Photosynthesis

Process by which carbon is reduced from CO$_2$ to organic carbon

Provides all energy for the biosphere (except for chemosynthesis at hydrothermal vents)

Affects composition of atmosphere, development of soils, is responsible for differences between geochemistry on neighbour planets and biogeochemistry on Earth

Rates of plant growth vary widely from ~0 to >1000 g C m$^{-2}$ yr$^{-1}$
Chemical mechanism

Chlorophyll molecule oxidised by light
NADP reduced to NADPH -- photosystem 1
Water split: $2\text{H}_2\text{O} \rightarrow 4\text{H}^+ + 4\text{e}^- + \text{O}_2 \uparrow$ -- photosystem 2
NADPH and ATP used to reduce CO$_2$ via Rubisco
CO$_2$ + H$_2$O $\rightarrow$ CH$_2$O + O$_2$

Carbon dioxide enters leaves via stomates on lower side of leaf
Stomatal conductance (cm/sec) controlled by water availability
Rubisco controls photosynthetic rate under optimal conditions
Water-use efficiency

Stomate conductance controls: CO$_2$, O$_2$ and H$_2$O transfer

H$_2$O loss is transpiration, main mechanism of water transfer to atmosphere

e.g. 25% of precipitation in NH lost by transpiration
-water often limiting

Water Use Efficiency (WUE) = mmoles CO$_2$ fixed/ moles H$_2$O lost
Typical values 0.86 - 1.50, lower stomatal conductance, higher WUE
Higher atmos CO$_2$ can use lower conductance, higher WUE

Number of leaf stomates may be getting smaller as atmospheric CO$_2$ increases

C isotope fractionation can be used to determine WUE

1.1% of atm CO$_2$ is $^{13}$C but $^{12}$C diffuses faster than $^{13}$C

Plant tissue contains ~ 2% less $^{13}$C than atmos = -20‰ (per mil)

$$\delta^{13}C = \frac{^{13}C/^{12}C_{\text{sample}} - ^{13}C/^{12}C_{\text{std}}}{^{13}C/^{12}C_{\text{std}}} \times 1000$$

Atm $\delta^{13}C = -8‰$, most plants -20‰ + -8‰ = -28‰
When stomatal conductance is high, $\delta^{13}$C is more negative, more discrimination. When conductance is low, less discrimination, as more of total CO$_2$ inside leaf used. $\delta^{13}$C in preserved plant material show WUE has increased in plants since last glacial max as atmos CO$_2$ rose, also increased since Industrial Revolution.

WUE can be calculated using the eddy co-variance technique.
Nutrient-Use Efficiency

In many species nitrogen limitation affects Rubisco content $\rightarrow$ photosynthetic rate

$P$ may be limiting for some species

$Mg$ and $Mn$ rarely limiting

N limitation is most common

Rate of photosynthesis/ $N$ in leaf = NUE

Similar for most species, inversely related to WUE

Figure 5.3 Relationship between net photosynthesis and leaf nitrogen content among 21 species from different environments. From Field and Mooney (1986).
Net primary Production and Respiration

Respiration is a result of mitochondrial activity and scales well with plant N content

Photosynthesis measured is usually Net, i.e. amount of CO₂ taken up or O₂ released

Respiration approx. 50% of photosynthesis
So gross photosynthesis ~ 2x net
Gross Primary Production (GPP) - plant respiration 
\( R_p \) = Net Primary Production (NPP)

NPP does not all go to plant growth, herbivores, litterfall etc.

Annual accumulation of organic matter in g m\(^{-2}\) yr\(^{-1}\) 
C \( \sim \) 50\% by weight

Relative to intercepted light NPP \( \sim \) 1\% of energy

NPP measured by harvesting at peak growth or by 
seasonal change in mass of tissue -- correct for in-season 
consumption and loss

NPP separated into above ground and below ground

Above ground split between leaves and stem (woody) growth

Forests \( \sim 25\% \) of above ground NPP in leaves, in 
shrublands 35-60\%

Old forests smaller % in leaves than young forests
Boreal forests have a higher proportion of woody growth than in tropics -- more respiration at higher temperatures

Above ground NPP correlates with leaf biomass

Root growth difficult to measure but can be high fraction (>50%) of total NPP

In forests higher % for root growth in least fertile soils

![Graph showing NPP vs Leaf biomass](image)

Figure 5.5 Using data from a variety of ecosytems in North America, Webb et al. (1995) found a strong relation between the annual aboveground net primary production and the biomass of foliage.

<table>
<thead>
<tr>
<th>Table 5.1</th>
<th>Net Primary Production in 25- and 180-year-old Alerce snubilo forests in the Cascade Mountains, Washington*</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>25-year-old</td>
</tr>
<tr>
<td>g m⁻² yr⁻¹</td>
<td>g m⁻² yr⁻¹</td>
</tr>
<tr>
<td>Biomass increment</td>
<td></td>
</tr>
<tr>
<td>Tree total</td>
<td>426</td>
</tr>
<tr>
<td>Shrub stems</td>
<td>6</td>
</tr>
<tr>
<td>Total</td>
<td>432</td>
</tr>
<tr>
<td>Decomposer production</td>
<td></td>
</tr>
<tr>
<td>Litterfall</td>
<td>151</td>
</tr>
<tr>
<td>Mortality</td>
<td>50</td>
</tr>
<tr>
<td>Herb layer turnover</td>
<td>37</td>
</tr>
<tr>
<td>Total</td>
<td>213</td>
</tr>
<tr>
<td>Total aboveground</td>
<td>645</td>
</tr>
<tr>
<td>Belowground</td>
<td></td>
</tr>
<tr>
<td>Root</td>
<td></td>
</tr>
<tr>
<td>Fine (&lt;2 mm)</td>
<td>650</td>
</tr>
<tr>
<td>Fibrous (bast tissue)</td>
<td>571</td>
</tr>
<tr>
<td>Coarse (&gt;2 mm)</td>
<td>79</td>
</tr>
<tr>
<td>Angiosperm fine root turnover</td>
<td>506</td>
</tr>
<tr>
<td>Total root turnover</td>
<td>1581</td>
</tr>
<tr>
<td>Mycorrhizal fungal component</td>
<td>526</td>
</tr>
<tr>
<td>Total belowground</td>
<td>1707</td>
</tr>
<tr>
<td>Ecosystem total</td>
<td>2352</td>
</tr>
</tbody>
</table>

Can estimate NPP in forests via CO\textsubscript{2} depletion during the day and enrichment during the night--eddy correlation

GPP in Massachusetts 1070-1210 g C m\textsuperscript{-2} yr\textsuperscript{-1}

plant and soil respiration = 810-1140 g C m\textsuperscript{-2} yr\textsuperscript{-1}

True increment 140-280 g C m\textsuperscript{-2} yr\textsuperscript{-1}

NPP is greater since it includes leaves etc.

Global estimates of NPP and biomass
Need detailed regional coverage for global models harvest techniques, v. expensive
Chlorophyll absorbs light $\rightarrow$ use ratio of surface reflectance in two wavebands to estimate chlorophyll inventory
Ground truth satellite data: reflectance ratio $\propto$ Leaf area $m^2/m^2$

Leaf area Index $\propto$ NPP, therefore colour $\propto$ NPP.
Pixel size and regional validity of ground-truthing are still big issues

Woody tissues hard to estimate by colour, but water filled tissue can be estimated via reflected microwave from SAR
Global annual NPP $\sim 45\text{--}65 \times 10^{15}$ g C yr$^{-1}$, total biomass $\sim 560 \times 10^{15}$ g C

**FIGURE 5.12** Distribution of global NPP on land for 2002, computed from MODIS data. Source: FromRunninget al. 2004, Figure 5 in BioScience, June 2004; used with permission.
Mean residence time C in plant tissue = biomass/NPP
= 9 yrs

Varies from ~4 yrs in deserts to > 20 yrs in forests

Values average short turn over materials e.g. leaves < 1 yr, with tree wood equals decades to centuries

Global estimates still based on harvest methods, are biased by selection of representative regions

Current values of biomass may be too high
NPP values indicate:
Tropical forests > boreal forests > shrub tundra i.e. latitude effect decreases with decreasing precipitation forests > grasslands > deserts

**TABLE 5.3 Biomass and Net Primary Production in Terrestrial Ecosystems**

<table>
<thead>
<tr>
<th>Biome</th>
<th>Area (10^6 km^2)</th>
<th>NPP (g C m^{-2} yr^{-1})</th>
<th>Total NPP (10^9 g C yr^{-1})</th>
<th>Biomass (g C m^{-2})</th>
<th>Total plant C pool (10^9 g C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tropical forests</td>
<td>17.5</td>
<td>1250</td>
<td>20.6</td>
<td>19,400</td>
<td>320</td>
</tr>
<tr>
<td>Temperate forests</td>
<td>10.4</td>
<td>685</td>
<td>7.6</td>
<td>13,380</td>
<td>120</td>
</tr>
<tr>
<td>Boreal forests</td>
<td>13.7</td>
<td>450</td>
<td>2.4</td>
<td>41.50</td>
<td>54</td>
</tr>
<tr>
<td>Mediterranean shrublands</td>
<td>2.8</td>
<td>500</td>
<td>1.3</td>
<td>6.0</td>
<td>16</td>
</tr>
<tr>
<td>Tropical savannas grasslands</td>
<td>27.6</td>
<td>5.0</td>
<td>14.0</td>
<td>28.50</td>
<td>74</td>
</tr>
<tr>
<td>Temperate grasslands</td>
<td>15.0</td>
<td>3.5</td>
<td>5.3</td>
<td>37.5</td>
<td>6</td>
</tr>
<tr>
<td>Deserts</td>
<td>27.7</td>
<td>125</td>
<td>3.3</td>
<td>330</td>
<td>9</td>
</tr>
<tr>
<td>Arctic tundra</td>
<td>5.6</td>
<td>60</td>
<td>0.5</td>
<td>325</td>
<td>2</td>
</tr>
<tr>
<td>Crops</td>
<td>13.5</td>
<td>315</td>
<td>3.9</td>
<td>315</td>
<td>4</td>
</tr>
<tr>
<td>Ice</td>
<td>15.5</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>149.3</td>
<td>58.9</td>
<td>615</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

From data compiled by Seager et al. 2001, assuming a 5% carbon content in plant tissues.
NPP vs T

\[ NPP_{MAT(\circ C)} = \frac{-17.6243}{(1 + e^{1.3496 - 0.071548\text{MAT(\circ C)}})} \]

Net primary productivity (Mg C ha\(^{-1}\) yr\(^{-1}\))

Mean annual temperature (\(^\circ C\))

NPP vs precipitation

\[ NPP_{MAP(\text{mm})} = \frac{0.005212(\text{MAP}^{0.1236})}{e^{0.00459532(\text{MAP})}} \]

Net primary productivity (Mg C ha\(^{-1}\) yr\(^{-1}\))

Mean annual precipitation (mm)
NPP decreases with elevation, this is a temperature effect.

NPP can increase with elevation though if precipitation increases with elevation.

Used relationships to develop a global map. Good agreement with satellite image implies T and water are main NPP limiting factors.

Global estimate $63 \times 10^{15}$ g C yr$^{-1}$
Models: e.g. Melillo (1993)

$$\text{NPP} = \text{NPP}_{(\text{max})} \times \text{PAR} \times \text{LAI} \times \text{T} \times \text{CO}_2 \times \text{H}_2\text{O} \times \text{NA}$$

PAR is radiation, LAI, leaf area, T is temp, H$_2$O is soil moisture, NA nutrient availability

Get $52 \times 10^{15} \text{ g C yr}^{-1}$.

Using AVHRR to calculate LAI get $48 \times 10^{15} \text{ g C yr}^{-1}$

(70% 30S to 30N)

Models can be used to predict changes in NPP as CO$_2$ and precipitation vary

2-year movie reveals some fantastic seasonal cycles of plant growth, especially at high latitudes across North America, Europe, and Asia. The movie also reveals the almost immediate response of land plants to changing daily weather patterns.

http://earthobservatory.nasa.gov/Newsroom/NPP/npp.html
Global change effects

11-24% of NPP supports human activities

NPP may have been reduced 25-40% by anthropogenic activity

Changes in isotopic composition of atmospheric CO$_2$ recorded in ice cores, tree rings etc. can be used to estimate fossil fuel usage (no $^{14}$C, negative $^{13}/^{12}$C) biomass burning (normal C negative $^{13}/^{12}$C)

Atmospheric CO$_2$ increasing from fossil fuel $5 \times 10^{15}$ g C yr$^{-1}$, and forest clearing $\sim 1.6 \times 10^{15}$ g C yr$^{-1}$ (1980's)

Biomass decreased by $110 \times 10^{15}$ g C (13%) since 1860

Some forest regrowth will act as CO$_2$ sink

+200 ppm CO$_2$ expts show + 12-20% in forests/crops

In practice growth usually limited by other factors, water, nutrients etc.

Ozone, acid rain reduce NPP, but N deposition increases

See increase in NPP at N latitudes-growing season effect
Northward migration of productive forests may increase C storage by $180 \times 10^{15}$ g C when fully adjusted for an atm. doubling.

Alternatively, net source of CO$_2$ from land as earlier warming of land than ocean leads to desertification results in net release of CO$_2$.

During LGM C storage in land plants and soils 30-50% lower.

MODIS shows a decrease in global NPP -- drought in S Hemisphere.

FIGURE 5.16 Change in terrestrial NPP from 2000 to 2009 from MODIS. Source: From Zhao and Running 2010. Used with permission of the American Association for the Advancement of Science.
Fate of NPP

As long-lived plants age, biomass reaches a maximum.

Net Ecosystem Production (NEP) = NPP - (R_h + R_d)

R_h = respiration of herbivores, R_d = respiration of decomposers

As NPP = GPP - R_p, then

NEP = GPP - R_t where R_t is total respiration.
As long-lived plants age NPP is not incorporated into biomass but is delivered to the soils

Herbivory <20% of NPP ~ 3 x10^{15} g C yr^{-1}

Fires also consume net production ~2-5 x 10^{15} g C yr^{-1}

Up to 1.2 x 10^{15} g C yr^{-1} of reduced C cpds are emitted from plants to atmos. e.g. CO, isoprene from pine forests etc.

Detritus (cellular organic C)

Most NPP delivered to soils as dead organic matter

Root turnover, dead leaves, also woody parts as forest ages

Decomposition in upper layers of soil releases nutrients, produces humus which accumulates in lower soil profile

Use litterbags to monitor decay, fraction left after 1 yr

X/X_0 = e^{-k}
Mass balance, litterfall = k(detrital mass)

At steady state input = decay

Mean residence time = 1/k

When decomposition is fast e.g. wet tropical regions k ≥ 1

In contrast in peatlands k ~ 0.001

Global (Mean Residence Time) MRT ~ 3yrs i.e. k= 0.33, for surface of soils

Decomposition is a function of water and temperature (Q₁₀ = 2 for microbiological activity) i.e. doubles every 10°C increase

In arid and semi-arid systems soil moisture limits rates, but UV and termites may be important here

Evapotranspiration used to model k, results agree with observations

Figure 5.15: Rates of decomposition of fresh litter in the United States predicted by a simulation model using actual evapotranspiration as a predictor variable. Simpleth columns are the fractional loss rate (% of mass from fresh litter during the two year of decay. From Robison (1976a).
Humus and soil organic carbon
Humus, non-cellular remnant of detritus
Large number of aromatic rings, C=C=C=C units and
-COOH and -OH groups
Characterised by separation method
Acid soluble fraction - fulvic acid transports Fe and
Al in soils

Are complexed with clays
and are resistant to microbial attack

MRT ~ 30 years but
some fractions are old,
hundreds to
thousands of years

Inventory of soil org C 1456 x 10^{15} g C, is > than overlying biomass

<table>
<thead>
<tr>
<th>Biome</th>
<th>World area (10^6 km²)</th>
<th>Mean soil profile carbon (kg C/ha)</th>
<th>Total soil carbon pool (10^{15} g C)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>0-100 cm</td>
<td>0-300 cm</td>
</tr>
<tr>
<td>Tropical grasslands</td>
<td></td>
<td>15.2</td>
<td>21.4</td>
</tr>
<tr>
<td>Savannas</td>
<td></td>
<td>14.5</td>
<td>20.6</td>
</tr>
<tr>
<td>Temperate grasslands</td>
<td></td>
<td>13.2</td>
<td>19.0</td>
</tr>
<tr>
<td>Deserts</td>
<td></td>
<td>11.3</td>
<td>16.4</td>
</tr>
<tr>
<td>Arid lands</td>
<td></td>
<td>11.2</td>
<td>17.2</td>
</tr>
<tr>
<td>Total</td>
<td>136.5</td>
<td></td>
<td>2341</td>
</tr>
</tbody>
</table>

Note: Includes soil carbonates, chalky limestone, carbonates and detrital. 30.5 x 10^{15} g C, estimated 1980.
$^{14}$C data suggest 16% of organic matter in a pasture soil at least 5700 yrs old. Most turnover in surface soil layers only 17% from below 15 cm.

Can use of CO$_2$ flux to estimate turnover, but is complicated by root respiration.

Figure 5.17 Turnover of litter and soil organic fractions in a grassland soil. Note that mean residence time can be calculated for each fraction from measurements of the quantity in the soil and the annual production or loss (respiration) from that fraction. Flux estimates are in kg C m$^{-2}$ yr$^{-1}$. From Schlesinger (1977).

Figure 5.18 Latitudinal trends for carbon dynamics in forest and woodland soils of the world. The dashed line shows the mean annual input of organic carbon to the soil by litterfall. The solid line shows the loss of carbon, measured as the flux of CO$_2$ from the surface. The difference between these lines represents the loss of CO$_2$ from root respiration and from the respiration of roots detritus and mycorrhizae. From Schlesinger (1977).
Accumulation of organic matter is greatest in wetlands, least in deserts, is part of NEP

Accumulation of organic matter is least in tropical forests, more in boreal forests, is opposite to NPP

Microbiological activity is driven by temperature and moisture

Accumulation of soil organic matter is driven by decomposition not by NPP

During soil development humus accumulates at 1-12 g C m\(^{-2}\) yr\(^{-1}\)

At steady state humus production = loss through decomp and erosion

Global humus production < 0.4 x 10\(^{15}\) g C yr\(^{-1}\) = C in river run-off

<table>
<thead>
<tr>
<th>Ecosystem type</th>
<th>Vegetation as terminal state</th>
<th>Soil origin</th>
<th>Accumulation interval (yr)</th>
<th>Long-term rate of accumulation (g C m(^{-2}) yr(^{-1}))</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tundra</td>
<td>Polar desert</td>
<td>Glacial errir</td>
<td>8,000</td>
<td>0.2</td>
</tr>
<tr>
<td></td>
<td>Polar desert</td>
<td>Glacial errir</td>
<td>9,000</td>
<td>0.3</td>
</tr>
<tr>
<td></td>
<td>Polar desert</td>
<td>Glacial errir</td>
<td>7,600</td>
<td>2.4</td>
</tr>
<tr>
<td></td>
<td>Sedge mat</td>
<td>Glacial errir</td>
<td>1,000</td>
<td>0.4</td>
</tr>
<tr>
<td></td>
<td>Sedge mat</td>
<td>Glacial errir</td>
<td>9,000</td>
<td>1.1</td>
</tr>
<tr>
<td></td>
<td>Sedge mat</td>
<td>Glacial errir</td>
<td>8,700</td>
<td>0.7*</td>
</tr>
<tr>
<td>Boreal forest</td>
<td>Spruce</td>
<td>Glacial errir</td>
<td>5,500</td>
<td>1.7</td>
</tr>
<tr>
<td></td>
<td>Spruce-fir</td>
<td>Glacial errir</td>
<td>5,450</td>
<td>0.8</td>
</tr>
<tr>
<td></td>
<td>Spruce-fir</td>
<td>Glacial errir</td>
<td>2,740</td>
<td>2.2</td>
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<tr>
<td>Temperate forest</td>
<td>Broadleaf evergreen</td>
<td>Volcanic ash</td>
<td>1,277</td>
<td>12.0</td>
</tr>
<tr>
<td></td>
<td>Coniferous</td>
<td>Volcanic mudflow</td>
<td>1,000</td>
<td>10.0</td>
</tr>
<tr>
<td></td>
<td>Coniferous</td>
<td>Alluvium</td>
<td>1,500</td>
<td>5.1</td>
</tr>
<tr>
<td></td>
<td>Deciduous</td>
<td>Dunes</td>
<td>10,000</td>
<td>0.7</td>
</tr>
<tr>
<td></td>
<td>Podocarpus</td>
<td>Dunes</td>
<td>10,000</td>
<td>2.1</td>
</tr>
<tr>
<td></td>
<td>Angophora</td>
<td>Dunes</td>
<td>4,500</td>
<td>1.7</td>
</tr>
<tr>
<td></td>
<td>Eucalyptus</td>
<td>Dunes</td>
<td>6,500</td>
<td>1.4</td>
</tr>
<tr>
<td></td>
<td>Eucalyptus</td>
<td>Dunes</td>
<td>5,500</td>
<td>2.1</td>
</tr>
<tr>
<td></td>
<td>Low forest</td>
<td>Glacial deposits</td>
<td>9,000</td>
<td>2.5</td>
</tr>
<tr>
<td>Tropical forest</td>
<td>Montane</td>
<td>Volcanic ash</td>
<td>8,500</td>
<td>2.5</td>
</tr>
<tr>
<td></td>
<td>Rain forest</td>
<td>Volcanic ash</td>
<td>8,400</td>
<td>2.3</td>
</tr>
<tr>
<td>Temperate grassland</td>
<td>Coniferous</td>
<td>Glacial deposits</td>
<td>9,000</td>
<td>2.2</td>
</tr>
<tr>
<td>Temperate desert</td>
<td>Grassland</td>
<td>Alluvium</td>
<td>3,600</td>
<td>0.8</td>
</tr>
</tbody>
</table>

From Schlesinger (1990); citations to original literature are given therein.
* Corrected from value given in original publication.
Since last glaciation soil organic carbon accum. ~ 1.35 g C m\(^{-2}\) yr\(^{-1}\)

Now contain 300 x 10\(^{15}\) g C >10% of org C in all soils

Current storage rate (0.04 x 10\(^{15}\) g C m\(^{-2}\) yr\(^{-1}\)) is too small to act as a sink for anthropogenic CO\(_2\)

Total organic C in soils (1456 x 10\(^{15}\) g C) = 0.03% of Atmos O\(_2\), marine C storage accounts for most of the O\(_2\)
Global change effects

Cultivation reduces organic C in soil (20-30%) in first few decades

Estimates give $0.8 \times 10^{15} \text{ g C yr}^{-1}$ added to atmosphere from land-use changes

Abandonment of agricultural land leads to rapid increase in soil organic C

Table 5.5: Accumulation of Soil Organic Matter in Abandoned Agricultural Soils and in Other Disturbed Sites, Which are Allowed to Return to Native Vegetation

<table>
<thead>
<tr>
<th>Ecosystem type</th>
<th>Previous land use</th>
<th>Period of abandonment (yr)</th>
<th>Rate of accumulation (g C m$^{-2}$ yr$^{-1}$)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Subtropical forest</td>
<td>Cultivation</td>
<td>40</td>
<td>30–50</td>
<td>Lugo et al. (1986)</td>
</tr>
<tr>
<td>Temperate deciduous forest</td>
<td>Cultivation</td>
<td>100</td>
<td>45</td>
<td>Jenkinson (1990)</td>
</tr>
<tr>
<td>Temperate coniferous forest</td>
<td>Diked soils</td>
<td>50</td>
<td>21–26</td>
<td>Schiffman and Johnson (1989)</td>
</tr>
<tr>
<td>Temperate deciduous forest</td>
<td>Mine spoils</td>
<td>100</td>
<td>55</td>
<td>Beke (1990)</td>
</tr>
<tr>
<td>Temperate grassland</td>
<td>Mine spoils</td>
<td>28–40</td>
<td>28</td>
<td>Leisman (1957)</td>
</tr>
<tr>
<td>Temperate grassland</td>
<td>Cultivation</td>
<td>55</td>
<td>1.55</td>
<td>Anderson (1977)</td>
</tr>
<tr>
<td>Temperate grassland</td>
<td>Cultivation</td>
<td>5</td>
<td>110.0</td>
<td>Burke et al. (1998)</td>
</tr>
<tr>
<td>Temperate grassland</td>
<td>Cultivation</td>
<td>5</td>
<td>110.0</td>
<td>Gebhart et al. (1994)</td>
</tr>
</tbody>
</table>
Charcoal from forest fires is also resistant C, not likely important part of global C flux

Warming of soils will increase decomposition rates, CO$_2$ fluxes from tundra are large if warmed and water table lowered

If atmos CO$_2$ levels also increase tundra may be site of net storage as more nutrients released from increased rates of decomposition