(*2*), we prefer Johnston's (*13*) more neutral label, area superficialis basalis, even though it must be admitted that the structure is immediately adjoined by olfactory projection areas. The evidence that the area superficialis basalis receives fibers ascending from levels caudal to the mesencephalon recalls the quintofrontal tracts of birds. Should this suggested similarity be confirmed, it would seem conceivable that the basal forebrain region in the wider sense subserves the integration of sensory information of several modalities.

A telencephalic projection to the deep layers of the optic tectum likewise has not been described in elasmobranchs before. Except for the contralateral nature of this pathway, it appears quite comparable to certain corticotectal projections of mammals (*14*) and to a similar pathway identified in the avian brain (*15*).

The lesions in our experiments were too large and too few to provide information about the exact source of the various fiber systems. Consequently, only general patterns of organization have emerged. At present it cannot be stated, for example, whether the thalamo-telencephalic and telencephalo-thalamic connections are reciprocal as they predominantly are in mammals.

In summary, the principal evidence emerging from the present study has been that of a massive thalamo-telencephalic projection in the selachian brain. This projection is distributed to areas of the telencephalon well outside the structures receiving fibers of the olfactory tract. Apart from the curious fact that the projection is almost entirely crossed, it is of obvious interest to ask what the nature of the recipient telencephalic cell territories could be. Somewhat comparable—although uncrossed—thalamic projections to nonpallial components of the telencephalon have recently been identified in birds (*15*) and reptiles (*16*). In these forms the recipient cell regions have traditionally been interpreted as part of the corpus striatum, but it has been suggested recently (*15, 16*) that their neuronal populations might be homologous, in the phylogenetic sense, to certain cell systems of the mammalian neocortex. The present findings bear no clue to this intriguing question; they do suggest, however, that the telencephalon of the shark is more directly comparable to that of amniotes and considerably less completely monopolized by the olfactory system than earlier studies by inadequate methods had seemed to indicate.

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Plant Response to Carbon Dioxide Enrichment under Field Conditions: A Simulation

Abstract. *A comprehensive soil-plant-atmosphere computer simulation model (SPAM) predicted up to a 45 percent increase in carbon dioxide uptake by a crop enriched with carbon dioxide at ground level. Enrichment rates of 225 and 450 kilograms of carbon dioxide per hectare per hour were used. Simulations covered a wide range of wind speed, crop height, and leaf area display.*

We have simulated crop CO_2 uptake under optimum conditions of high light intensity and adequate plant moisture. We simulated a crop with high photosynthetic light saturation of the leaves (such as corn) and also with high CO_2 saturation. We used a comprehensive soil-plant-atmosphere computer simulation (SPAM) which was developed by Stewart and reported by Stewart and Lemon (*1*). This model predicts light penetration, thermal radiation exchange, sensible heat flux, latent heat flux, and net photosynthesis (CO_2 exchange) by a crop canopy for short time periods (for example, 1 hour).

The model treats the crop system as a two-boundary problem, with one boundary being defined at a reference height of 6 m above ground within the aerodynamic boundary layer and the other boundary being the soil surface. The input parameters at the top boundary are wind speed, air temperature, vapor content, net radiation, solar elevation angle, direct shortwave radiation, and diffuse shortwave radiation. The crop architecture parameters are leaf area distributions with respect to height in nine classes of leaf angles. For computations, the total leaf area was divided into 15 equal horizontal sublayers. The soil, or lower boundary, input parameters are soil heat flux, soil moisture tension at the surface, CO_2 flux from the soil, and aerodynamic roughness of the soil surface. The reference height parameters, crop architecture, and soil boundary parameters are used to predict, by iteration, the light, wind, and eddy diffusivity within the crop canopy. This model is more complete and complex than other published crop-climate models (*2*).

The boundary layer resistance of the leaf as a function of wind speed and the stomatal resistance as a function of light intensity and a water stress parameter are included in the calculations which partition the energy flux from the crop into sensible (temperature) and latent (water vapor) heat components. The CO_2 uptake of the crop is predicted for 20 radiation load classes of the leaves in each horizontal sublayer from experimentally determined (*1*) curves of CO_2 uptake as a function of light intensity for individual leaves.

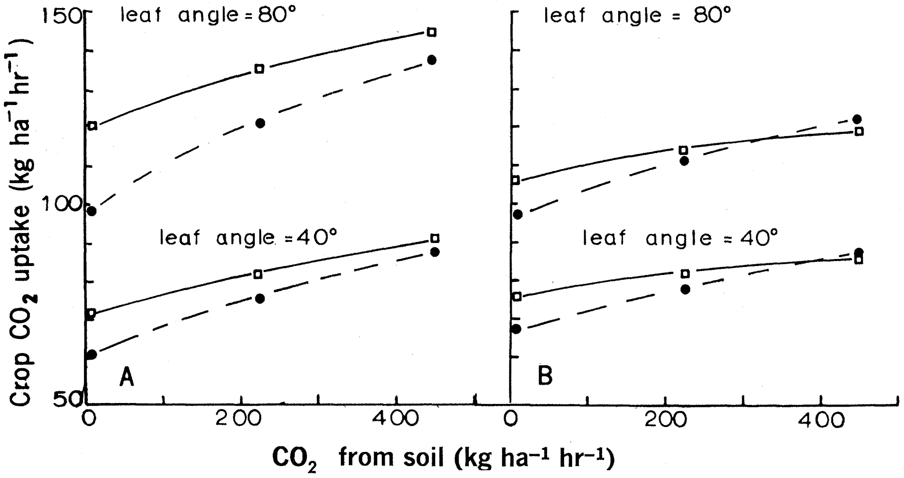

Fig. 1. Simulated crop CO_2 uptake as a function of the ground level CO_2 enrichment rate, leaf angle, leaf area index (LAI), and wind speed at the reference height (600 cm). The height of (A) the simulated crop with LAI = 10 was 50 cm, and the height of (B) the simulated crop with LAI = 4 was 215 cm. (Open squares) High wind, 600 cm sec^{-1}; (solid circles) low wind, 100 cm sec^{-1}.

Respiration is predicted as a function of leaf temperature (*3*). Using a simplified CO_2 diffusion model for a leaf (*4*), we combined the effects of boundary layer resistance, stomatal resistance, respiration, and light response curves to compute the net CO_2 uptake by successive approximation processes.

The SPAM computer simulation model was tested by the use of experimental field data and predicted the photosynthetic activity of a corn crop to within 10 to 20 percent of that computed by energy balance methods based on field data (*1*).

Carbon dioxide enrichment in greenhouses has been studied and practiced for several years (*5*). Recently CO_2 enrichment in the field has been attempted. A single line source at ground level at this project and a uniform area source (*6*) have been used in aerodynamic transport studies. Carbon dioxide is a by-product of many industrial processes such as the manufacture of ammonia. Underground reservoirs of CO_2 in the Mississippi Delta region have stimulated interest in agricultural applications (*6*).

Upward CO_2 flux at the soil surface is an input that can be varied in the SPAM model. Crop architecture parameters and minimum stomatal resistance are other easily varied inputs of the model. Thus this model is well suited to simulate the effects of CO_2 added uniformly at ground level.

Two crop configurations, each with two leaf angles, were selected for simulations. A low-growing (height = 50 cm) crop (such as bermuda grass) with a high leaf area index (LAI = 10) was chosen to "trap" released CO_2 from the ground surface. The other crop configuration (for example, a corn crop) was more open, with a height of 215 cm and an LAI of 4. Leaf angles of 40° and 80° represent, respectively, a "normal" distribution and an erect distribution of leaf angles in the canopy. The model assumes a uniform distribution of leaves in the horizontal direction throughout the canopy. This case is ideal, and is rarely, if ever, found in nature. Thus the response of a crop to CO_2 enrichment is simulated here under the most ideal conditions of horizontal leaf distribution.

Carbon dioxide release rates of 225 and 450 kg ha^{-1} hr^{-1} were tested and compared with a typical soil CO_2 flux rate of 10 kg ha^{-1} hr^{-1}. Two wind speeds were tested, a low wind speed (100 cm sec^{-1}) typical of a quiet day in the eastern states and a high value (600 cm sec^{-1}) typical of winds in the Great Plains on a summer day.

Figure 1 shows the results from the simulated CO_2 enrichment. The base rate net photosynthesis ranged from 61 to 121 kg ha^{-1} hr^{-1}. Carbon dioxide uptake increased from 12 to 45 percent at the highest release rates, with the degree of increased uptake dependent upon the characteristics of the crop and the wind speed. The largest effect was the increased CO_2 uptake with erect leaves (80°) as compared to the case with normal leaves (40°) (*7*).

We also considered the effect of CO_2 liberated from decaying organic

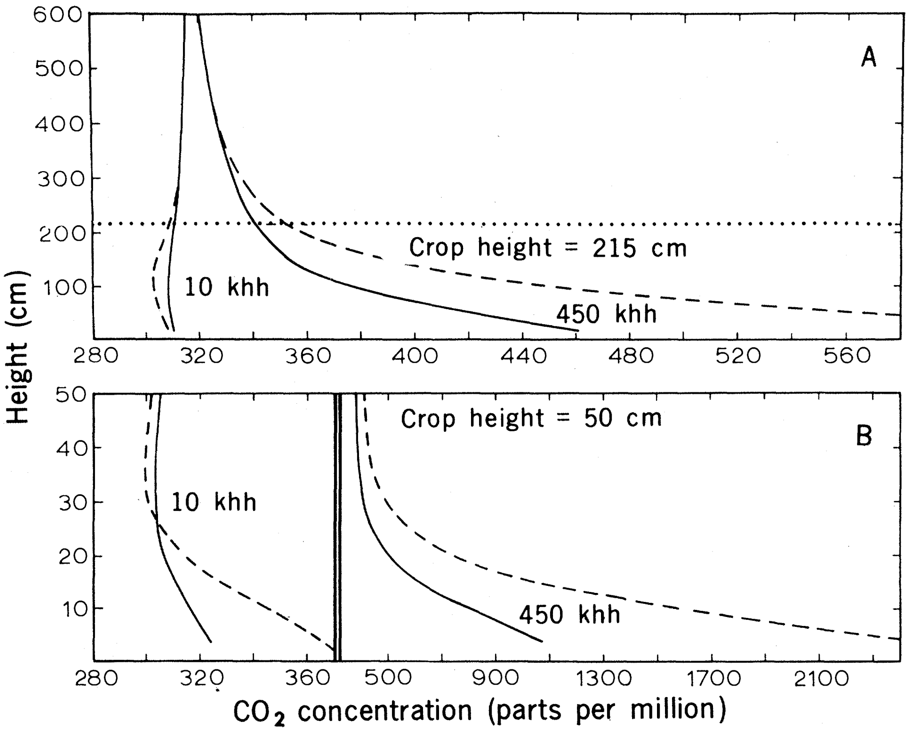

Fig. 2. Simulated CO_2 concentration profiles for the cases with a leaf angle of 40° for (A) the tall, open crop (height = 215 cm, LAI = 4) and (B) the short, dense crop (height = 50 cm, LAI = 10) for normal soil CO_2 flux density rates of 10 kg $ha^{-1}hr^{-1}$ (*khh*) and enrichment rates of 450 kg $ha^{-1}hr^{-1}$. (Dashed lines) Wind speed, 100 cm sec^{-1}; (solid lines) wind speed, 600 cm sec^{-1}. Note the scale changes.

Table 1. Carbon dioxide enrichment simulations. Entries in column 4 represent the percent increase in CO_2 uptake based on normal uptake rates at the same leaf angle and wind speed. Columns 5 and 6 show, respectively, the percent of released CO_2 taken up by the crop and lost to the atmosphere. Column 7 lists the efficiency of uptake, that is, the increased CO_2 uptake divided by the total added CO_2.

Leaf angle	Wind speed (cm/sec)	CO_2 release rate (kg/ha)	Increased uptake of CO_2 (%)	Amount of CO_2		Efficiency
				Taken up by crop (%)	Lost to atmosphere (%)	
		LAI = 4, height = 215 cm				
40°	100	225	15	35	65	4.5
40°	100	450	28	20	80	4.2
40°	600	225	7	37	63	2.5
40°	600	450	13	19	81	2.3
80°	100	225	14	50	50	6.2
80°	100	450	25	27	73	5.4
80°	600	225	6	51	49	3.0
80°	600	450	12	27	73	2.8
		LAI = 10, height = 50 cm				
40°	100	225	24	34	66	6.6
40°	100	450	45	20	80	6.2
40°	600	225	14	37	63	4.4
40°	600	450	25	20	80	4.1
80°	100	225	23	54	46	10.1
80°	100	450	38	31	69	8.5
80°	600	225	12	60	40	6.3
80°	600	450	22	32	68	5.6

sources. Applications of 15 to 30 metric tons of sewage sludge or animal manure per hectare of soil per year (dry weight) are high but not excessive. Typical CO_2 flux rates from such applications are 10 to 20 kg ha^{-1} hr^{-1}. Figure 1 shows that additional CO_2 from such sources would increase the net photosynthesis by only a negligible amount.

Table 1 shows the percentage increase in the uptake of CO_2 by the simulated crops when CO_2 is added at ground level. Each of these percentage increases was based on crop CO_2 uptake rates computed under the same tabulated meteorological and crop input conditions as before, but with a typical soil CO_2 flux rate of 10 kg ha^{-1} hr^{-1}. Table 1 also shows the relative amounts of released CO_2 that were taken up by the crop or lost to the atmosphere. The efficiency E of uptake was defined as:

$$E = \frac{\text{Increased } CO_2 \text{ uptake rate}}{CO_2 \text{ enrichment rate}}$$

The efficiency, given in the last column of Table 1, ranged from about 2 to 10 percent, depending upon the input conditions. The highest efficiencies were obtained with erect leaves (80°), low wind speed (100 cm sec^{-1}), and short, dense vegetation (height = 50 cm, LAI = 10). The lowest efficiencies were obtained with a normal leaf display (40°), high wind speed (600 cm sec^{-1}) and tall, open vegetation (height = 215 cm, LAI = 4). On the other hand, the largest percent increase in CO_2 uptake was obtained with a normal leaf display (40°) and the smallest with an erect leaf display (80°), other conditions being the same as those described above, respectively.

Some simulated CO_2 concentration profiles for the 40° angle leaf display are shown in Fig. 2. The model computes 15 values within the plant canopy and 5 values above. The cases with a leaf angle of 80° gave similar profiles. The profiles on the left side of Fig. 2 are typical of those with no CO_2 enrichment. The profiles on the right side are those computed for an enrichment rate of 450 kg ha^{-1} hr^{-1} at the soil surface. These profiles are similar to those obtained with actual CO_2 release (*6*). The CO_2 concentration decreased rapidly with height within the crop canopy in spite of the high enrichment rate.

Wind is necessary to supply CO_2 to the crop from the atmosphere under normal conditions. However, Fig. 2 shows that wind disperses the added CO_2 and decreases the potential benefits of CO_2 enrichment under conditions of natural ventilation. With the source of CO_2 at the bottom of the crop, the concentration drops steadily from the bottom to the top. The potential benefits of a high concentration of CO_2 at the bottom of the crop are not realized, since crop photosynthesis is greatest in the top layers where light is most plentiful.

We have not allowed for partial stomatal closure by high concentrations of CO_2 (*8*) in these simulations. Mutants of potato and tomato (*9*) have been reported which do not close all their stomata in response to water stress or darkness. Thus it is likely, although it has not been demonstrated as yet, that these or other mutants may not close their stomata in response to a high concentration of CO_2. Thus we think it is reasonable to simulate plants with stomata that remain open in a high CO_2 environment. Even if stomata partly close and restrict the supply of CO_2 to the chloroplasts, this result will reduce transpiration by an even greater amount and will increase the ratio of photosynthesis to transpiration. In this case, CO_2 would be a beneficial antitranspirant.

The efficiency of uptake of artificially supplied CO_2 (Table 1) is very low. The simulations show that CO_2 uptake could be increased up to 45 percent (Fig. 1), but the efficiency of the applied CO_2 was never greater than 10 percent. These simulations indicate that CO_2 enrichment under natural field conditions would be very inefficient because of the rapid loss of added CO_2 to the atmosphere and the resulting relatively small buildup of CO_2 near the leaves of the top canopy where the most light is available.

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