Response of Agronomic and Forest Species to Elevated Atmospheric Carbon Dioxide

Abstract. *The effects of atmospheric carbon dioxide on corn, soybeans, loblolly pine, and sweetgum were studied in the field during a growing season. The plants were exposed to a range of concentrations of carbon dioxide day and night in open-topped, flow-through chambers. At a mean daytime carbon dioxide concentration of 910 parts per million, increases in total biomass ranged from 157 to 186 percent of the control values. Seed yield and wood volume increased and there were changes in plant anatomy and form. Net photosynthesis increased with increasing carbon dioxide concentration in soybeans and sweetgum, but was unaffected in corn. Water use efficiency also increased in corn, soybeans, and sweetgum.*

It is widely considered that atmospheric CO_2 concentrations are rising and that this is chiefly due to increased consumption of fossil fuels (*1*). There is, however, considerable debate over the climatic and biological consequences of this change in the earth's atmosphere (*2, 3*).

The essential role of plants in the carbon cycle makes them a logical starting point for assessing the impact of elevated CO_2 on living systems. Through photosynthesis, plants form the support system for the rest of the biosphere. Since carbon is a chief input in this food-producing process, any appreciable response of plants to changing CO_2 concentrations could have far-reaching implications. The gradual accumulation of CO_2 in the atmosphere and the paucity of long-term field data on CO_2 and plant growth suggest an immediate need for research in this area.

In this report we describe the design and implementation of a system permitting study of the effects of CO_2 on vegetation in the field and give the results of our first experiments with two agronomic and two forest species.

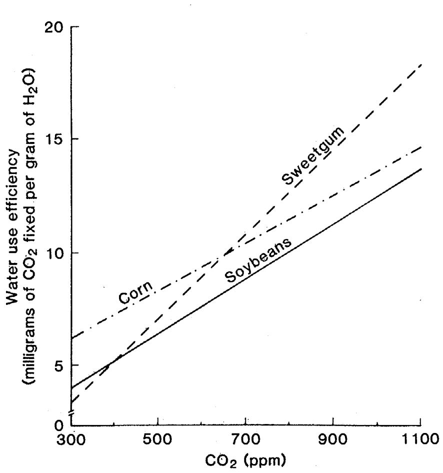

Fig. 1. Water use efficiencies for corn, soybeans, and sweetgum at various CO_2 concentrations. Values were fitted by the method of least squares and are based on 46 observations for soybeans, 50 for corn, and 15 for sweetgum.

Test atmospheres containing 340 ± 12 (background level), 520 ± 30, 718 ± 52, and 910 ± 52 parts per million (ppm) CO_2 (daytime values) were generated in transparent, open-topped chambers (2.4 m high by 3.0 m in diameter) (*4–6*) located in the field. Each chamber, essentially an open-ended cylindrical baffle, was constructed of a structural aluminum frame covered by Roll-A-Glass, a clear film of polyvinyl chloride. The bottom half of each chamber cover was double-walled, with the inside wall being perforated to distribute air uniformly into the chamber. A plenum box equipped with a 0.75-horsepower fan and a particulate filter supplied air at a rate of about 1.06 m^3/sec. Pure CO_2 from a liquid receiver weighing 12.7 metric tons was metered day and night through a high-pressure manifold into the ventilation airstream to generate the three elevated CO_2 concentrations. The pressure of each delivery line was regulated separately. Background exposures with and without chambers were established, and all treatments were replicated three times. Carbon dioxide levels were continually monitored with an infrared CO_2 analyzer by sequentially sampling air from each open-topped chamber.

Four plant species—corn [*Zea mays* (L.) 'Golden Bantam'], soybean [*Glycine max* (L.) Merr. 'Ransom'], loblolly pine (*Pinus taeda* L.), and sweetgum (*Liquidambar styraciflua* L.)—were grown in 16.5-liter pots containing one part peat-lite, one part coarse sand, and two parts clay loam soil and exposed to the various CO_2 levels in the chambers for 3 months. The plants were watered and fertilized throughout the study. The soybeans received a nitrogen-free nutrient solution to prevent inhibition of nodulation and nitrogen fixation.

Stomatal conductance and net photosynthesis were measured with a steady-state minicuvette system (*7*). All measurements were made at 25° ± 0.1°C, 70 ± 1 percent relative humidity, a photon flux density of 1600 to 1800 $\mu E/m^2$-sec, and a CO_2 concentration equal to that present in a given treatment. Stomatal conductance decreased with increasing CO_2 for each species. Conductance for corn decreased from 1.8 to 0.8 cm/sec between 340 and 910 ppm CO_2. The rate of decrease dropped steadily as the concentration of CO_2 increased. No significant change in photosynthetic rate was observed for corn; the regression suggested a slight decrease (−0.006 mg of CO_2 per square decimeter per hour for each 1-ppm increase in CO_2). However, net photosynthesis increased linearly with CO_2 concentration for soybeans. The regression indicated that the rate increased by 0.036 mg of CO_2 per square decimeter per hour for each 1-ppm increase in CO_2. This difference in the photosynthetic response to CO_2 concentrations between C_3 and C_4 plants was observed previously (*8, 9*).

Growth was enhanced in all four species (Table 1). Yield increased for the two crop species and wood volume increased for the tree species. Substantial changes in seed quality (such as in the content of fat, protein, fiber, and moisture) did not occur.

There is a seeming discrepancy between the photosynthetic rates for corn (no significant CO_2 effect) and that species' increased biomass (Table 1). This increase in biomass without a concomitant increase in the photosynthetic rate per unit of leaf area is attributable to increased leaf area and increased water use efficiency. Plants growing in atmospheres containing 520 to 910 ppm CO_2 did not undergo the wilting that we commonly observed for control plants on hot summer afternoons, when the rate of water uptake was exceeded by the rate of water loss. Wilting on hot afternoons inhibits leaf expansion and photosynthesis at a time when other environmental factors are most favorable for rapid carbon fixation. Thus a corn plant growing in an atmosphere with a high level of CO_2 was able to continue fixing carbon

Table 1. Final dry weights of the test species as percentages of the control weights. There were 18 observations for corn, pine, and sweetgum and six for soybeans.

Species	Concentration of CO_2 (ppm)				
	340				
	Chamber	No chamber (background)	520	718	910
Corn	100	93	158	148	160
Soybean	100	103	157	179	186
Pine	100				157
Sweetgum	100				160

and avoided wilting even though it had a greater leaf area.

Water use efficiency, defined as milligrams of CO_2 fixed per gram of water transpired, increased dramatically with increasing CO_2 concentrations for the species tested (Fig. 1). Although plants grown at high CO_2 levels were larger, they used available soil water at a much lower rate because of stomatal closure. For corn, water use efficiency was improved in CO_2-enriched atmospheres through lower transpiration rates. For soybeans and sweetgum, enhancement of photosynthesis also contributed to this improvement.

The leaves of soybeans, pine, and sweetgum thickened steadily as CO_2 levels rose. At 910 ppm CO_2, leaf thickness in these three species was 131, 110, and 121 percent of the control values, respectively. Thickness increased in all of the cell layers of pine and sweetgum leaves. In soybeans the greatest effect was the appearance of a well-developed third layer of palisade cells. As CO_2 levels increased for soybeans, more nodes, earlier anthesis, and less floral abscission were observed. Germinability of soybean seeds was not affected, however. Leaf thickness, node number, and reproduction in corn were not significantly altered by the CO_2 treatments.

These findings suggest positive growth responses to CO_2 enrichment for the agronomic and forest species studied. Further studies are needed to improve the experimental system and to provide additional data on the effect of CO_2 enrichment on vegetation.

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Psychological Stress Induces Sodium and Fluid Retention in Men at High Risk for Hypertension

Abstract. *Exposure to competitive mental tasks significantly reduced the urinary sodium and fluid excreted by young men with one or two hypertensive parents or with borderline hypertension. In this high-risk group, the degree of retention was directly related to the magnitude of heart rate increase during stress, suggesting common mediation by way of the sympathetic nervous system. Thus, psychological stress appears to induce changes in renal excretory functions that may play a critical role in long-term blood pressure regulation.*

Psychological stress has long been hypothesized to be one of the set of interacting elements that may influence the development of primary hypertension in humans, but its role remains unclear (*1*). Certain authorities contend that a critical factor in the establishment of hypertension is the failure of the kidneys to maintain blood pressure (BP) within normal limits by excreting sufficient salt and water (*2*). Abnormal retention of sodium may contribute to hypertension in other ways as well (*3*). Studies in the dog (*4*) and rat (*5*) show that psychological stress reduces renal excretion of sodium and fluid. This stress-induced retention is greater among young spontaneously hypertensive rats than among rats with no genetic predisposition for hypertension (*5*). Thus, such retention may be one mechanism whereby stress contributes to the pathogenic process, particularly in individuals with genetic or acquired predispositions.

In humans, evidence that psychological stress may induce sodium and fluid retention is primarily indirect. Reports that stressful mental tasks increase plasma renin activity and decrease renal blood flow in certain individuals, particularly those with one or two hypertensive parents and those showing high heart rate responses to stress, suggest but do not demonstrate that excretion of sodium and fluid may be reduced (*6–8*). High heart rate response in humans reflects enhanced sympathetic nervous system activity during competitive and other mental tasks (*7*); in animals, stress-induced sodium retention is sympathetically mediated (*4, 5*). The purpose of the present study was to determine whether exposing young men to competitive mental stress reduces their excretion of sodium and fluid, and whether any observed reductions are greater among those with known risk factors for hypertension [for example, parental or borderline hypertension (*9, 10*)] or those demonstrating high heart rate responses to stress.

Forty male college students (18 to 22 years old) participated in the study, 24 of them being subjected to the "stress" and 16 to the "nonstress" condition. All had resting diastolic pressures less than 90 mmHg and no clinical signs of any cardiovascular or renal disorder. During the 5-hour experiments, high rates of fluid excretion were established and maintained by requiring the subjects to drink 1 liter of water during the first hour and 200 ml every 30 minutes thereafter. Urine collections were obtained by voluntary voiding every 60 minutes; the subjects were reminded each time to empty their bladders completely. Samples from each collection were assayed in duplicate for sodium concentration (Beckman Electrolyte 2 Analyzer) and osmolality (Model 3DII Digimatic Osmometer, Advanced Instruments). Sodium concentration was multiplied by fluid excretion rate to derive sodium excretion rate. Cardiovascular measures were sampled during each of the last 3 hours. Each sample included 5 minutes of heart rate, scored from the electrocardiogram (EKG) in beats per minute, and four to six BP determinations obtained by means of a remotely controlled inflation cuff with a Narco Korotkoff Sounds microphone fixed on the left brachial artery. The EKG, cuff pressure, and Korotkoff sounds were recorded on a Beckman Dynograph located in an adjacent room.

The subjects were separated into high risk (HR) and low risk (LR) groups depending on the presence or absence of borderline systolic hypertension (*11*) or parental history of hypertension (*12*). In the nonstress condition, nine LR and