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Carbon Sequestration: Photosynthesis and Subsequent Processes

The increase in the global atmospheric CO₂ concentration projected for 2050 increases the productivity of temperate forests by a quarter; but it is by no means clear that such increased productivity will lead to more long-term carbon sequestration.

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Man's activities have increased, and will continue to increase, the fraction of the atmosphere composed of CO₂. From values of about 280 μmol mol⁻¹ between the end of the last glaciation and about 1750, atmospheric CO₂ has increased to about 380 μmol mol⁻¹ today, and the value in 2050 will be about 550 μmol mol⁻¹. Small-scale experiments show that these higher CO₂ levels increase the rate of photosynthesis and plant productivity. Field enrichments with CO₂ also show increases in plant productivity. In a recent paper, Norby *et al.* [1] report a meta-analysis of four Free Air Carbon dioxide Enrichment (FACE) studies on temperate forests. They conclude that the primary productivity of these communities at predicted 2050 CO₂ levels is 23 ± 2% (median ± error derived from regression analysis) higher than at today's CO₂ level; however, such increases in productivity do not necessarily mean an increase in long-term sequestration of carbon.

We need to know how plants will respond to the inevitable increase in CO₂ over the next few decades and beyond. Such knowledge is important in understanding the influence of global environmental change on plants and the biota dependent on them, and is needed to analyze the role of vegetation in

sequestering part of the anthropogenic input of CO₂ to the atmosphere. About half of the CO₂ released since 1750 remains in the atmosphere, with much of the rest sequestered in the ocean and the remainder sequestered in terrestrial ecosystems for periods of decades to centuries [2,3]. With an estimated 60% of terrestrial carbon stored in forest ecosystems [4], it is vital that we get indications of whether such terrestrial sequestration will continue with further increases in CO₂ production.

We need FACE experiments because work in growth cabinets can never really mimic the real world environment either in variability or scale. FACE experiments permit comparisons to be made between present day conditions and the predicted CO₂ level for 2050 (or whenever) for natural stands of vegetation. Initially confined to low-growing vegetation (pastures or arable crops), FACE experiments have subsequently been extended to forests [1]. FACE experiments involve a ring of CO₂-release points; points are activated depending on wind speed and direction. This enables the experimenter to maintain the required mean CO₂ level, although there can be changes in CO₂ concentrations of 200–300 μmol mol⁻¹ over periods of 5–20 s [5].

The results of experiments in which such fluctuations were mimicked in controlled environment conditions in

comparison with the same, invariant, mean CO₂ concentration showed that the fluctuating environment in FACE experiments could significantly under-estimate the effects of steady increased CO₂ concentrations [5]. There is also the problem that some FACE experiments economize on CO₂ by not applying CO₂ enrichment at night, although non-photosynthetic effects of CO₂ (on respiration) may not be as large a problem as was initially thought [6,7]. Despite these problems, FACE is rightly the method of choice for studying the effect of enhanced CO₂ on terrestrial communities.

Perhaps the most surprising outcome of Norby *et al.*'s [1] meta-analysis is the consistency among the four studies in the degree of stimulation of productivity by increased CO₂. This similarity occurred despite differences in tree species, including evergreen conifers and annually deciduous dicotyledons, absolute productivity, soil type, age of the stand, and local climate. The independence of absolute productivity is important: to the extent that it is imposed environmentally rather than by tree genotype, it is consistent with demonstrations that enhancement of productivity by augmenting CO₂ can occur even when productivity is constrained in the present atmosphere by the availability of some other resource [3,8].

Gifford [8] specifically addressed limitation by water supply in semi-arid and arid areas, and by the supply of photosynthetically active radiation in the humid tropics, in modelling the response of global terrestrial productivity to increased CO₂. Future work could profitably integrate CO₂ effects with the change from nitrogen to phosphorus limitation with time after colonization of 'new'

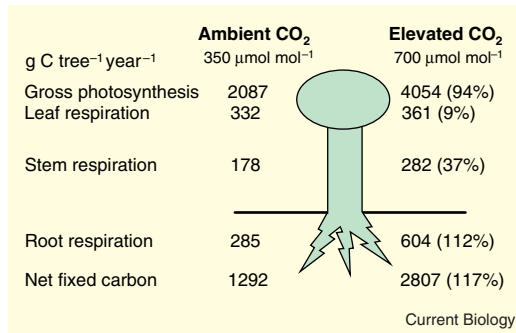


Figure 1. Annual carbon fluxes (g C tree⁻¹ year⁻¹) for young birch trees during the fourth year of growth in ambient or elevated CO₂.

Numbers in brackets denote the percentage increase in carbon flux, compared to ambient conditions, when atmospheric CO₂ concentrations are doubled. Note that a higher concentration of CO₂ used in the 'elevated

CO₂ treatment, together with differences in canopy closure and mode of CO₂ application, are likely to explain the disparity between this example and Norby *et al.* [1] in stimulation of net carbon flux. (Adapted with permission from [6].)

terrestrial habitats by, for example, retreat of ice after glaciation, or cooling of lava flows [9,10]. Given that productivity responses to elevated CO₂ might be constrained by the availability and transpirational delivery of mineral nutrients to the root [11], it would be interesting to examine decreased productivities with lower atmospheric CO₂ in the last glaciation [12] in the context of the availability of other resources.

Increased primary productivity under elevated CO₂ has implications for the food-web. Although organic carbon availability might be improved, the dilution of other plant components by carbon in high-CO₂ environments might reduce the nutritional quality of plant tissues for consumers [13]. Furthermore, changes in resource allocation to physical and allelochemical defences might occur, particularly if tissue nitrogen levels are altered. The interaction of these effects with changes in nutritional value might elicit a range of herbivore behavioral and growth performance responses to altered food quality: even within one herbivore group, the phloem feeders, plants grown under elevated CO₂ had positive, zero and negative impacts on the population growth of five aphid species [14].

The consequences of tissue carbon-enrichment for herbivores and other trophic groups have implications for the extent of carbon sequestration in response to increased atmospheric CO₂. The long-term sequestration of some of the additional CO₂ fixed

as organic carbon requires that there is neither a more than proportionate increase in CO₂ loss in ecosystem respiration with increasing primary productivity (Figure 1), nor a stoichiometric (with plant content) sequestration of nutrients such as nitrogen and phosphorus which would limit the use of these nutrients in further primary productivity [13].

Norby *et al.* [1] wisely caution against extrapolating from their demonstration of increased productivity in the four forest areas to a prediction of increased long-term carbon sequestration. One reason is uncertainty over the impact of climate change on respiration. Although photosynthesis does not appear to acclimatize in a range of tree species after several years of CO₂ exposure, respiratory responses are not entirely clear [6,7], and long-term effects on carbon sequestration might be influenced by acclimatization of either process to changes in additional factors, such as temperature [15], that accompany CO₂ increases.

One potential outcome of plant responses to elevated CO₂ is an improved capacity to capture energy and nutrients as allocation is increased to leaf and fine root tissues (Figure 1), and to root exudates [4]; this will be particularly true if the accompanying architectural changes allow more effective radiation interception or mining of the substrate, or improved interaction with microbial symbionts. The impact of increased CO₂ on plant architecture, and also on plant

development and phenology — effects that have often confounded the interpretation of CO₂ enrichment studies — are likely to be crucial to our understanding of carbon sequestration in forest ecosystems. Although changes in plant phenology in response to elevated CO₂ can be variable [6], plant development tends to accelerate under CO₂ enrichment [16], while net carbon fixation rate can vary with the plant developmental stage at the time of CO₂ enrichment [6,16].

What is known of the terrestrial carbon sink which is responsible for some of the discrepancy between known anthropogenic CO₂ emissions and the sum of accumulation of CO₂ in the atmosphere and in the ocean [2,3]? Gielen *et al.* [17] have shown net carbon storage during a three year FACE study on *Populus*; but further longer-term studies are needed. Even recycling of any increased below-ground productivity into soil CO₂ could become sequestered by increased rock weathering [18] rather than escaping back to the atmosphere.

Much remains to be discovered about the links between increased terrestrial primary productivity resulting from higher atmospheric CO₂ and carbon sequestration. The same applies to the possibility of greater carbon sequestration in the ocean as a result of higher biological productivity, in addition to the solution of atmospheric CO₂ in the surface ocean [12,19,20].

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Visual Optics: The Shapes of Pupils

The eyes of many terrestrial vertebrates have slit-shaped pupils. A new hypothesis links this pupil shape to the way that vertebrate lenses compensate for chromatic aberration.

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Human eyes have circular pupils, but a great many animals have pupils that are oval or slit-shaped. These slits/ovals may be oriented vertically (as in crocodiles, vipers, cats and foxes), or horizontally (as in some rays, flying frogs, mongooses and ungulates such as sheep and hippopotami). The explanation usually given for the use of a slit pupil is that it can exclude light more effectively than a circular pupil, and so slit pupils tend to be found in the eyes of animals with a crepuscular or nocturnal lifestyle that need to protect their eyes during daylight [1]. The slit pupil of a cat, for example, can change the intensity on the retina 135-fold, compared to 10-fold in man [2]. This has never seemed to be an entirely convincing explanation, however, as some animals (such as the tarsier) have circular pupils that can close down very effectively, to a diameter of about half a

millimeter [1], and in many ungulates the rather rectangular pupils do not close to a narrow slit in bright light. A recent paper by Malmström and Kröger [3] offers a much more intriguing explanation of the oval pupil; it relates to the way that vertebrate lenses have evolved to handle color.

It has been known at least since James Clerk Maxwell, who famously contemplated the eye of his breakfast herring [4,5], that spherical fish lenses are well corrected for spherical aberration – the tendency for peripheral rays to be focused too close to the lens. This correction results from the lens having a particular near-parabolic gradient of refractive index [5,6]. Chromatic aberration, however, in which blue light is focused substantially closer to the lens than red light, was thought until recently to be uncorrected. This is because protein solutions cannot be produced with different chromatic dispersions, and thus achromatic

lens combinations cannot be made from biological lens material.

Fish lenses, however, have found another way round the problem. In 1999, Kröger and his colleagues [7] showed that the gradient in fish lenses is not exactly that predicted for perfect spherical correction. It has a systematically lumpy profile, which results in the lens having several different focal lengths for concentric zones at different distances from the center. Each of these focal zones produces an image at a different distance from the lens, and each such image has its own chromatic aberration, which one would think would make a bad situation even worse. But the beauty of the arrangement is that the red image from one zone actually coincides with the green image from another zone and the blue image from the third zone, meaning that there is one plane in which there is a sharp image for all the wavelengths relevant to the fish's color vision system (Figure 1A). Of course much of the light is not well focused in this plane and this will reduce image contrast, so this is not a perfect solution, but it is much better than the alternative of having a single focal length with a sharp image for only one wavelength.