of soil resources <u>and</u> length of growing season
    - Plants adjust Ps capacity and LAI to soil resources
      - Which then determines the limits of potential C input & sequestration

Carbon Cycling - Production Processes

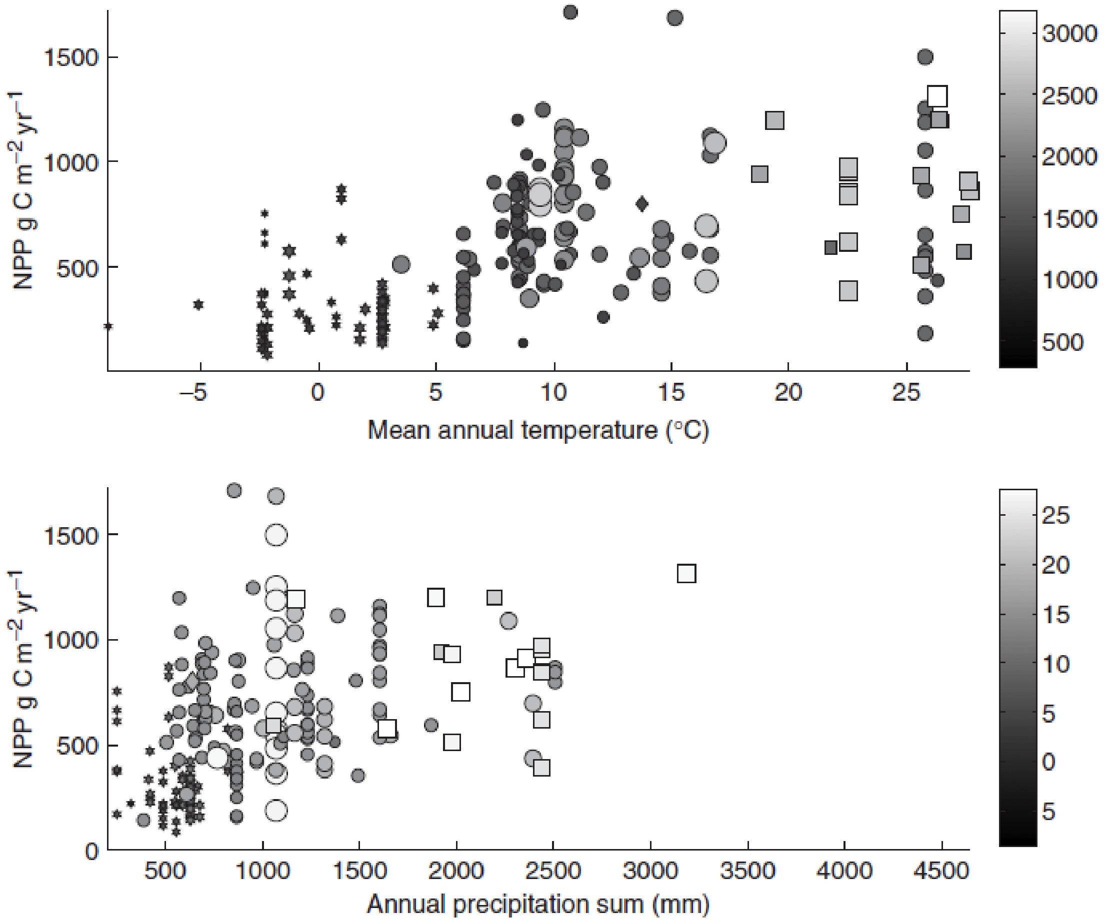
- Environmental controls over NPP
  - Climate strongly impacts NPP



(Schuur 2003)

Carbon Cycling - Production Processes

- Environmental controls over NPP
  - Climate strongly impacts NPP



(Luyssaert et al. 2007)

Carbon Cycling - Production Processes

- Environmental controls on NPP are complex
  - Climate impacts plant physiology and largely determines resource/nutrient availability (soil water & nutrient limitations)
  - Also very important impacts of species, stand age & structure, etc.
- Climate controls on NPP are largely mediated through climatic impacts on the availability of belowground resources (water & nutrients)

Carbon Cycling - Production Processes

- High LAI is needed to maximize GPP (or NPP), yet GPP (& NPP) is constrained by belowground resources…

- How do plants deal with this dilemma?
  - Allocate growth and biomass to leaves (to maximize C gain) or to roots (to maximize belowground resource capture)

Carbon Cycling - Production Processes

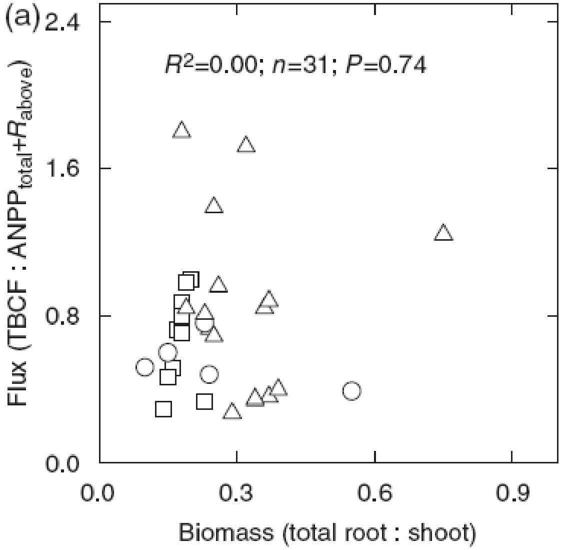
- Liebig’s Law of the Minimum
  - Plants allocate growth to tissues that maximize capture of the single most limiting resource
    - Allocate to roots when dry or nutrient poor
    - Allocate to stem (…or leaves) when light is limiting
      - (a) more biomass, (b) more efficient, or (c) longer retention
- Plants can adjust allocation in response to resource availability
  - Prevents overwhelming limitation by any one resource
  - Tends to result in plants being limited by multiple resources simultaneously

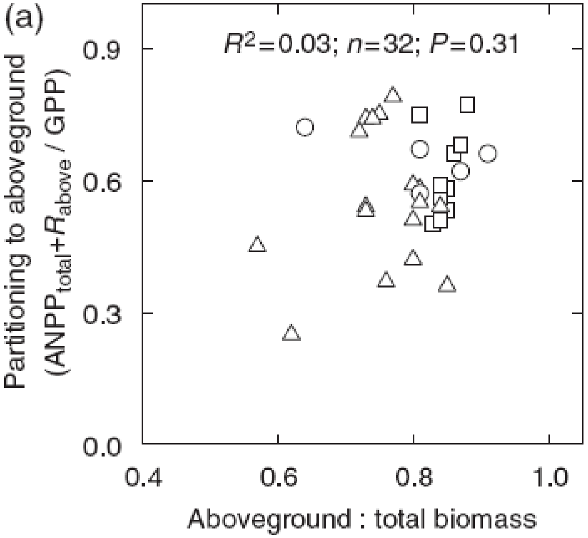
Carbon Cycling - Production Processes

- Global forest C allocation patterns
  - *R* vs. NPP?
  - Aboveground vs. Belowground?
  - Foliage vs. Wood?
- Examined a diverse global dataset of forest stand C budgets (Litton et al. 2007)
  - Biomass, flux, and partitioning
  - Response of C allocation to stand age, belowground resource availability (H_2O & nutrients), competition (stand density)

Carbon Cycling - Production Processes

- Global forest C allocation patterns
  - Biomass ≠ flux or partitioning
  - Why?
  - Who cares?

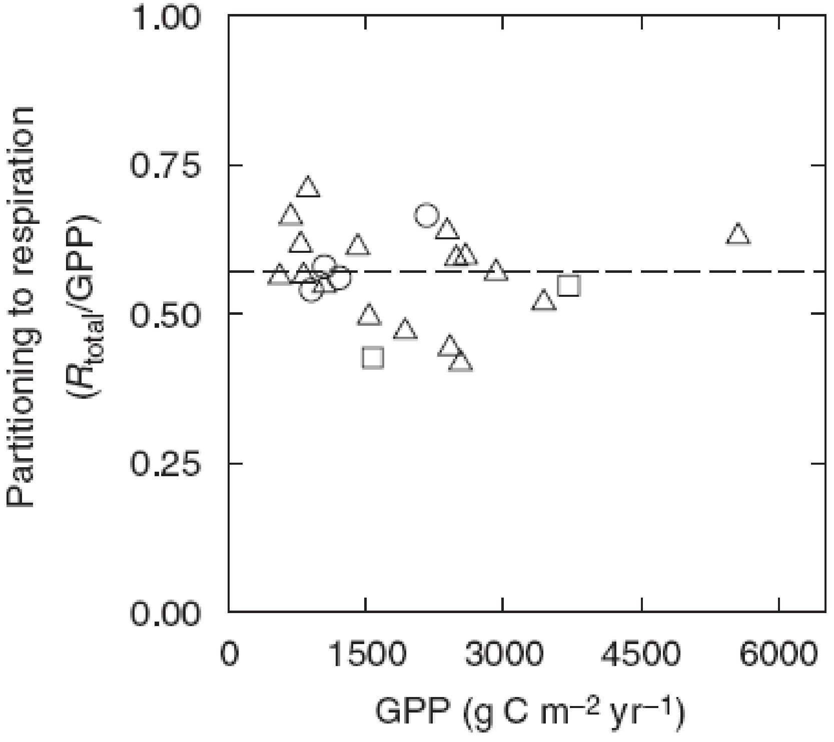




(Litton et al. 2007)

Carbon Cycling - Production Processes

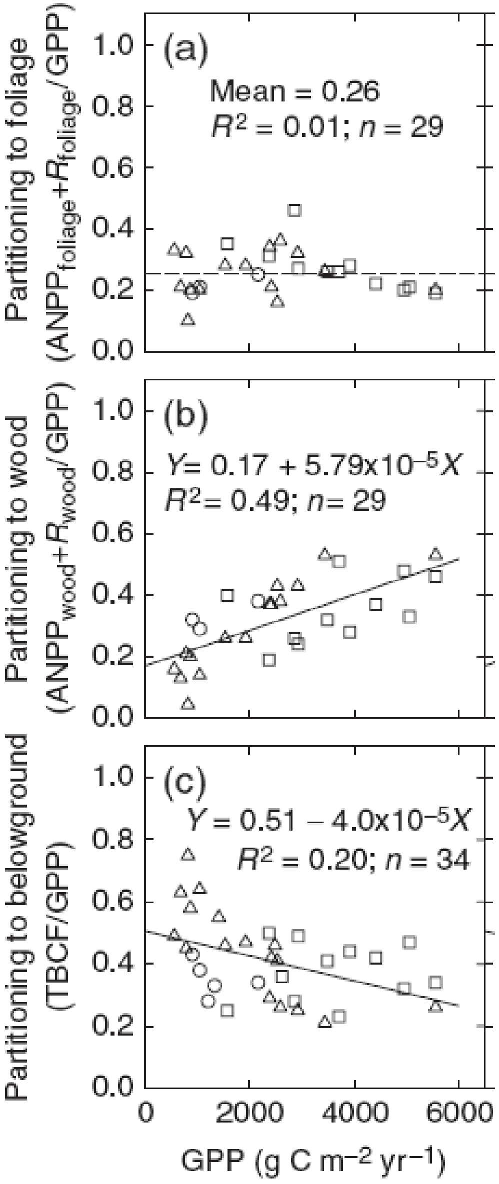
- Global forest C allocation patterns
  - *R* uses a relatively constant fraction of GPP



(Litton et al. 2007)

Carbon Cycling - Production Processes

- Global forest C allocation patterns
  - Partitioning to foliage remarkably constant
  - As resources (GPP) increase, partitioning shifts from below- to aboveground
  - Since partitioning to foliage is ~constant, resources increase partitioning to wood
  - Very, very useful for models



(Litton et al. 2007)

Carbon Cycling - Production Processes

- Why is NPP often limited by multiple resources?
  - Adjust allocation to prevent limitation by the most limiting resource
  - Environment changes seasonally and from year to year
    - Different factors limit NPP at different times
  - Plants can increase supply of limiting resources
    - How?
  - Retain a larger proportion of resources in short supply
  - Different resources limit different species that make up the ecosystem

Carbon Cycling - Production Processes

- Storage buffers plants from variation in resource availability associated with environmental variability
  - Plants accumulate CHOs & resources when they are abundant
    - Leaf CHOs accumulate during day and decline at night
    - Seasonal variability in storage
  - Plants use CHOs & resource stores when supply declines

Carbon Cycling - Production Processes

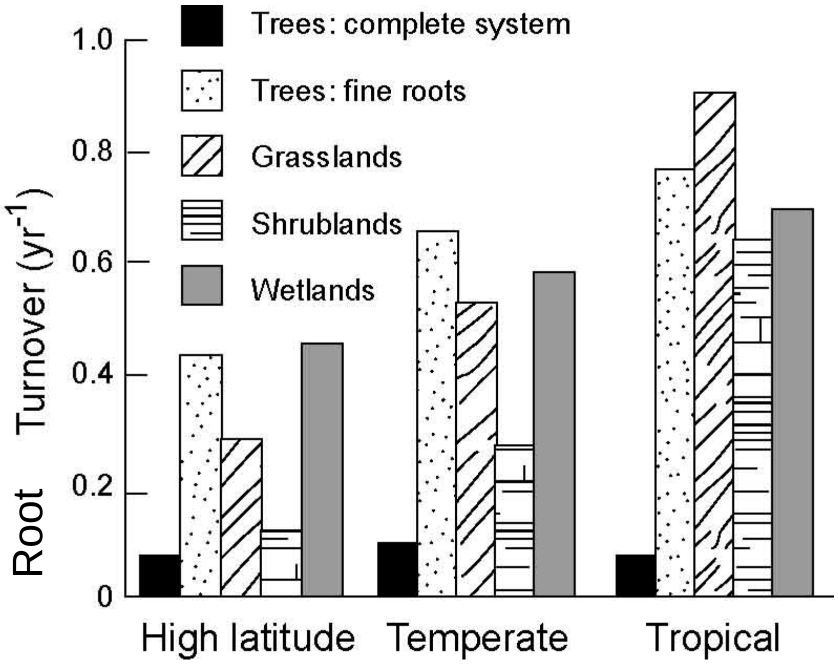
- How can a plant increase resource supply?
  - 1) Growth into resource-rich areas
    - Leaves or roots
  - 2) Symbionts
    - N fixation
    - Mycorrhizae
  - 3) Rhizodeposition (labile C deposition at root surface)
    - Stimulate microbial mineralization
    - “Priming” of microbes that then degrades more recalcitrant SOM and release nutrients

Carbon Cycling - Production Processes

- Why do plants lose tissues they work so hard to produce (i.e., why do I have to rake my yard)?
  - Pathogens, herbivores, etc.; disturbances (fire)
  - Mortality
  - Senescence to balance resource requirements with resource supply (if you can't pull your own weight…)
- Results in exploitation of resource rich areas and/or seasons
- Translocation prior to senescence minimizes loss of limiting nutrients

Carbon Cycling - Production Processes

- Why is root turnover faster in high-resource environments?
  - They can afford to



Carbon Cycling - Production Processes

Live Biomass distribution of the major terrestrial biomes[a].

Biome	Shoot ($g\ m^{-2}$)	Root ($g\ m^{-2}$)	Root (% of total)	Total ($g\ m^{-2}$)
Tropical forests	30,400	8,400	0.22	38,800
Temperate forests	21,000	5,700	0.21	26,700
Boreal forests	6,100	2,200	0.27	8,300
Mediterranean shrublands	6,000	6,000	0.5	12,000
Tropical savannas and grasslands	4,000	1,700	0.3	5,700
Temperate grasslands	250	500	0.67	750
Deserts	350	350	0.5	700
Arctic tundra	250	400	0.62	650
Crops	530	80	0.13	610

[a] Data from [Roy, 2001 #3858]. Biomass is expressed in units of dry mass.

- 50-fold variation across biomes; 80% in forests
- Biomass is greatest in tropical and temperate forests
- Tropical forests have ~50% of global biomass, but occur on only ~12% of ice-free land area

Carbon Cycling - Production Processes

Global distribution of terrestrial biomes and their total carbon in plant biomass[a].

Biome	**Area (10^6 km$^{2)}$**	**Total C pool (Pg C)**	**Total NPP (Pg C yr^{-1})**
Tropical forests	**17.5**	**340**	**21.9**
Temperate forests	**10.4**	**139**	**8.1**
Boreal forests	**13.7**	**57**	**2.6**
Mediterranean shrublands	**2.8**	**17**	**1.4**
Tropical savannas and grasslands	**27.6**	**79**	**14.9**
Temperate grasslands	**15.0**	**6**	**5.6**
Deserts	**27.7**	**10**	**3.5**
Arctic tundra	**5.6**	**2**	**0.5**
Crops	**13.5**	**4**	**4.1**
Ice	**15.5**		
Total	**149.3**	**652**	**62.6**

[a] Data from [Roy, 2001 #3858]. Biomass is expressed in units of carbon, assuming that plant biomass is 50% carbon.

- ~50% of global biomass and ~35% of NPP is in tropical forests

Carbon Cycling - Production Processes

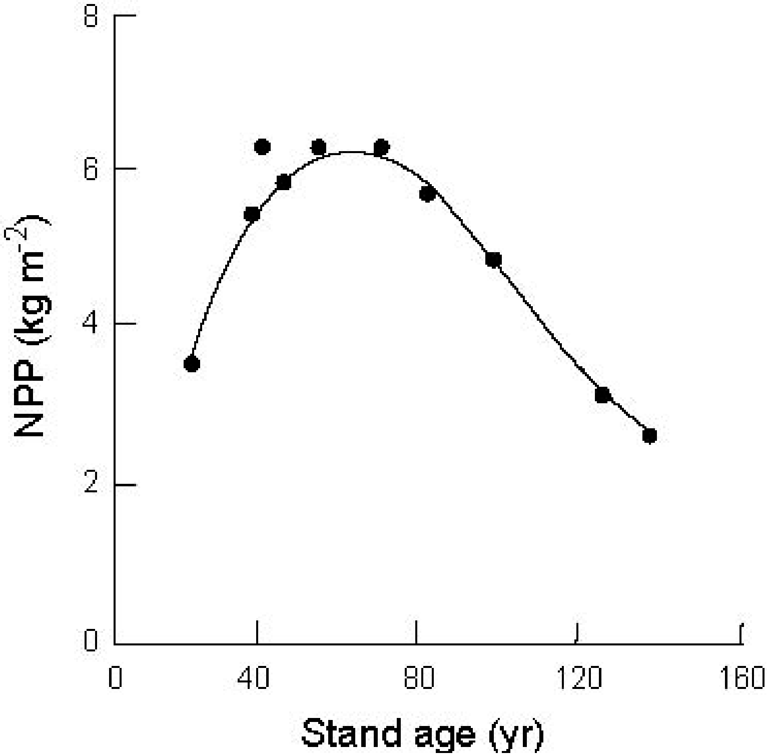
Table 5.4. Productivity per day and per unit leaf area[a].

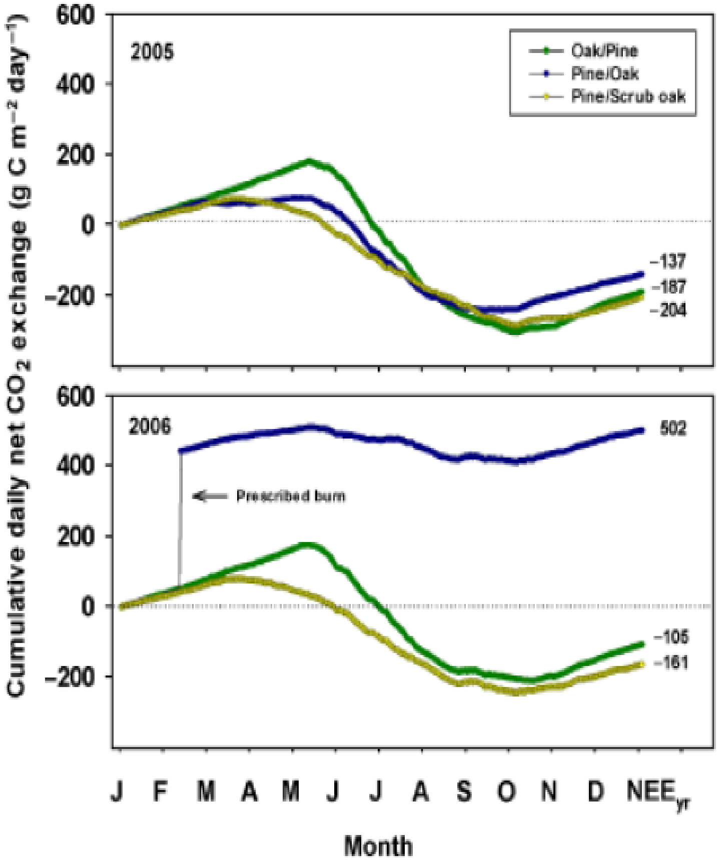
Biome	Season length[b] (days)	Daily NPP per ground area ($g\ m^{-2}\ d^{-1}$)	Total LAI[c] ($m^2\ m^{-2}$)	Daily NPP per leaf area ($g\ m^{-2}\ d^{-1}$)
Tropical forests	365	6.8	6.0	1.14
Temperate forests	250	6.2	6.0	1.03
Boreal forests	150	2.5	3.5	0.72
Mediterranean shrublands	200	5.0	2.0	2.50
Tropical savannas and grasslands	200	5.4	5.0	1.08
Temperate grasslands	150	5.0	3.5	1.43
Deserts	100	2.5	1.0	2.50
Arctic tundra	100	1.8	1.0	1.80
Crops	200	3.1	4.0	0.76

- Daily NPP per unit LAI relatively consistent
- ***LAI and growing season length largely explain NPP biome diff.

Carbon Cycling - Production Processes

- Disturbance and succession are major causes of spatial and temporal variation in NPP within ecosystems and biomes





(Clark et al. 2010)