revolution the distinction between energy and information was less clear, and the term brightness was used to refer to both lightness and brightness, without distinction. Sometimes the term brightness is used for the perceived brightness of the illumination level. But perceived illumination and perceived luminance are separate, and by consensus, the term brightness is now used to refer only to the latter.

Why are there so many theories of brightness?

There is little adaptive value in determining the intensity of light reflected by a surface. It is far more useful to know if the surface is black, white or gray. Thus, just as the perception of object properties requires a theory of perceived object size, not a theory of perceived visual angle, doesn't this also require a lightness theory rather than a brightness theory? The answer is obviously yes. But why then are there more theories of brightness than of lightness? Because brightness theorists make the tacit assumption that lightness is based on brightness. This assumption has its roots in the old sensation/perception distinction, with brightness values serving as sensations that correspond to local stimulation. But this remains an assumption. And there is little reason to reject the claim of gestalt theory that lightness is perceived directly, without a prior stage of raw sensations.

Where can I find out more?

Adelson, E.H. (2000). Lightness perception and lightness illusions. In The New Cognitive Neuroscience, Second Edition, M. Gazzaniga, ed. (Cambridge, MA: MIT Press), pp. 339–351.
Blakeslee, B., and McCourt, M.E. (2003). A multiscale spatial filtering account of brightness phenomena. In Levels of Perception, L. Harris and M. Jenkin, eds. (New York: Springer), pp. 47–72.
Gilchrist, A. (2006). Seeing Black and White (New York: Oxford University Press).
Hering, E. (1874/1964). Outlines of a Theory of the Light Sense (Cambridge, Mass.: Harvard University Press).

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Primer

Global primary production

F.I. Woodward

The primary source of carbon dioxide released to the atmosphere by human activities derives from fossil carbon fixed by prehistoric photosynthesis. Carbon dioxide is the dominant greenhouse gas that drives global warming, while also being the substrate for photosynthesis. Globally and annually, photosynthesis fixes an order of magnitude more CO_2 than is released by human activities. In this primer I shall consider the extent to which natural systems act as a sink for CO_2 human emissions.

Gross primary production (GPP) refers to the photosynthetic conversion of solar radiation to produce adenosine triphosphate (ATP) and reduced adenosine dinucleotide phosphate (NADPH). The chemical energy stored in these metabolites is used in large part to synthesise plant biomass from carbon dioxide and water, a process known as net photosynthesis that can be determined for a green leaf, or a suspension of algae, by measuring changes in either carbon dioxide or oxygen concentration as a consequence of the photosynthetic activity. Some of the chemical energy is also used in the processes of photorespiration and the reduction of nitrate and sulphate. Although GPP is the rate of production of chemical energy, for measurements and modelling of plants and vegetation GPP is generally taken to be equal to net photosynthesis, the energy remaining for CO_2 fixation, after its use for photorespiration and the reduction of nitrate and sulphate.

Primary production provides the energy source and substrates for virtually all of the major food chains of the world and is measured in units of carbon. A range of primary production terms are used (Box 1). Over a year only about one half of GPP is fixed into biomass, the other half is lost by respiratory processes (distinct from photorespiration): this defines net primary production (NPP). Biomass is the key product of NPP as this is now available for consumption by secondary consumers. Over an annual time scale, NPP is often measured by the difference in biomass sampled one year apart. This implies that all NPP is fixed and remains as biomass. In fact some biomass is also lost as dead litterfall (Box 1), causing

Box 1

Terminology.

Gross primary production (GPP) = photosynthetic CO_2 fixation

Net primary production (NPP) = GPP – autotrophic respiration

Net ecosystem production (NEP) = NPP – heterotrophic respiration

Net biome production (NBP) = NEP – losses through disturbance

Biomass = Σ(NPP – losses through litterfall)

Units of production are in mass of carbon dioxide or carbon and either per unit of surface area (ground or photosynthetic tissue) per unit of time, for example gC m^{-2} day^{-1}, or integrated for a large area, for example. PgC $year^{-1}$, where P = 10^{15} g.

Unit of carbon dioxide concentration is part per million of air by volume (ppm).

NPP to be underestimated if the lost biomass is not quantified. This litterfall provides material for the activity of decomposer organisms, whose activity is measured as carbon losses by heterotrophic respiration (Box 1).

Measuring global net primary production

The NPP of a single plant can be measured by enclosing the whole plant (including roots in the case of a land plant) in an airtight and air conditioned container, while constantly recording changes in carbon dioxide concentration. Daytime photosynthetic uptake of CO_2 will be followed by nocturnal release of CO_2 by respiration. Continuing such a measurement programme to provide an annual NPP would be practically difficult and at best achieved for a very small sample of plants.

On land, NPP can be calculated in the field for a larger sample of plants by measuring the biomass increment over a year. This approach may miss unaccounted losses of new biomass through litterfall, and other possible losses such as through herbivory or root exudates, and so would underestimate NPP. The measurements also suffer from sampling errors, as different plants would be sampled to calculate biomass changes and individuals differ in terms of biomass, even in an even aged uniform stand of plants. NPP is impossible to measure by harvesting at large spatial scales such as by countries, because of the need to harvest material and to sample in large numbers. Non-destructive approaches have been used to circumvent this problem and, with longer-term averaging, can smooth errors at the expense of temporal resolution.

The obvious limitations of destructive and non-destructive approaches have led to the use of satellite remote sensing measurements to drive models of NPP and provide global scale coverage, at daily to monthly frequencies. The approach also lends itself to measurements on land and ocean using the same basic NPP model (1), with appropriate units on a unit surface area basis (2):

$$\text{NPP} = \text{photosynthetic biomass} \times \text{growth efficiency} \times \text{light} \quad (1)$$

$$\text{gC m}^{-2}\text{ day}^{-1} = [\text{g}_A\text{ m}^{-2}] \times [(\text{gC g}_A^{-1}\text{ mol}^{-1}) \times E] \times \text{mol day}^{-1} \quad (2)$$

Photosynthetic biomass is made up of either green leaves or chlorophyll in algal cells and expressed per unit area of surface (g_A m^{-2}), and light is solar radiation (mol day^{-1}) in the photosynthetically active waveband (400–700 nm). Total photosynthetic biomass is integrated throughout the column of leaves in a vegetation canopy or through the euphotic zone — the depth in which there is sufficient light for photosynthesis — of the ocean. Growth efficiency is a measure of the conversion of solar radiation, by photosynthetic biomass, to the carbon units of NPP (gC g_A^{-1} mol^{-1}), accounting for the quantum efficiency of photosynthesis and other dimensionless efficiency factors (E). These latter factors include limitations by temperature and nutrients and drought and low humidity on land.

Radiometric measurements by satellites of radiation reflected from the earth's surface can be used to quantify critical components of the NPP model. For land and ocean, reflected radiation at different wavebands between 400 and 700 nm are used to calculate the amount of photosynthetically active radiation incident on the photosynthetic biomass. Over land, measurements of reflected radiation in the red and near infra-red wavebands are used to calculate the density of leaves through the vegetation canopy. Over the oceans, different wavebands of reflected blue light are used to calculate phytoplankton chlorophyll and biomass and the depth of the euphotic zone. Additional data sources are used to calculate temperature and, where necessary, other key climatic variables such as humidity and wind.

The global view

Satellite-based estimates of NPP show clear regional patterns (Figure 1), with terrestrial NPP being, on a per unit area basis, on average three times that of the oceans. However, the current total NPP by the two biospheres is approximately equal, at about 60 PgC yr^{-1} for the terrestrial biosphere and 65 PgC yr^{-1} for the oceanic biosphere.

High oceanic NPP is observed in areas where there is coastal upwelling of nutrients, such as off the west coasts of South America and Africa, and globally these regions account for about 14–30% of oceanic NPP. The generally low rates of productivity for the deep and open oceans reflect the critical limitation of nutrients (nitrogen, phosphate and iron) needed to support high productivity.

On land, NPP is highest in the rain forests between the tropics, where precipitation is greater than 1500 mm yr^{-1} and temperature is uniform through the year (typically 22–26°C). Seasonal variations of temperature or precipitation reduce NPP. For example, moving in any direction from the rain forest of Zaire, a 1% reduction in annual precipitation leads to a 1% reduction in NPP, with no change in annual temperature. Temperature limitation becomes more dominant at the higher latitudes of the northern hemisphere. Over Europe NPP is reduced by about 4% for each 1°C reduction in mean annual temperature, with little change in annual precipitation.

The total NPP of the Pacific Ocean is about equal to that of the tropical rain forests (~20 PgC yr^{-1}), while the same total is achieved by the Atlantic plus the Indian Ocean. The total NPP of the Southern and Arctic Oceans is about equal to that of the Boreal forests (~3 PgC yr^{-1}).

The carbon cascade

If the World were at climatic equilibrium then carbon fixed by

NPP would be exactly balanced by carbon losses due to plant respiration plus other processes. These processes are another reality of life — decomposition. All plants may die and be decomposed or be consumed by herbivores and parasites, which in turn may also be consumed or die. The end result of this chain of events is decomposition of dead plant-derived carbon by heterotrophic respiration. A small fraction escapes decomposition and becomes a future fossil fuel. Small though this fraction may be it actually becomes a crucial component of the global carbon cycle over geological time scales.

Burning fossil fuels and deforestation together currently emit about 9 PgC yr^{-1} into the atmosphere. This amount seems small relative to the combined 125 PgC yr^{-1} of NPP by the biosphere. Accounting for heterotrophic respiration, however, reduces NPP considerably, with a net ecosystem production (Box 1) of 11 PgC yr^{-1} for the oceans and 5 PgC yr^{-1} for the land (Figure 2) — similar magnitudes to human derived emissions. On land, further losses of carbon occur as a consequence of disturbance, such as by fire and soil erosion, reducing the carbon actually removed from the atmosphere, the net biome production, to about 2–3 PgC yr^{-1}. This accounts for about 20–30% of human emissions, varying from year to year due to climatic fluctuations.

Net ecosystem production by the oceans represents the sinking of dead organisms and detritus through the water column. If this particulate organic matter, plus any dissolved organic matter, penetrates below the mixed layer of the ocean (the thermocline), then its carbon content may be sequestered from the atmosphere for centuries or longer. This process is known as the biological pump, and serves to maintain high concentrations of dissolved carbon in the ocean. It is calculated that the absence of this pump would cause atmospheric carbon dioxide concentrations to be 200 ppm higher than the present. This accumulation represents the long-term activity of the biological pump, while continuous upwelling of deep waters returns dissolved carbon back to the ocean surface and atmosphere.

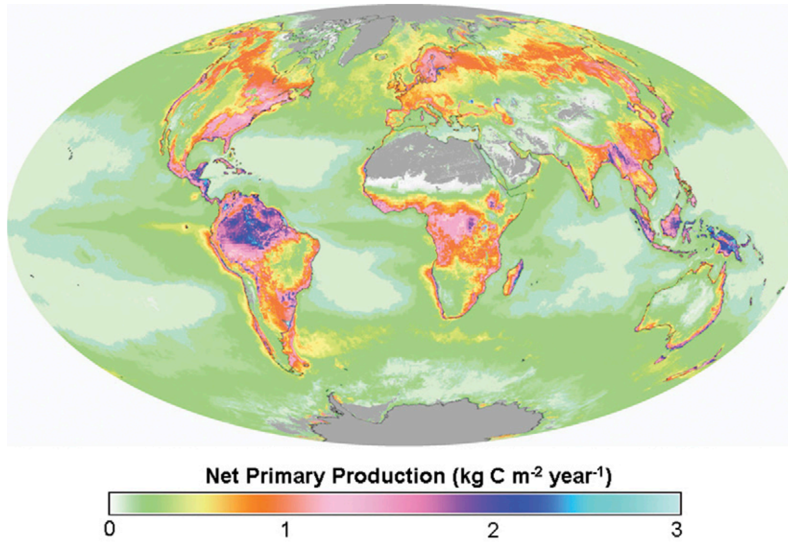

Figure 1. Net primary production based on reflectance measurements from the MODIS satellite with growth models to provide a full global coverage for 2002.
Image from NASA Observatory with colour scale inverted from the original.

It is uncertain how much of the anthropogenic emissions of carbon are sequestered by the biological pump, primarily because this will entail an enhanced supply of nutrients that is not readily measured at the global scale. It is likely that sequestration is a relatively small fraction of emissions. By contrast, uptake by another oceanic pump, the solubility pump, accounts for about 2–3 Gt C yr^{-1} of human emissions.

The solubility pump is a global-scale process which depends on the negative temperature dependence of CO_2 solubility in water. Solubility is greatest in the cold waters of high latitude oceans, where the dense water sinks, removing CO_2 to depth. Ocean currents move this cold water towards the tropics, where upwelling forces water to the surface and the loss of CO_2, which is less soluble at the higher temperatures. These higher temperature waters are then cooled as they move back to the higher latitudes, completing the cycle of the pump.

Dissolved CO_2 is about 1% of the inorganic carbon in the ocean and is the only component that is exchanged with the atmosphere and is not yet at equilibrium with the atmosphere, because of the continued accumulation of fossil carbon dioxide. Bicarbonate and carbonate ions constitute the other 99%, of which bicarbonate is 91%. The chemical interchange of CO_2 with water and its uptake as bicarbonate ions is described as follows:

$$CO_2 + H_2O + CO_3^{2-} \leftrightarrow 2\ HCO_3^- \quad (3)$$

Rising atmospheric CO_2 concentrations increase the dissolved CO_2 concentration in sea water, but warming reduces this solubility. It is estimated that oceanic NPP by the biological pump has declined by about 6% over the last 20 years and this is strongly correlated with an increase in global sea surface temperatures of 0.2°C. Increasing the dissolved CO_2 concentration also increases the bicarbonate ion concentration, but this is associated with a decrease in the carbonate ion concentration (and pH), which decreases the effectiveness of the solubility pump. The contemporary solubility pump is already working at a 25–40% reduction in efficiency compared to before the industrial revolution.

The biospheric challenge

Global warming occurs though the accumulation of greenhouse gases in the atmosphere. Rounding various estimates of climatic sensitivity provides an average relationship between carbon accumulation in the atmosphere, the atmospheric CO_2 concentration and global warming with a ratio of 200:100:1. Therefore, a 200 PgC accumulation in the atmosphere would lead to an increase in atmospheric CO_2 concentration of 100 ppm and 1°C of global warming. This relationship has considerable uncertainty bounds, but provides a useful rule of thumb for assessing climatic impacts of CO_2 emissions.

A further rule of thumb, using rounded totals, indicates the importance of the land and ocean for naturally mitigating anthropogenic impacts on the carbon cycle. Over the last one to two centuries, human changes in land use, such as deforestation, have caused the release of 200 PgC from the land to the atmosphere, in addition to fossil fuel emissions of 300 PgC. The atmospheric carbon content has increased by 200 PgC, indicating that 300 PgC has been taken up by the oceans and the land, in approximately equal amounts. Global climate has therefore been sheltered from the full effect of human emissions by these two natural carbon reservoirs.

Model simulations of future terrestrial and oceanic carbon fluxes depend strongly on future fossil fuel emission scenarios and models also differ in their quantitative outcomes. Experiments have demonstrated that increasing CO_2 concentrations stimulate NPP on land. Doubling CO_2 concentration stimulates NPP by about 20%. This fertilisation effect will be diminished, under any future warming where precipitation is either reduced or even remains unchanged, through the effects of drought. Under a business-as-usual scenario the terrestrial and oceanic biospheres are likely to be carbon sinks through the 21st century, but with a decreasing capacity through time as a result of the increasingly negative impacts of warming on both land and ocean, in addition to increasing drought limitation on land.

Concluding actions

The idea of planting trees to reduce carbon emissions is often discussed. The scope of the problem can be nicely illuminated at the global scale. If all land use changes of the previous two centuries were reversed, then carbon accumulation in the atmosphere would be 80 PgC less than the present, leading to a global cooling of 0.4°C. By contrast, total deforestation could add as much as 400 PgC to the atmosphere, leading to a global warming of 2°C. Although these are rough estimates they indicate quite clearly that global scale management of forests, particularly in terms of increasing afforestation and reducing deforestation, has a part to play in future global climate.

The global nature of the problem becomes clear when considering sequestration at the country scale. If the whole of the UK were reforested then this would be equivalent to a sequestration of about 1 PgC. If this directly impacted the atmospheric CO_2 concentration then there would be a global cooling of 0.005°C. The approximate annual rate of carbon uptake would be 1 PgC, divided by the time to forest maturity. So if the time to maturity were 25 years, then the annual cooling would be 0.0002°C. Annual UK emissions of fossil fuel carbon to the atmosphere cause a global warming of ~0.0003°C yr^{-1}, while current global emissions of 7.9 PgC yr^{-1} may cause an estimated 0.016°C yr^{-1} of warming, using the above rule of thumb. The small contribution of the UK to the global change indicates that global mitigation of climatic change can only be achieved by internationally concerted action to reduce carbon emissions.

The oceanic and terrestrial sinks for carbon currently sequester 60% of anthropogenic emissions, but this fraction is likely to decline through the 21st century. There is limited potential to stimulate this sequestration, such as with iron fertilisation of the ocean. Increasing iron stimulates plankton growth and carbon uptake — initially. Herbivores then increase in abundance leading to little change in plankton density and subsequent additions of iron will cause only a limited stimulation of carbon sequestration. There is some suggestion, however, that restoring fish diversity in the over-fished global oceans can enhance production and the resistance of this production to perturbations. As was the case for afforestation the key to success will be concerted global action in controlling and enhancing species diversity.

The natural carbon cycle could also be enhanced by human intervention higher up the carbon cascade (Figure 2). For example, terrestrial NPP could be harvested to manufacture ethanol as a replacement, or partial replacement for petrol (gasoline) in vehicles. Brazil, for example, produces ethanol from sugar cane that replaces 20–25% of petrol in fuel. The plant source, such as sugar cane, grows and sequesters carbon which is then released again in the car exhaust gases. The ideal net result of this method is a neutral effect on the atmospheric CO_2 concentration for using the ethanol, but there would still be CO_2 accumulation from the fossil fuel component. At the current fossil fuel emission of 7.9 PgC yr^{-1}, globally, and assuming 1.6 PgC yr^{-1} as emissions from vehicle transport, then a 22% use of ethanol, globally, would reduce fossil fuel emissions by 0.35 PgC yr^{-1}, broadly equivalent to a cooling of 0.0007°C yr^{-1};

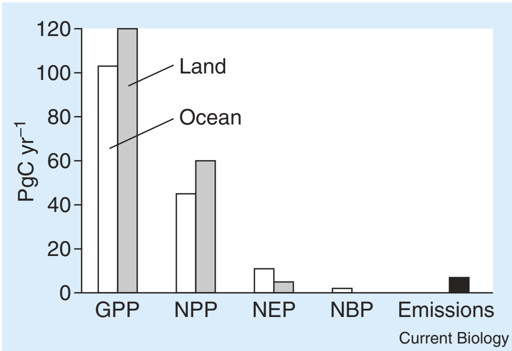

Figure 2. The average carbon cascade from gross primary production (GPP), to net primary production (NPP), to net ecosystem production (NEP) to net biome production (NBP), for land and ocean, and in comparison with emissions due to human activities.

although small this is more than twice the fossil fuel emissions of the UK. But there are hidden carbon costs in terms of fossil fuel requirements for growing, harvesting and converting sugar cane to ethanol, which means the process is not carbon neutral and, furthermore, ethanol has about 65% of the energy content of petrol.

Growing crops for biofuels is area intensive while mining for fossil fuels is much less so. Nearly 4% of Brazil is used to grow sugar cane for producing ethanol. In the UK, wheat would be the likely source of ethanol, but it is about as half as productive as sugar cane. There are 26 million registered car owners in the UK who, on average, drive 15000 km yr^{-1}. Petrol with 22% ethanol has an average fuel economy of about 9 km l^{-1}. Wheat produces 0.43 t ethanol ha^{-1}. These data imply that one car owner driving an average annual distance would require annually the ethanol from 0.67 ha of wheat crop. For all drivers in the UK this adds up to nearly 75% of the land area of the UK to grow wheat for ethanol production. This is clearly not a practical approach to reducing carbon emissions, using the current technologies for producing biofuels such as ethanol. Increasing the area of crops for biofuel production would exert unacceptably severe impacts on the area under food crops and on the diversity of species in natural and semi-natural vegetation.

There are many alternative opportunities to use primary production in order to mitigate the serious consequences of anthropogenic climatic change. The benefit will always be fractional where the real need is to find methods of significantly reducing fossil fuel emissions of carbon dioxide at source and globally. Time is ticking on and many models indicate that the natural oceanic and terrestrial sinks for carbon will slow through the current century. The reduced primary production of the terrestrial biosphere results in particular from warmer and drier conditions on land, increasing the frequency of droughts. Warming the oceans leads to stratification of the warm low density upper ocean water that increasingly reduces the upward movement of nutrients from the denser and colder water beneath. This stratification will reduce the supply of nutrients to the phytoplankton and the solubility of CO_2 in the warmer upper waters, leading to a reduction in primary production.

The natural sinks for human emissions of CO_2 are therefore most likely to slow through the current century, increasing the fraction of CO_2 that remains in the atmosphere and its associated warming potential. Area-based human modifications of the carbon cycle, such as by increasing the area of crops for producing biofuels, will exert some mitigating impact on emissions. Their use to mitigate all emissions is unrealistic. For example, with a business-as-usual rate of CO_2 emissions fulfilling the aim of stabilising atmospheric CO_2 concentration at 550ppm would require a land area about the size of the whole of South America to grow crops for biofuels.

Methods for using or enhancing biological productivity to reduce human CO_2 emissions, and their climatic consequences, can only be a small part of the mitigation strategy. The only answer is improved methods of reducing emissions from all CO_2 sources plus a move away from an energy system based on carbon, such as to hydrogen.

Further reading

Behrenfeld, M.J., Boss, E., Siegel, D.A., and Shea, D.M. (2005). Carbon-based ocean productivity and phytoplankton physiology from space. Global Biogeochem. Cy. *19*, GB1006. 10.1029/2004GB002299.

Behrenfeld, M.J., O'Malley, R.T., Siegel, D.A., McClain, C.R., Sarmiento, J.L., Feldman, G.C., Milligan, A.J., Falkowski, P.G., Letelier, R.M., and Boss, E.S. (2006). Nature *444*, 752–755.

Falkowski, P.G., Barber, R.T., and Smetacek, V. (1998). Biogeochemical controls and feedbacks on ocean primary productivity. Science *281*, 200–206.

Friedlingstein, P., Cox, P., Betts, R., Bopp, L., von Bloh, W., Brovkin, V., Cadule, P., Doney, S., Eby, M., Fung, I., *et al.* (2006). Climate-carbon cycle feedback analysis: results from the C4MIP model intercomparison. J. Climate *19*, 3337–3353.

Orr, J.C., Fabry, V.J., Aumont, O., Bopp, L., Doney, S.C., Feely, R.A., Gnanadesikan, A., Gruber, N., Ishida, A., Joos, F., *et al.* (2005). Nature *437*, 681–686.

Prentice, I.C., *et al*. (2001). The carbon cycle and atmospheric carbon dioxide. In Climate Change 2001: The Scientific Basis, J.T. Houghton *et al*., eds. (Cambridge: Cambridge University Press) pp. 183–237.

Richardson, A.J., and Schoeman, D.S. (2004). Climate impacts on plankton ecosystems in the northeast Atlantic. Science *305*, 1609–1612.

Running, S.W., Nemani, R.R., Heinsch, F.A., Zhao, M., Reeves, M., and Hashimoto, H. (2004). A continuous satellite-derived measure of global terrestrial primary productivity. BioScience *54*, 547–560.

Sims, R.E.H., Hastings, A., Schlamadinger, B., Taylor, G., and Smith, P. (2006). Energy crops: current status and future prospects. Global Change Biol. *12*, 2054–2076.

Tilman, D., Hill, J., and Lehman, C. (2006). Carbon-negative biofuels from low-input high-diversity grassland biomass. Science *314*, 1598–1600.

Woodward, F.I., and Lomas, M.R. (2004). Vegetation dynamics – simulating responses to climatic change. Biol. Rev. 79, 643–670.

Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Jackson, J.B.C., Lotze, H.K., Micheli, F., Palumbi, S.R. *et al*. (2006). Impacts of biodiversity loss on ocean ecosystem services. Science *314*, 787–790.

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