

Increase in C3 plant water-use efficiency and biomass over Glacial to present CO₂ concentrations

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ATMOSPHERIC CO₂ concentration was 160 to 200 μmol mol⁻¹ during the Last Glacial Maximum (LGM; about 18,000 years ago)¹, rose to about 275 μmol mol⁻¹ 10,000 years ago^{2,3}, and has increased to about 350 μmol mol⁻¹ since 1800 (ref. 4). Here we present data indicating that this increase in CO₂ has enhanced biospheric carbon fixation and altered species abundances by increasing the water-use efficiency of biomass production of C₃ plants, the bulk of the Earth's vegetation. We grew oats (*Avena sativa*), wild mustard (*Brassica kaber*) and wheat (*Triticum aestivum* cv. Seri M82 and Yaqui 54), all C₃ annuals, and selected C₄ grasses along daytime gradients of Glacial to present atmospheric CO₂ concentrations in a 38-m-long chamber. We calculated parameters related to leaf photosynthesis and water-use efficiency from stable carbon isotope ratios (¹³C/¹²C) of whole leaves. Leaf water-use efficiency and above-ground biomass/plant of C₃ species increased linearly and nearly proportionally with increasing CO₂ concentrations. Direct effects of increasing CO₂ on plants must be considered when modelling the global carbon cycle and effects of climate change on vegetation.

The shoots of plants grown in the 38-m chamber were enclosed by a transparent cover through which air was moved in one direction. Photosynthesis by enclosed plants progressively depleted the CO₂ concentration ([CO₂]) and increased the ¹³C/¹²C of air (B.D.M. *et al.*, manuscript in preparation) as it moved the 38 m from the air intake to outlet of the chamber. The δ¹³C values (see Fig. 1 legend) of leaves of C₃ species and of concurrently grown C₄ grasses, grassbur (*Cenchrus incertus*), crabgrass (*Digitaria ciliaris*) and Gaspé yellow flint maize (*Zea mays*),

were linearly correlated with [CO₂] (Fig. 1). The difference between the δ¹³C of atmospheric CO₂ and leaf carbon of maize (and certain other C₄ species) is conservative across environments⁵ and did not vary significantly with [CO₂] (B.D.M. *et al.*, manuscript in preparation), enabling us to use the δ¹³C of C₄ leaves as a proxy for the δ¹³C of chamber air⁶.

Leaf intercellular [CO₂] (*c_i*), calculated from leaf δ¹³C values, increased linearly and nearly proportionally (by the same ratio) with higher ambient [CO₂] (*c_a*) in each C₃ species. As a result, intercellular [CO₂] was a constant but different fraction of *c_a* in oats (*c_i/c_a* = 0.70) and mustard (*c_i/c_a* = 0.65) grown at mean [CO₂] from 330 to 160 μmol mol⁻¹ (Fig. 2). The *c_i/c_a* of wheat cultivars increased only slightly from 0.63 and 0.66 at 225 μmol mol⁻¹ to 0.66 and 0.69 at 350 μmol mol⁻¹ for Yaqui 54 and Seri M82, respectively. A similar result has been reported⁷ in young wheat plants exposed to CO₂ partial pressures between 120 and 500 μbar. Others have demonstrated that coordination of stomatal and mesophyll functions minimizes variation in *c_i/c_a* to similar values in C₃ species⁸, but this is the first demonstration of such for C₃ plants grown over a [CO₂] range characteristic of Last Glacial Maximum (LGM)-to-present atmospheric concentrations. Intrinsic water-use efficiency, defined as the ratio of leaf photosynthesis or net assimilation (*A*) to stomatal conductance to water vapour (*g*), increased by the same (oats and mustard) or nearly the same (wheat) relative amount as did [CO₂], a consequence of conservative *c_i/c_a* in these C₃ species (Fig. 3).

Leaf assimilation should have increased substantially at the higher *c_i* that accompanied increasing [CO₂], unless photosynthetic capacity (the relationship of *A* to *c_i*) declined. The positive linear relationship of *A* to *c_i* at subambient [CO₂] that is typical of C₃ species did not differ between oat plants grown at extremes of the [CO₂] gradient⁹. We estimate from that relationship that with a constant *c_i/c_a* of 0.70, net assimilation of oat leaves would have increased ~40% with the 75 μmol mol⁻¹ rise in [CO₂] since 1800. That the increase in leaf *c_i* was correlated with greater plant carbon gain is evidenced by the positive linear relationships between *c_i* and aboveground biomass per plant of all C₃s studied (Fig. 4).

Climate¹⁰, and particularly site water balance¹¹, largely control the structure and productivity of vegetation. This control is determined in part by plant water-use efficiency (WUE), biomass produced per unit transpiration. Our results imply that WUE of C₃ plants may have increased by 27% over the past 200 years

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and ~100% since the LGM. Water-use efficiency calculated from $\delta^{13}\text{C}$ is often highly correlated with the ratio of biomass to transpiration of C3 plants¹², but the correlation is influenced by leaf-to-air vapour pressure differences. Little of the CO_2 -induced increase in potential WUE might be realized if higher A/g resulted entirely from stomatal closure. Then, transpirational cooling of leaves would decline and leaf temperature and transpiration rate per unit g would rise¹³. Any decline in water loss might also be partly offset by the resulting increase in atmospheric water vapour pressure deficit. But the c_i and biomass/plant of C3 annuals increased by the same ratio as $[\text{CO}_2]$, indicating that much of the CO_2 -induced increase in A/g (and WUE) was realized as higher A and ultimately as greater plant biomass (Fig. 4). This increase in plant A/g from the LGM to present must have extended the geographic ranges of some

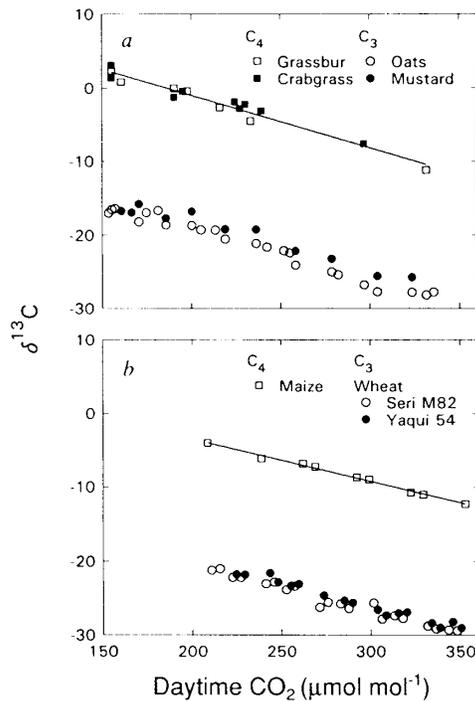


FIG. 1 The stable carbon isotope composition of upper leaves from C3 and C4 plants that were grown at daytime $[\text{CO}_2]$ from near $350 \mu\text{mol mol}^{-1}$ to a. 150 (19 January to 3 May, 1989) or b. $200 \mu\text{mol mol}^{-1}$ (12 February to 23 May, 1991). The C-isotope composition of whole leaves was determined by mass spectrometry (ISOMASS; VG Isogas) and expressed as $\delta^{13}\text{C}$, ‰ (parts per thousand) ^{13}C relative to a PeeDee belemnite reference standard: $\delta^{13}\text{C} = \left(\frac{^{13}\text{C}/^{12}\text{C}}{^{13}\text{C}/^{12}\text{C}}_{\text{standard}} - 1 \right) \times 10^3$. Lines are linear regressions of $\delta^{13}\text{C}$ of C4 species on mean daytime $[\text{CO}_2]$ during growth: $\delta^{13}\text{C} = 13.30 - 0.07[\text{CO}_2]$, $r^2 = 0.96$, $P < 0.0001$ for grassbur and crabgrass, and $\delta^{13}\text{C} = 7.91 - 0.06[\text{CO}_2]$, $r^2 = 0.99$, $P < 0.0001$ for maize. Plants were grown from seed in a 38-m long chamber in a ventilated glasshouse²⁷. Soil water was restored weekly to field capacity. The chamber consisted of a 0.6-m-high polyethylene cover attached to the top of a 0.76-m-deep and 0.45-m-wide soil container. A desired $[\text{CO}_2]$ gradient was maintained in the chamber during daylight (9–10 h daily) by automatically varying the rate of unidirectional air flow through the cover in response to changes in photosynthetic CO_2 depletion by enclosed plants and sunlight intensity. Standard deviation of the minimum daytime $[\text{CO}_2]$ was less than $35 \mu\text{mol mol}^{-1}$ on more than 80% of days. Drybulb and dewpoint temperatures of air were regulated at each 7.6 m along the chamber to track temporal variation in the glasshouse. The daytime drybulb temperature and vapour pressure deficit of air after regulation at each 7.6 m along the chamber were a mean 26°C ($N = 34$) and 1.94 kPa ($N = 33$) during the time sampled leaves of oats and mustard expanded and 20.6°C ($N = 24$) and 1.13 kPa ($N = 19$) during wheat growth.

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species into areas where precipitation was formerly too low to support growth. We calculate from regression that A/g of oats and mustard would have increased 14.1 to 16.4 mmol CO_2 per $\text{mol H}_2\text{O}$, respectively, with the increase from 275 to $350 \mu\text{mol mol}^{-1} \text{CO}_2$ that has occurred since 1800. The increase is comparable to the mean 27.6% rise in A/g of $21.9 \text{ mmol mol}^{-1}$ of C3 species from moist wash to drier slope habitats in the Sonoran desert, where the change in A/g was associated with a shift in species composition¹⁴.

Our results and those of others^{15,16}, if representative for C3 species, imply that the rise in $[\text{CO}_2]$ since the LGM greatly increased potential productivity of most of Earth's vegetation. Many believe, however, that higher $[\text{CO}_2]$ has a negligible effect

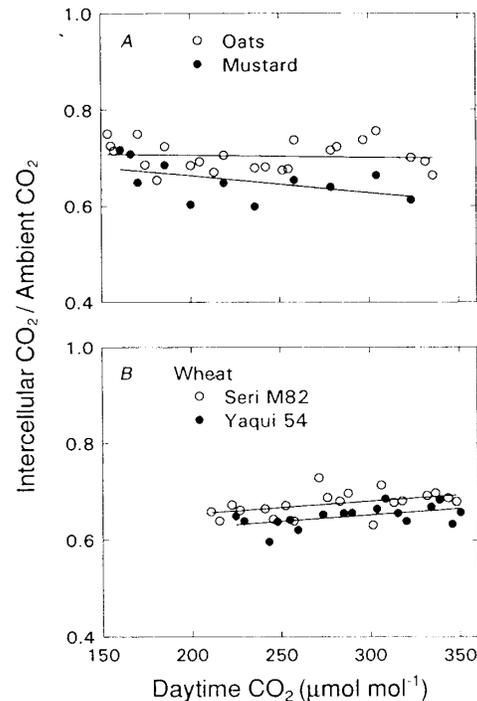


FIG. 2 The ratio of leaf intercellular $[\text{CO}_2]$ (c_i) to ambient $[\text{CO}_2]$ (c_a), calculated from the $\delta^{13}\text{C}$ of leaves, as a function of the daytime $[\text{CO}_2]$ at which C3 plants were grown. The slopes of regressions of c_i/c_a on c_a did not differ significantly from zero for (A) oats ($P = 0.70$) or mustard ($P = 0.11$); the c_i/c_a of B, the two wheat cultivars, was positively related to c_a (Seri M82, $c_i/c_a = 0.60 + (2.66 \times 10^{-4})c_a$, $r^2 = 0.22$, $P = 0.04$ and Yaqui 54, $c_i/c_a = 0.57 + (2.71 \times 10^{-4})c_a$, $r^2 = 0.27$, $P = 0.04$). The stable C isotope composition of plants ($\delta^{13}\text{C}$) reflects that of atmospheric CO_2 ($\delta a^{13}\text{C}$) and fractionation during photosynthesis²⁸. For C3 plants, $\delta p^{13}\text{C} = \delta a^{13}\text{C} - a - (b - a)c_i/c_a$, where a is a fractionation resulting from the greater diffusivity of $^{12}\text{CO}_2$ than $^{13}\text{CO}_2$ across leaf stomata (4.4‰ (ref. 29); positive values indicate discrimination against ^{13}C or ^{12}C -enrichment) and b is discrimination by ribulose 1,5-bisphosphate carboxylase against ^{13}C in CO_2 fixation (29‰; ref. 30). Leaf c_i/c_a can be deduced from the above equation when $\delta p^{13}\text{C}$ and $\delta a^{13}\text{C}$ are known. We calculated $\delta a^{13}\text{C}$ as a function of c_a in the 38-m chamber from the $\delta^{13}\text{C}$ of leaves from C4 plants that were grown with oats, mustard and wheat using a fractionation by C4 plants relative to air of 3.136‰. Isotope fractionation by maize grown across a 350 – $200 \mu\text{mol mol}^{-1} \text{CO}_2$ gradient in an additional experiment did not vary significantly with $[\text{CO}_2]$ ($\bar{x} = 3.136\%$, s.e. = 0.06% , $N = 9$; B.D.M. *et al.*, manuscript in preparation). Regressions of $\delta^{13}\text{C}$ on daytime $[\text{CO}_2]$ did not differ significantly for grassbur and crabgrass grown with oats and mustard (Fig. 1a; $F_{(2,12)} = 2.6$, $P < 0.10$) or for maize and crabgrass grown with wheat (data not shown; $F_{(2,29)} = 2.7$, $P > 0.10$). The small changes in drybulb and dewpoint temperatures between points of regulation at each 7.6 m along the chamber⁹ had no significant influence on the relationship of c_i/c_a of individual species or cultivars to c_a .

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on global carbon fixation because factors other than CO_2 limit productivity of most unmanaged vegetation^{17,18}. Some recent research suggests that a step increase in $[\text{CO}_2]$ above the current $350 \mu\text{mol mol}^{-1}$ produces little or no short-term (≤ 3 years) increase in plant or ecosystem carbon storage where low temperatures or nutrient (particularly nitrogen) availability currently restrict plant growth^{19,20}. Extrapolation from these studies to the past is difficult, for only superambient $[\text{CO}_2]$ and a limited range of processes and temporal scales were considered. Plant water- and light-use efficiencies²¹ were lower at subambient $[\text{CO}_2]$, implying that sustainable biomass and plant nutrient requirements were also lower in the past. Species and genetic change, fixation of atmospheric N_2 , and nitrogen deposition may have facilitated plant response to CO_2 in the past when concentrations rose more slowly or with a greater relaxation time between change than today, but data are lacking.

Increased widths of annular rings of some trees²², global CO_2 models²³, calculations of carbon accumulation in temperate forests²⁴, and the increased amplitude of the annual cycle of atmospheric $[\text{CO}_2]$ ²⁵ in recent decades, all suggest that rising $[\text{CO}_2]$ has stimulated biospheric carbon fixation. Effects of $[\text{CO}_2]$, however, cannot readily be distinguished from those of human impact and concurrent climate change²⁴. Resolution of what fraction has been realized, if any, of the potentially great increase in plant productivity since the LGM demands that effects of $[\text{CO}_2]$ on the processes that influence plant growth be

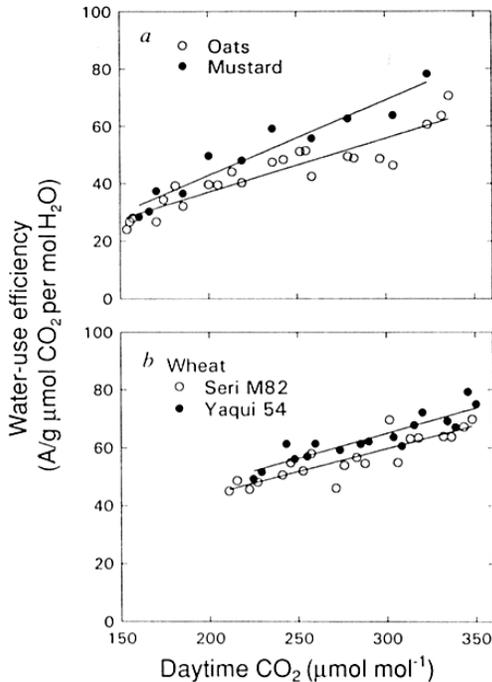


FIG. 3 Relationships between intrinsic water-use efficiencies of C3 plants (net assimilation (A)/stomatal conductance to water (g)) derived from the $\delta^{13}\text{C}$ of leaves and the daytime $[\text{CO}_2]$ (c_a) at which plants were grown. Linear regressions differed significantly ($P < 0.005$) between a. oats ($A/g = -0.70 + 0.19c_a$, $r^2 = 0.86$) and mustard ($A/g = -9.91 + 0.26c_a$, $r^2 = 0.92$), and b. two cultivars of wheat, Seri M82 ($A/g = 12.05 + 0.16c_a$, $r^2 = 0.77$) and Yaqui 54 ($A/g = 13.29 + 0.17c_a$, $r^2 = 0.82$). $P < 0.0001$ for each regression. Intrinsic water-use efficiency of C_3 leaves is directly proportional to c_a and negatively correlated with the ratio of leaf intercellular $[\text{CO}_2]$ (c_i) to c_a : $A/g = c_a(1 - c_i/c_a)/1.6$, where 1.6 is the ratio of gaseous diffusivities of CO_2 and water vapour in air. The c_i/c_a was determined from the stable C isotope compositions of leaves.

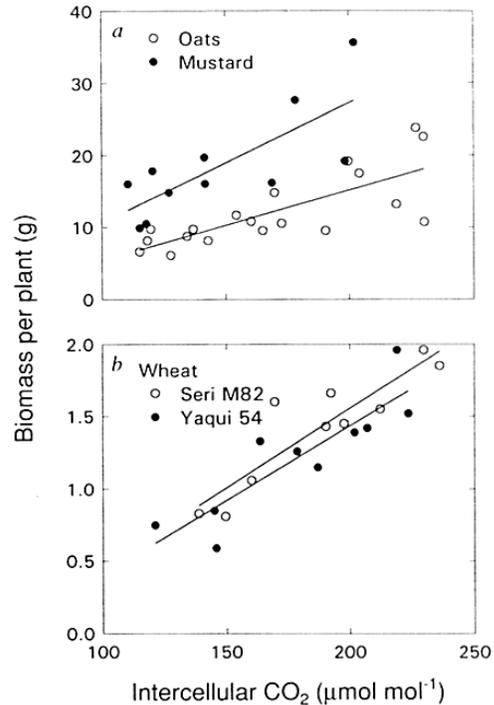


FIG. 4 Relationships of above-ground biomass per C3 plant at maturity to leaf intercellular $[\text{CO}_2]$ (c_i). Leaf c_i was determined from the stable C isotope composition of plants grown from current atmospheric $[\text{CO}_2]$ to a near $150 \mu\text{mol mol}^{-1}$ (oats, mustard; 20 plants m^{-2}) or b. 200 $\mu\text{mol mol}^{-1}$ CO_2 (wheat; 350 plants m^{-2}). Note that the scale of the ordinate differs in a and b. Lines are linear regressions of above-ground biomass per plant on leaf c_i : biomass = $-4.42 + 0.10c_i$ for oats ($N = 19$) and biomass = $-6.00 + 0.17c_i$ for mustard ($N = 11$), $r^2 = 0.58$, $P < 0.01$ and biomass = $-0.63 + 0.01c_i$, $r^2 = 0.81$ and biomass = $-0.62 + 0.01c_i$, $r^2 = 0.77$ for Seri M82 and Yaqui 54 cultivars of wheat, respectively, $P < 0.001$, $N = 10$.

understood within an ecosystem context and over relevant periods. Our results nonetheless demonstrate the risks inherent in using present vegetation-climate relationships to reconstruct past climates from pollen or fossil records without incorporating potential direct effects of $[\text{CO}_2]$ ²⁶. □

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