

RESPONSE OF VEGETATION TO RISING
CARBON DIOXIDE: PHOTOSYNTHESIS,
BIOMASS, AND SEED YIELD OF SOYBEAN

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Abstract. Elevated carbon dioxide throughout the lifespan of soybean causes an increase in photosynthesis, biomass, and seed yield. A rectangular hyperbola model predicts a 32% increase in soybean seed yield with a doubling of carbon dioxide from 315 to 630 ppm and shows that yields may have increased by 13% from about 1800 A.D. to the present due to global carbon dioxide increases. Several other sets of data indicate that photosynthetic and growth response to rising

carbon dioxide of many species, including woody plants, is similar to that of soybean. Calculations suggest that enough carbon could be sequestered annually from increased photosynthesis and biomass production due to the rise in atmospheric carbon dioxide from 315 ppm in 1958 to about 345 ppm in 1986 to reduce the impact of deforestation in the tropics on the putative current flux of carbon from the biosphere to the atmosphere.

INTRODUCTION

Recent increases in carbon dioxide of the earth's atmosphere from 315 parts per million (ppm), mole fraction basis [1 ppm = 1 μ mol (carbon dioxide) per mol (air)], in 1958 to a projected 345 ppm at present are well-documented [Keeling et al., 1982; Gammon et al., 1985]. Analyses of entrapped gases in ice cores from Antarctica and Greenland show that atmospheric carbon dioxide concentration may have been as low as 160-200 ppm during the period 20,000 to 15,000 years ago [Delmas et al., 1980]. Ice core comparisons between two laboratories gave a mean value of about 260 ppm for the period 800 to 2500 years ago [Barnola et al., 1983] and carbon dioxide concentrations in the range of 258-283 ppm have been measured from ice core samples dated between 1000 and 1900 A.D. [Oeschger and Stauffer, 1983]. More recent studies based on tree ring data [Stuiver et al., 1984] and ice core data

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[Neftel et al. 1985; Raynaud and Barnola, 1985] probably limits the 1800 A.D. concentration to a range of 260-285 ppm [Gammon et al., 1985]. Current views suggest two important sources of carbon that have contributed to the atmospheric carbon dioxide since about 1800 A.D.: a nonfossil fuel source from about 1800 A.D. to the present based on time series of $^{13}\text{C}/^{12}\text{C}$ data of tree rings which suggest a very broad peak of about 2 Pg C/yr [2 quadrillion (USA system) g C/yr] that has declined to less than 1 Pg C/yr in recent decades [Peng et al., 1983], and a fossil fuel source that has increased markedly since around 1850 to about 5 Pg C/yr [Bojkov, 1983; Marland and Rotty, 1984]. If we assume that a level of 276 ppm is a reasonable average pre-1800 A.D. carbon dioxide concentration [Stuiver et al., 1984], then the increase to present would be about 25%. Furthermore, a 14% increase would have occurred prior to 1958.

Potential climatic responses to increasing atmospheric carbon dioxide were suggested years ago [Callendar, 1940, 1958; Dingle, 1954; Plass, 1959; Kaplan, 1960; Möller, 1963], and models have been developed to predict global climatic effects [Manabe and Weatherald, 1980; Washington et al., 1980; Gates et al., 1981; Hansen et al., 1981; Cess and Potter, 1984]. Recently, the direct effects of rising carbon dioxide on global vegetation and agricultural crops have received increasing attention [Allen, 1979; Rosenberg, 1981; Baker et al., 1982; Kimball, 1983a, b; Lemon, 1983; Wittwer, 1980, 1983; Waggoner, 1984]. Although soil nutrients have been considered to be more limiting than atmospheric carbon dioxide for unmanaged vegetation [Goudriaan and Ajtay, 1979; Kramer, 1981], growth chamber and greenhouse studies suggests that increased carbon dioxide causes increased plant growth at low as well as high levels of nutrients [Gifford, 1979a, b; Wong, 1979; Sionit et al., 1981; Luxmoore et al., 1986] or light [El-Sharkawy et al., 1968; Wittwer, 1983]. Resolution of proposed scenarios of interactions of carbon dioxide levels and mineral nutrient cycling and availability effects on ecosystems response awaits further research [Oechel and Strain, 1985]. Research objectives to determine direct effects of carbon dioxide on vegetation have been defined and proposed because of the importance of increased atmospheric carbon dioxide to agriculture, the terrestrial

biosphere, and the global carbon cycle [Revelle, 1982; Lemon, 1983; Woodwell et al., 1978, 1983]. This paper focuses on possible effects of these carbon dioxide increases on C-3 plants, particularly on soybean photosynthesis, biomass, and seed yield. Soybean has the Calvin cycle (C-3 plant) biochemical pathway for photosynthetic carbon dioxide fixation [Tolbert and Zelitch, 1983]. Leaf photosynthetic carbon dioxide uptake rates of C-3 plants have been widely documented to increase considerably in response to increased levels of carbon dioxide, whereas photosynthetic rates of the Hatch-Slack C-4 system responds very little [Percy and Björkman, 1983] because of the internal carbon dioxide-concentrating mechanism of C-4 plant leaves [Tolbert and Zelitch, 1983].

SOYBEAN DATA AND MODEL

Data Set

Soybean [*Glycine max* (L.) Merr. cv. 'Bragg'] crop biomass and seed yield data from carbon dioxide enrichment studies at four locations have been obtained for several years [Dahlman et al., 1985]. The desired carbon dioxide levels were maintained for the entire growing season within outdoor controlled-environment chambers or open-top chambers exposed to natural sunlight [Phene et al., 1979; Rogers et al., 1983c; Jones et al., 1984b]. Soil water and mineral nutrients were maintained at high (nonlimiting) levels. Relative seed yield ranged from about 1.1 times the ambient at 405 ppm to about 1.5 times the ambient for 930 ppm. Seed yields were expressed as relative values with respect to nearambient control levels of carbon dioxide to minimize variability due to location, year, and population density effects. Soybean productivity increased about 30% for a carbon dioxide doubling (about 660 ppm which is expected about 50-100 years in the future, depending mainly upon the rate of fossil carbon dioxide emission). Results from some of these experiments suggest increased water use efficiency (WUE) by soybeans at elevated carbon dioxide [Rogers et al., 1983a, b; Jones et al., 1984a, 1985; Allen et al., 1985b]. Also since water stress (drought) usually results in larger relative growth increases of most plants [Kimball, 1985], these experiments may have resulted in

lower relative yield responses to carbon dioxide enrichment than would be expected in real-world agricultural systems.

Nonlinear Model

Rectangular hyperbolae. Models are needed for predicting growth and yield of various crop and native plants in response to rising atmospheric carbon dioxide [Dahlman, 1985]. These models can range in detail and complexity from dynamic, process level, mechanistic growth models through to simple regression models of yield as a function of carbon dioxide level. Complex, detailed models are needed to make extrapolative predictions about crop responses to carbon dioxide and interactions with environmental conditions, but simpler techniques can be used for first-order approximation of overall responses [World Meteorological Organization, 1984]. We adopted a simple, nonlinear model to describe plant photosynthesis, growth, and yield responses to carbon dioxide. Specifically, a form of the rectangular hyperbola (similar to the Michaelis-Menten equation of the kinetic theory of enzyme reactions) was used to fit relative crop yield responses to different levels of carbon dioxide after normalizing the response to recent concentrations of about 330-340 ppm. This equation has been used many times in the past to describe photosynthetic responses of leaves to carbon dioxide and light [Rabinowitch, 1956; Chartier, 1966; Acock et al., 1971; Lommen et al., 1971; Tenhunen et al., 1980], although the photosynthetic process is much more complex than a single-step, enzyme-mediated carboxylation reaction. It has also been adopted in many models of crop photosynthesis [Monsi and Saeki, 1953; deWit, 1965; Chartier, 1967; Duncan et al., 1967]. Although many other nonlinear models have been proposed and used to describe carbon dioxide and light response curves, namely, power functions [Smith, 1937, 1938], exponential formulations [Webb et al., 1974; Thornley, 1976], and quadratic functions [Chartier, 1966], the rectangular hyperbola [Baly, 1935; Smith, 1937] has generally become the most widely used. Acock et al. [1971] found that Michaelis-Menten types of formulations (rectangular hyperbolae) of Maskell [1928] and Rabinowitch [1951] were well-suited for net photosynthetic rate responses of Amaranthus edulis leaves to both light and

carbon dioxide concentration. These rectangular hyperbolae provided quantitative comparisons of soybean canopy light utilization efficiency and canopy conductance to carbon dioxide [Acock et al., 1985].

Modeling procedure. Recently available soybean seed and biomass yield data from 1980-1982 enrichment experiments were normalized to data at current ambient carbon dioxide levels and fitted by one of us (K.J.B.) with a rectangular hyperbola of the Michaelis-Menten form. Yield data were not collected in the subambient range of carbon dioxide concentrations during this 1980-1982 period. To provide information across the range of 0-1000 ppm on the shape of the nonlinear plant response to carbon dioxide, short-term experiments were conducted on soybean crop net photosynthetic rates (defined by net carbon dioxide exchange rates) measured in three outdoor, controlled-environment chambers in 1983 on plants grown at 330 ppm. Under midday, near-constant high light conditions, carbon dioxide concentration was changed and controlled at values ranging from 120 to 990 ppm until stable photosynthetic rates were obtained. The net photosynthetic rate data were normalized to the 330-ppm response and a rectangular hyperbola was fitted to these normalized data (Figure 1). In the terminology of ecology the response illustrated in Figure 1 is equivalent to gross primary production [Odum, 1983] minus both immediate photorespiration and all other above ground canopy respiration.

The Michaelis-Menten rectangular hyperbola was modified by including a Y-intercept term and programmed for fitting crop responses to carbon dioxide concentration in a statistical analysis system (SAS) nonlinear regression procedure (NLIN):

$$R = (R_m \times CD) / (CD + K_m) + R_i \quad (1)$$

where R is yield (or other response); CD is carbon dioxide concentration; R_m is the asymptotic response limit of $(R - R_i)$ at high CD; R_i is the intercept on the y axis; and K_m is the value of substrate concentration, i.e., CD, at which $(R - R_i) = 0.5 R_m$. Equation (1) can be converted to a form in terms of the x-axis intercept:

$$R = R_c \times (CD - \Gamma) / (CD + K_m) \quad (2)$$

where R_c , defined by $(R_m + R_i)$, is the

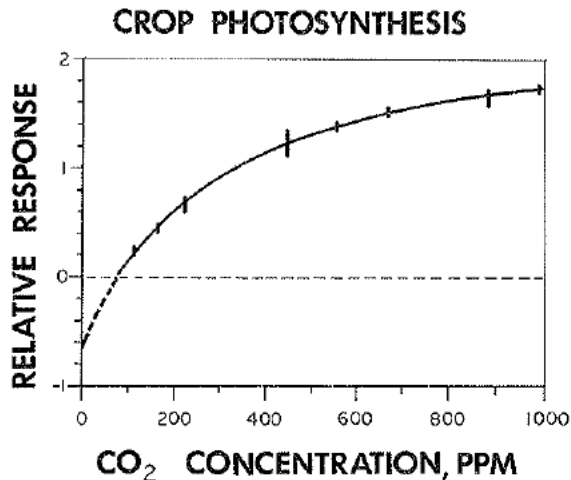


Fig. 1. Soybean crop canopy midday net photosynthetic rate response to carbon dioxide concentration, normalized to 330 ppm, obtained October 23-30, 1983 (56-61 days after planting), from plants grown at 330 ppm in outdoor controlled-environment chambers at Gainesville, Florida. Dots show data, and the solid line shows the fitted rectangular hyperbola.

actual yield asymptotic response ceiling, and Γ , the intercept on the x axis, is the crop net photosynthetic rate carbon dioxide compensation point.

Model parameters. Parameters of $R_m = 3.08$, $K_m = 279$ ppm, and $R_i = -0.68$ were obtained from the midday relative photosynthetic rate data of Figure 1, with an asymptotic photosynthetic response ceiling (R_c) of 2.40 projected for infinite atmospheric carbon dioxide concentration. The computed crop net photosynthetic rate carbon dioxide compensation point (Γ) was 79 ppm. The carbon dioxide compensation point is the concentration at which net carbon dioxide exchange is zero. In high light, Valle et al. [1985] reported an average Γ of 63 ppm for soybean leaves with low photosynthetic capacity and 42 ppm for soybean leaves with high photosynthetic capacity. Below the carbon dioxide compensation concentration, photorespiration plus metabolic respiration exceeds photosynthesis in bright light. In equation (1), when carbon dioxide is decreased to the point where $R = 0$, the $CD = \Gamma = -(R_i \times K_m)/(R_i + R_m)$. The value of Γ for the whole crop is slightly higher than the soybean leaf carbon dioxide compensation point probably because of additional respiration of nonleaf material

in the canopy (e.g., stems, pods). However, a reasonable estimate of Γ is desirable for any model because it represents the "starvation point global atmospheric carbon dioxide concentration" for a plant. For whole canopy photosynthesis rates these short-term measurements are satisfactory since Jones et al. [1985] found that cross-switching carbon dioxide levels for a day between soybeans grown at 330 and 800 ppm gave canopy photosynthetic responses which were dependent mainly on carbon dioxide exposure level regardless of the long-term pretreatment level of carbon dioxide.

Soybean biomass yield data are not illustrated, but model parameters were $R_m = 3.02$, $K_m = 182$ ppm, $R_i = -0.91$, $R_c = 2.11$, and $\Gamma = 78$ ppm. In this case, Γ was the same as for net photosynthesis, but R_c was about 12% less. A smaller asymptotic response ceiling for biomass productivity than for net photosynthesis would be expected if more nighttime respiration resulted from the higher photosynthetic rates at high carbon dioxide. The biomass yield response is proportional to net primary production as defined by Odum [1983].

Soybean seed yield data (Figure 2) gave parameters of $R_m = 2.55$, $K_m = 141$ ppm, $R_i = -0.76$, and $R_c = 1.79$. The model gave a crop carbon dioxide compensation point for seed yield of 60 ppm, which was somewhat less than the whole-canopy net photosynthetic carbon dioxide compensation point. Since seed yield data were not available at concentrations below 330 ppm, the model predictions cannot be reliable for the carbon dioxide compensation point for seed yield. Because seed production is an energy consuming process, we would actually expect a carbon dioxide compensation point for seed yield to be higher than for canopy photosynthesis. Since harvest index (the ratio of seed yield over seed plus podwall and stem yield) decreased with increasing carbon dioxide concentration [Allen et al., 1987; Rogers et al.; 1983a], the seed yield data over the 330-945 ppm range forced the model predictions to extrapolate to a higher value of R_i and hence a lower value of Γ than was found with the net photosynthesis and biomass yield data.

In a later experiment, Bisbal [1987] reported that the ratio of final soybean seed yield at 160 ppm to that at 330 ppm was 0.38, which is considerably less than the value of 0.58 predicted by the model

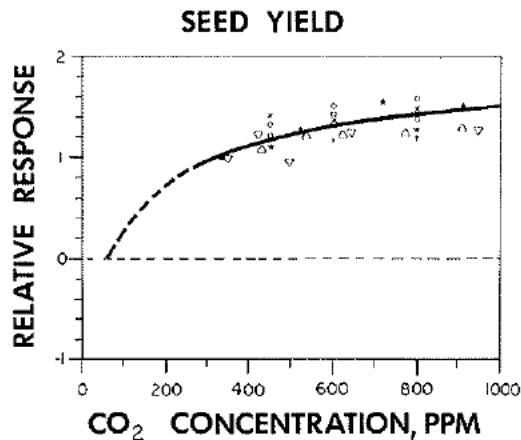


Fig. 2. Rectangular hyperbola response of normalized soybean seed yield data to carbon dioxide concentration for Ransom, Bragg, and Forrest cultivars. Data obtained from outdoor controlled-environment chamber experiments at three locations: Gainesville, Florida, 1981 (squares), 1982 (crosses); Mississippi State, Mississippi, 1981 (diamonds), 1982 (pluses); Clemson, South Carolina, 1982 (asterisks); and from open-top chamber experiments at Raleigh, North Carolina, 1980 (stars); 1981 (triangles); 1982 (inverted triangles). All data were normalized to 330-340 ppm = 1.0.

with a limited range of data. However, the model prediction fit the observations well over the carbon dioxide exposure range of 330-945 ppm in which seed yield data were collected which gives credence to this approach for obtaining yield responses. This nonlinear model is clearly superior to a linear regression model which predicted a yield ratio intercept (R_i) of 0.82 at zero carbon dioxide, a biological impossibility.

The β factor. The modified Michaelis-Menten rectangular hyperbola lends itself to other analyses, first, to the prediction of increased crop responses expected from a given increase in carbon dioxide concentration,

$$\% \text{ increase of } R = (\Delta R/R) \times 100 \quad (3)$$

and second, to the prediction of the "biotic growth factor" [Bacastow and Keeling, 1973; Siegenthaler and Oeschger, 1978; Wong, 1980] applied to yield or any other biotic response. The "biotic growth factor" β is the ratio of a relative

response change $\partial Y/Y$ to a relative stimulus change $\partial X/X$, i.e., $(\partial Y/Y)/(\partial X/X)$, which is the same as the ratio of a percentage change in Y to a percentage increase in X . It has been used in models to predict biologic responses to carbon dioxide changes. The specific form of β depends on the functional relationship of Y to X , which involves a response of Y to a function of X/X_0 , where X_0 is the value of the independent variable at a fixed reference condition. We define β_1 from the equation $Y = Y_0\{1 + \beta_1[\ln(X/X_0)]\}$ and β_2 from the power function $Y = Y_0(X/X_0)^{\beta_2}$ where Y_0 is the value of Y at the reference $X = X_0$.

By these functional definitions the "biotic growth factor" is

$$\beta_1 = (\partial R/R_0)/(\partial CD/CD) \quad (4)$$

when applied to a logarithmic response to CD/C_0 , or

$$\beta_2 = (\partial R/R)/(\partial CD/CD) \quad (5)$$

when applied to a power function response to CD/C_0 , where R_0 is a response at the reference carbon dioxide concentration C_0 .

However, with the modified type Michaelis-Menten rectangular hyperbola, the "biotic growth factor" has an explicit functional form derived from equation (1):

$$\beta_3 = (\partial R/R)/(\partial CD/CD) = [K_m/(CD + K_m)] \times \{R_m \times CD/[R_m \times CD + R_i(CD + K_m)]\} \quad (6)$$

which reduces to the approximation $\beta_3 \approx K_m/(CD + K_m)$ for small values of R_i . In this case, β_3 itself is a rectangular hyperbolic function of CD , and, furthermore, it is an explicit function of the Michaelis parameter K_m . Thus β_3 is a property of the response data fitted to the whole range of available treatment CD rather than to an arbitrary choice of C_0 . By manipulation, the rectangular hyperbolic function can also be expressed in terms of (X/X_0) , as $Y = Y_m \beta_3(X/X_0) + Y_i$, where X_0 is equivalent to K_m , the Michaelis parameter, and Y_m and Y_i have generic definitions shown in equation (1). β_3 has the property of being an explicit hyperbolic function of the Michaelis parameter of the rectangular hyperbola, whereas β_1 and β_2 do not have explicit definitions derivable from their formulations.

TABLE 1. Percent Increases and Ranges of Biotic Growth Factors (β_3) of Soybean Photosynthesis Rates, Biomass Yield, and Seed Yield Predicted by the Rectangular Hyperbola Model Across Selected Carbon Dioxide Concentrations Associated With Relevant Time Periods

Period A.D.	Initial-Final [CO ₂], ppm	Photosynthesis		Biomass Yield		Seed Yield	
		Increase, %	β_3	Increase, %	β_3	Increase, %	β_3
1800-1958	276-315	11.9	0.90-0.80	10.3	0.79-0.70	7.9	0.62-0.54
1800-1986	276-345	20.1	0.90-0.74	17.3	0.79-0.64	13.2	0.62-0.50
1958-1986	315-345	7.3	0.80-0.74	6.3	0.70-0.64	4.9	0.54-0.50
1958-2058?	315-630	52.6	0.80-0.45	42.7	0.70-0.36	32.2	0.54-0.29

Past and future predictions. Table 1 shows predicted increases in soybean photosynthesis rates, biomass yield, seed yield, and the ranges of the biotic growth factor β_3 calculated from the model using the parameters derived from data in Figures 1 and 2. Table 1 shows that we could have had an 8% increase in seed yield from about 1800 to 1958 due to increased carbon dioxide concentration, if the pre-1800 A.D. value of carbon dioxide were 276 ppm. (Since crop cultivars in most cases were not the same in 1958 as in 1800 A.D., this prediction is actually based on an extrapolation back in time based on a current cultivar.) From 1958 to 1986, when the carbon dioxide was documented as having increased from 315 to about 345 ppm, the model predicts that the yield would have increased 5%. When or if carbon dioxide doubles from the 1958 level, we may expect a further soybean yield increase of about 32%, all other factors being equal. This expectation is in agreement with estimates calculated from numerous, diverse crops and experiments by Kimball [1983a] of a 33% increase in yield with a doubling of carbon dioxide, with a 95% confidence from 28 to 39%. Also, the estimates of β_3 for seed yield are in general agreement with an estimate by Waggoner [1984] of increases (0.1% per ppm carbon dioxide) of soybean and other grain legume yields, which translates to a β factor of 0.34 at a carbon dioxide concentration of 340 ppm. The range of values of β_3 from 0.70 to 0.64 for biomass yield across the range of 315 to 345 ppm carbon dioxide (Table 1) are close to the value of 0.6 for β assumed by Gifford [1980] for all biomes.

Table 1 shows an apparent decrease in response to carbon dioxide as the physiological process advances from midday net photosynthesis through biomass yield to final seed yield. This also fits the pattern of decreasing R_c . However, net photosynthesis near midday may not represent integrated carbon dioxide exchange over the whole day and the whole season. Also, harvest index (the ratio of seed yield to biomass yield) has been observed to decrease with increasing carbon dioxide concentration [Allen et al., 1987; Rogers et al., 1983a] which indicates proportionately less partitioning of photoassimilate to seed growth. The first difference can be investigated with experiments on whole-season carbon input-output balance, whereas the second difference indicates a genetic condition which may be improved with plant breeding and selection for higher seed yield under increasing atmospheric carbon dioxide conditions. Indeed current cultivars have been selected as carbon dioxide concentration has been rising.

Model utility. Figures 1 and 2 and Table 1 provide a concise nonlinear model overview of our state of knowledge of response of soybean, a C-3 photoassimilation pathway plant, to rising atmospheric carbon dioxide. This nonlinear model has a strong theoretical base and history of use in biology; it predicts asymptotic upper limits for responses at high levels of carbon dioxide; the zero response intercept is near the photosynthetic carbon dioxide compensation point; and it provides an analytic formulation of the "biotic growth factor." These characteristics are desirable, if not essential, for

generalizing any crop response to carbon dioxide. We expect some similarities in response of other C-3 plants, but unique parameters may have to be determined for crops with C-4 or CAM photosynthetic metabolism (e.g., maize, a C-4 plant, has smaller responses to elevated carbon dioxide than does soybean [Rogers et al., 1983a, b]).

GLOBAL CARBON DIOXIDE FERTILIZATION

Predicted Carbon Sequestering

Production and sequestering. Recent increased carbon dioxide levels in the atmosphere could result in enhanced plant uptake of carbon dioxide which could account for the current perception of a "missing or unidentified global carbon dioxide sink" that appears to be needed to balance the global carbon cycle. The oceans do not appear to be taking up all of the injected fossil fuel carbon dioxide, and yet the terrestrial biosphere is also considered to be a source of carbon dioxide based on recent disturbances that include harvests of tropical forests and conversion of land to agriculture [Broecker et al., 1979; Woodwell et al., 1978, 1983]. Various estimates of annual net primary production (NPP) of the terrestrial biosphere range from 53 to 78 Pg C/yr [Bolin et al., 1979]. Data from our study as well as other compilations and analyses [Kimball 1983a, b; Cure, 1985; Strain and Cure, 1985] show increased NPP with more carbon dioxide. If the estimated 6.3% increase in biomass production of soybean from 315 to 345 ppm [Table 1, based on equation (3)] can be applied to the estimated range of annual dry matter production of the terrestrial biosphere, then we would predict an increase of 3.3-4.9 Pg C going into the biosphere in 1986 compared to 1958. If approximately 50% of this predicted increased carbon flux goes into long-term storage, then 1.6-2.4 Pg of additional C in 1986 may be sequestered for decades and partially diminish the effects of carbon dioxide sources to the atmosphere.

Uncertainties. There is considerable uncertainty about how much global NPP actually becomes sequestered by terrestrial ecosystems for long time periods. However, as pointed out by Gifford [1980] and by Oechel and Strain [1985], an incremental increase in flow of carbon to the biosphere should produce an increase

in net carbon storage. Minimum estimates of annual biomass increment of several tropical forests calculated from Allen and Lemon [1976] showed a wide range from 19 to 67%. Gifford [1980] estimated that a 26 ppm carbon dioxide increase since 1958 would increase NPP by 2.83 Pg C/yr and increase stored carbon by 1.65 Pg/yr, a 58% sequestering of carbon. The best estimates of carbon sequestering are derived from considering the residence times and the annual carbon budgets of various global carbon pools found in Table 8.3 of Olson et al. [1985]. They report respective carbon residence times and annual carbon pool incomes of 43-30 yr and 15-25 Pg/yr for slow plant turnover pools, 340-200 yr and 5.2-10.1 Pg/yr for soil pools, and 10,000-1,000 yr and 0.33-1.0 Pg/yr for subfossil pools. The estimated annual carbon sequestering into these three pools thus ranges from 20.5 to 36.1 Pg/yr, with an average of 28.3 Pg/yr. The average of all estimates of NPP listed in Table 6.2 of Houghton et al. [1985] is 55 Pg/yr. Therefore, the estimated percentage of NPP that is sequestered annually in "long-term" carbon pools is 51%, and could range from 37 to 66%. However, about 70% of the carbon is entering the long-term carbon pool with the shortest carbon residence time.

Storage versus release. In spite of the uncertainties, our estimates of 1.6-2.4 Pg of increased carbon storage in 1986 due to carbon dioxide fertilization effects since 1958 could compensate for roughly 60% of one estimate of 1.8-4.7 Pg C released to the atmosphere annually due to ecosystem disturbance [Woodwell et al., 1983] and could compensate for essentially all of the 0.6-2.6 Pg C released to the atmosphere annually estimated by Houghton et al. [1985] based in part on revised biomass estimates of tropical forests by Brown and Lugo [1984]. The predicted 6.3% increase in soybean biomass response to carbon dioxide is considerably less than the 16% increase in biospheric activity predicted by Keeling [1983] from 1958 up to 1982 based on the increasing amplitude of the annual carbon dioxide cycle at Mauna Loa, Hawaii. However, recent concepts and model developments suggest that several factors contribute to the amplification of the annual amplitude of the Mauna Loa carbon dioxide signal, including direct stimulation of vegetation by carbon dioxide (27%), increase in agricultural production (18%), seasonal

atmospheric transport of fossil fuel carbon dioxide (18%), net effect of regrowth and afforestation of temperate forests and deforestation of tropical forests (28%), seasonality of fossil fuel use (6%), and increase in ocean productivity (3%) [Kohlmaier et al., 1985]. Although this model predicts only 4.3% out of the 16% increase in annual amplitude would be due to direct carbon dioxide effects, the combination of biological factors could account for about 76% of the increase in annual amplitude. Recent unpublished analyses by these authors suggest that fertilization by airborne nitrogen compounds may also contribute to the increase in the annual amplitude of the carbon dioxide concentration cycle.

Experimental Evidence

Although no long-term measurements of net photosynthesis or growth have been made on full size trees or forest systems under a range of carbon dioxide levels, several sets of short-term data suggest that tree seedlings, shrub plants, and woody perennials respond similarly to soybean. For example, from data sets of Mooney et al. [1964, 1966] we averaged net photosynthetic rates of 28 observations at carbon dioxide concentrations of 200 ppm and at 100 ppm which gave values of 0.63 ± 0.07 and 0.17 ± 0.09 , respectively, compared to rates at 300 ppm. Another composite of five species gave photosynthetic rates at 600 ppm of about 1.40 ± 0.15 with respect to rates at 300 ppm carbon dioxide [Carlson and Bazzaz, 1980; Hiesey et al., 1971; G.E. Bingham and H.H. Rogers, personal communication, 1983]. Jurik et al. [1984] reported that bigtooth aspen leaf photosynthetic rates increased 2.5-fold when carbon dioxide was raised from ambient to about 1900 ppm. Allen et al. [1985a] found that daily photosynthetic rates of a dense canopy of citrus seedlings doubled when exposed to 840 versus 330 ppm carbon dioxide. These values are in general agreement with those of Figure 1. Koch et al. [1983, 1985] found an average tissue dry weight response of 1.64 after exposure of citrus seedlings to 660 versus 330 ppm carbon dioxide for 14 weeks, and 2.13 after exposure at these concentrations for 22 weeks. Sionit et al. [1985] reported that exposure at 500 ppm versus 350 ppm carbon dioxide for a 32-week season resulted in a total dry weight response of 1.59 in Pinus

taeda (loblolly pine) and 1.43 in Liquidamber styraciflua (sweetgum), although there was no additional mass gain at 650 ppm. Luxmoore et al. [1986] reported relative responses in dry weight gain of 1.37-1.99 for three species of seedling trees exposed at 695 ppm versus 365 ppm carbon dioxide for 16 to 64 weeks. Growth data from 22 observations of woody species over the range of 900-1250 ppm carbon dioxide gave relative responses of 1.57 ± 0.28 [Kimball, 1983b] which compare well with Figure 2. Although these data are variable, they suggest that we are justified in using the nonlinear model projections to predict the approximate biospheric photosynthetic and biomass increase responses to the recent sharp rise in atmospheric carbon dioxide concentration. Even when other nutrients are limiting, plants may still respond to this carbon dioxide fertilization effect [Gifford, 1979a, b; Wong, 1979; Sionit et al., 1981; Luxmoore et al., 1986]. Furthermore, recent tree ring data on high-altitude conifers suggests that growth rates have increased in the last few decades [LaMarche et al., 1984]. A recent review of response of native species to doubling of carbon dioxide shows much variability with increased photosynthesis, growth, biomass productivity, and carbon sequestering in some cases but not in others [Oechel and Strain, 1985]. Arctic tundra is expected to accumulate carbon, but little data are available for other ecosystems. Long-term net primary productivity of biomass and sequestering of carbon will likely be somewhat less than short-term photosynthesis and growth due to limiting factors other than carbon dioxide and many physiological and ecological controls on carbon flows [Strain, 1985].

Cumulative Fertilization Effects

If we assume that the parameters of the rectangular hyperbola model for soybean biomass response to carbon dioxide can be applied to global net primary production then we can compute the cumulative additional NPP due to the carbon dioxide fertilization effect over a series of years. We chose 315 ppm in 1958 as the base carbon dioxide concentration and the initial reference year, with reference NPPo for that year taken as 53 Pg C/yr [Bolin et al., 1979]. The relative response for 1958 was calculated from

Equation (1) and labeled R_0 . For each succeeding year, ΔR , $\Delta R/R_0$, and the cumulative sum of $(\Delta R/R_0)(NPP_0)$ were calculated, based on carbon dioxide concentrations published in Keeling et al. [1982] and Gammon et al. [1985]. The cumulative additional NPP above the 1958 reference level was 4.8, 21.5, 35.5, and 52.7 Pg C for 1968, 1978, 1983, and 1988 (estimated), respectively. After 30 years, the predicted cumulative additional NPP was equivalent to the reference single-year NPP of 1958.

Revelle and Munk (1977) developed a model for predicting to predict the partitioning of carbon dioxide among the atmosphere, biosphere, and ocean reservoirs. They considered fossil fuel combustion and land clearing as sources of carbon dioxide which could be added to the three reservoirs. Data in Table 10.8 of Revelle and Munk (1977) can be interpolated to estimate the input of additional carbon to the biosphere by the carbon dioxide fertilization effect for the period 1958-1988. During this modeled 30-year period, the cumulative additional C was about 64 Pg. Both of these examples illustrate the potential for the carbon dioxide fertilization effect to compensate for large fluxes of carbon from the biosphere to the atmosphere in the global carbon budget.

CONCLUSIONS

Most of the data and analyses presented here lead to the conclusion that the carbon dioxide fertilization effect is a real and growing factor, globally as well as locally, in the earth's carbon cycle. However, more data and careful interpretations are needed both for agricultural and unmanaged vegetation across a continuum of subambient and superambient carbon dioxide concentrations. This information would improve our predictions of yield and biomass response under scenarios of the future carbon dioxide concentration, elucidate probable global biospheric carbon dioxide uptake and potential sequestering of carbon, and enable retrospective predictions of yield and carbon cycling based on scenarios of earlier decades and centuries.

In summary, the rectangular hyperbola model provides one rapid, simple approach for predicting responses of plants to future (and past) scenarios of atmospheric carbon dioxide when they are grown under nonstress conditions. Obviously, further

experimental data and mechanistic models are required to ultimately understand and predict in greater detail crop responses and ecosystem responses to carbon dioxide as they may interact with other biologic, environmental, and soil factors.

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