Marvin R. Lamborg, Chairman
Ralph W. F. Hardy, Co-Chairman
E. A. Paul

6. Microbial Effects

Panel Members: G. Bethlenfalvey, Peter Dart, C.L. Luh,
R.J. Luxmoore, Barbara Mazur, J.H. McBeath, Yaacov Okon,
W.H. Patrick, Jr., W.J. Payne, G.A. Peters, T. St. John.

RESEARCH RECOMMENDATIONS AND SUMMARY

The recommendations for microbiological research needs
are based on the following general scenario: a) increased
atmospheric CO_2 will increase crop productivities by 10-40%,
depending on crop and geographic area, which in turn will
increase biomass and soil organic matter by 5-40%; b)
additional root-derived materials and crop residue in the
soil will increase soil microbial activities, producing a
greater flux in most major cycles and possibly some changes
in pool sizes of -10% to +30%; c) these effects will
increase biological N_2 fixation, and the increased demand
for N will place significant limitations on phosphorus and
other mineral nutrients; d) no significant changes will
occur in soil O_2 or CO_2.

1) Quantification of the key soil components, proces-
ses and structure, as a function of increased atmospheric
CO_2, is essential. Components and processes to be measured
includes mycorrhiza, nitrogen fixation, biomass production,
mineralization-immobilization, nitrification, denitrifi-
cation, organic matter, available phosphorus and other
nutrients, soil CO_2 and O_2, and soil structure. These
determinations should be carried out in the key agricultural
and forest ecosystems of the tropical and temperate zones.
Information should also be collected on microbial
mobilization of limiting nutrients and on the sensitivity
of mobilization to atmospheric CO_2. Organisms of note are
those involved in N_2 fixation, nitrification, and
denitrification, as well as mycorrhiza. Rhizosphere
changes will probably precede those in the root-free zone.

Some of these measurements will of necessity be long term, perhaps 5-10 years.

2) Soil limitations should be defined in terms of N, P, and other nutrients. The N_2-fixing organisms and mycorrhiza are especially important to study. The latter can scavenge P and perhaps other limiting nutrients in unfertilized areas, and there is insufficient information on them. Development of inoculants composed of nitrogen-fixing organisms, and especially mycorrhiza, are essential.

3) Minimum tillage is suggested as a large-scale operating model resembling the conditions of soils which may occur under elevated CO_2.

4) On the assumption that additonal P and N will be needed to obtain crop production increases from elevated atmospheric CO_2, alternative economical sources of N and P should be developed with emphasis on biological systems.

5) Among the questions to be addresed are: Is there a significant increase in the amount of N_2O released to the atmosphere? Are soil-borne plant diseases increased or decreased? What is the effect of possible decreased litter quality?

6) The rapid rate of technological change, especially in molecular genetics, dictates the need to develop scenarios for the impact of increased CO_2 based on the use of futuristic rather than current technologies. The recently established molecular biology and recombinant DNA technologies should be applied to increase the beneficial interaction of soil microbes and plants. In this way, the postulated nitrogen, phosphorus, and nutrient limitations may be reduced, and the requirement for multiple interacting organisms may be eliminated.

Summary

The postulated doubling of atmospheric CO_2 is not likely to have a direct effect on soil microbial activity because during the growing season, the concentration of CO_2 in the soil atmosphere is already ten to fifty times higher than existing atmospheric CO_2. Based on all available experimental information, it is estimated that a doubling of atmospheric CO_2 will cause an increase in primary productivity of ten to forty percent, depending on locale. The increase in biomass will, in turn, produce a limitation of available soil nutrients, especially nitrogen

and phosphorus. Increased organic carbon together with nitrogen and/or phosphorus limitation will result in a preferential increase in nitrogen fixation and mycorrhizal activities as the expedient means for supplying required nutrients to sustain the predicted increase in primary productivity. Therefore, increased emphasis should be placed on fundamental research related to soil microbiology with special reference to nitrogen-fixing, nitrifying and denitrifying bacteria, and to the mycorrhizal fungi.

1. Global Effects. The biogeochemical cycle of carbon which integrates aerial, soil, and aquatic activities constitutes the basic mechanism for the production of renewable resources such as food, fiber, and fuel, and for the removal of organic detritus through mineralization. Man is increasingly affecting the carbon cycle by burning fossil fuels, by intensifying agriculture and forestry, and by destroying segments of the earth's plant cover. Soil microorganisms are an important determinant in defining the extent to which plants can respond to the increased level of atmospheric CO_2. Because the concentration of CO_2 in the soil is already an order of magnitude higher than the atmospheric concentration, soil microbes are unlikely to be affected by the anticipated atmospheric change. They will, however, be affected by the primary plant response, increased CO_2 fixation and increased biomass. Predicting the response of soil microbes to this secondary extent was the charge given to the "Microbial Inputs" group. The major conclusion of the group's discussions is that soil microorganisms will provide the major source of nutrients required by plants in response to the increased atmospheric CO_2. The extent of the plant response will be dictated by the soil activities. Increased knowledge of the soil changes may enable beneficial management for improved plant productivity under increased atmospheric CO_2. A summary of our knowledge and postulated changes in the various soil activities and recommendations for future research follows.

1.1 Microorganisms and Photosynthesis. At first glance, bacterial and cyanobacterial photosynthesis may not loom as large in cultivated and non-cultivated ecosystems as green plant photosynthesis, but the contributions of microbes to carbon fixation cannot be ignored (Karagouni and Slater, 1978). Microbial CO_2 fixation is reviewed in this chapter (see Section 3). Nitrogen fixation, the second most significant source of energy potential and nutrients for plants (Hardy and Havelka, 1975), is tied both directly and indirectly to photosynthesis. The photosynthetic prokaryotes which form the base of many food chains also

fix nitrogen. In addition, the photosynthate generated by legumes and many other plants contributes the energy and electrons used by the nodule-forming and associative heterotrophic bacteria that fix nitrogen.

Carbon dioxide, a product of both aerobic and anaerobic metabolism, is important not only because it completes the carbon cycle but also because of its direct influence on microbial growth. Chemoautotrophic and photoautotrophic microorganisms must have CO_2, as it is their sole carbonaceous nutrient. CO_2 is stimulatory to, and often required by, many heterotrophs. Frequently growth will not proceed in its absence. Yet high levels can be toxic.

1.2 CO_2 Concentrations in Soil and Factors Affecting It.

The CO_2 concentration in soil is much higher than that in the atmosphere because of the continued generation of CO_2 by biological processes. General soil levels under aerobic conditions usually approximate 3,000 ppm where active microbial or plant growth occurs. Under waterlogged conditions, soil CO_2 levels of 10,000-30,000 ppm are usually considered to be the average. All measurements of CO_2 are made on the air in the macropores between soil aggregates. The actual microsite could be much higher; however, because respiring roots and microorganisms are usually on the outside of aggregates in larger pores, the inside of aggregates probably do not generate large amounts of CO_2.

The movement of CO_2 from reactive sites follows the general laws of gaseous diffusion (Fick's law). The diffusion rates of gases are linearly related to the concentrations in the air, the soil depth, and the diffusion constant in soil. The solubility of gases in the water phase depends on the type of gas, the temperature, the salt concentration, and their partial pressure in the atmosphere. CO_2 has a diffusion constant in air similar to O_2 and N_2 (0.2 cm^2 sec^{-1}). The relative diffusion constant of all gases in water is lower by a factor of 10^{-4}. Because CO^2 can become ionized, it has a much higher solubility in water than 0^2 (0.9 cm /liter vs. 0.031 cm^3/liter for oxygen at $10°C$ and 760 mm of mercury).

As concluded from Fick's law, the diffusion rate across water films will control O_2 and CO_2 content relative to the fluxes associated with O_2 use and CO_2 production in soil. Calculations based on the diffusion coefficients and solubilities of CO_2 and O_2 in water indicate that CO_2 should move away from the respiring root 23 times more

quickly than O_2 will move in (Greenwood, 1970). Thus, under normal circumstances O_2 will become limiting before growth of plant roots and microorganisms is inhibited by an excess of CO_2 (Garrett, 1981). This could change, however, if a proliferation of microbial, fungal, and other plant material raises the below-ground concentration of CO_2 above 100,000 ppm by elevating HCO_3^- concentrations to the range known to inhibit fungal metabolism (see Section 5.6) (Griffin, 1972).

The soil volume is approximately half solid and half pore space. The water content of the pore space controls the proportion of soil air, with an average medium textured soil having approximately 25% air space (one half of the pores are water filled). The proportion of pore space may increase with increased organic matter (Russell, 1973). Any associated increase in total porosity would be expected to increase the gas diffusion coefficient, favoring rapid gas exchange.

During the growing season, the CO_2 concentration in soil is usually much higher than that of the atmosphere because of the generation of CO_2 by biological processes. On the average, the CO_2 concentration of the soil atmosphere varies from 10 to 50 times higher than the atmospheric CO_2. The seasonal change is the most important variable. Temperature has a major influence on plant productivity and litter decomposition rates. Moisture, while having the same effect as temperature, also has a major influence, in that CO_2 concentrations can become very high when major pore spaces are filled during or immediately after rainfall or irrigation. Table 1 shows the range of CO_2 concentrations in a North American grassland during the growing season. Diffusion during the winter had equalized soil CO_2 levels at various depths. Initiation of plant growth increased CO_2 at the surface, with two rainfall events in June and July resulting in CO_2 concentrations above 10,000 ppm occurring in the surface layers. As the winter approached, surface layers had less CO_2 due to decreased plant growth and microbial activity. The CO_2 content at lower depths could have been due to slow diffusion rates or continued microbial activity in soils that were still relatively warm during this time of the year.

The position of the water table is a major factor controlling CO_2 in the soil profile. In contrast to the data shown in Table 1, the highest CO_2 concentrations in Figure 1 occurred adjacent to the water table. The high gradient between 35 and 60 cm, illustrated in Figure 1 is

Table 1. CO_2 concentrations in a native grassland during the growing season (from de Jong, et al., 1974).

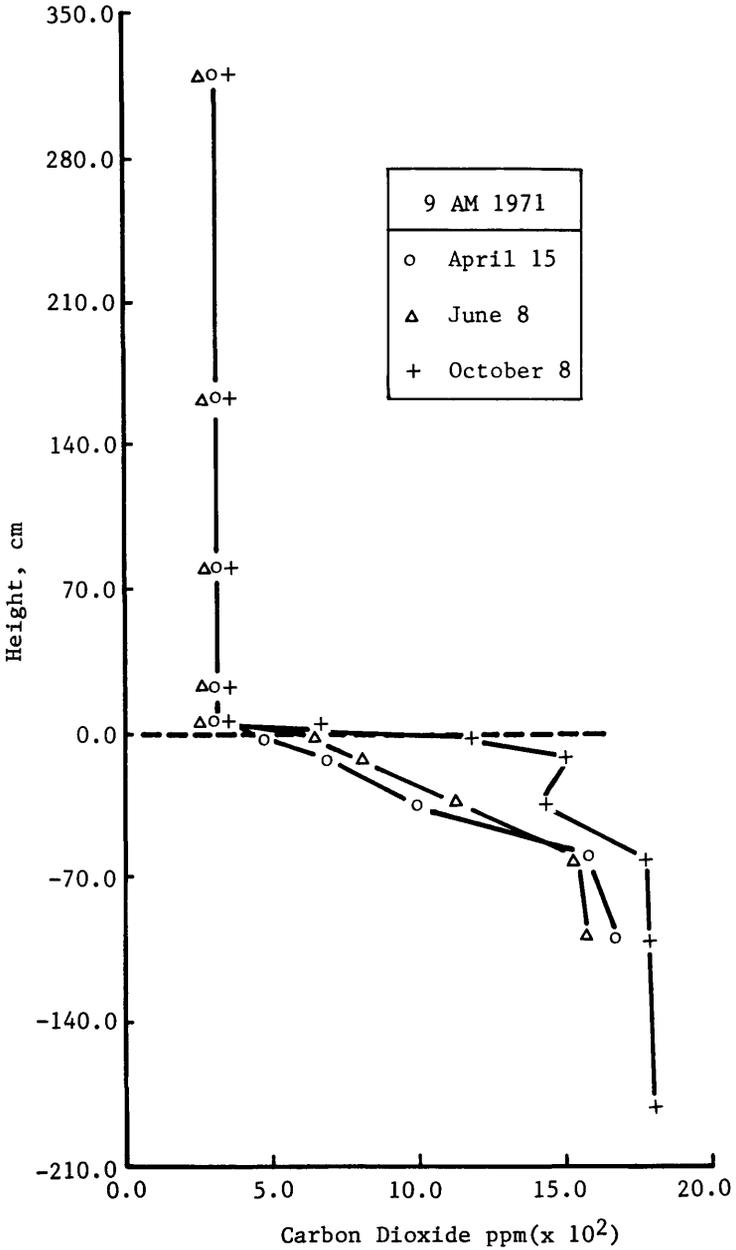| Soil depth (cm)	CO_2 ppm (x 10^2)					
	May 24	June 6	July 6	Aug. 5	Sept. 9	Oct. 10
15	15	109	161	33	10	3
30	12	41	123	73	9	4
45	10	14	40	92	6	4
90	10	13	30	23	14	33
150	7	18	24	30	38	29

Figure 1. Representative profiles of carbon dioxide concentration above the ground-water table on three selected dates. From Schwartz and Bazzaz (1977).
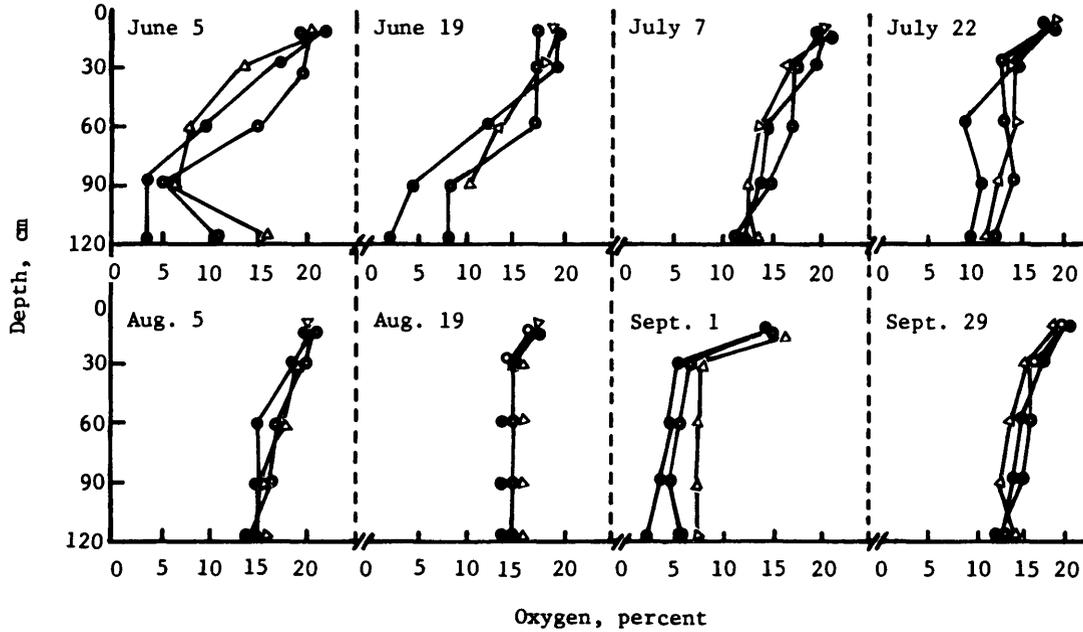
Figure 2. Oxygen content during the growing season in three replicated profiles in soil planted to cotton (Gossypium hirsutum L.). From Patrick (1977).

related to clay content and vegetative growth resulting
from the development of root structures.

On a macro basis, O_2 curves are generally reciprocal
to the CO_2 curves, justifying the assumption that O_2 is
consumed in the production of CO_2. But the agreement is
not absolute and the discrepancies are considerably beyond
the limit of experimental error. Oxygen content of
Louisiana soils were low in the sub-soil of silty clay loam
growing cotton early in the spring, but increased as the
season progressed. Heavy rains between the 19 August and 1
September samplings interfered with oxygen exchange in soil
and caused a temporary decrease in oxygen content (Figure
2).

Roots are the major contributors to total soil
respiration, with an average of 20 to 50% of the total soil
respiration being attributed to roots and the closely
associated microflora (Johnen, 1974; DeJong and Paul,
1979). Similar values are obtained for forests as for
agricultural sites (Reichle et al., 1973; Coleman, 1973).

In summary, soil CO_2 under aerobic conditions
approximate 3000 ppm where active microbial or plant growth
is occurring. Under waterlogged conditions, CO_2 levels of
10,000 to 30,000 ppm are usually considered to be an
average that plant roots and microorganisms are exposed
to. No significant change in soil microbial activity is
likely as a direct result of the projected increase in
atmospheric CO_2, since soil CO_2 is always several orders of
magnitude higher than ambient CO_2. In wetland soils that
are marginally aerated, increased plant residue decompo-
sition resulting from higher plant production may further
restrict aeration and cause a shift toward microbial
activity which uses electron acceptors other than O_2. This
should affect sensitive microbial reactions such as
denitrification, and possibly result in the production of
some inhibitory metabolites as well as decrease the decay
of plant residues.

1.3 Effect of Increased Levels of CO_2 on Solution
Equilibrium Reactions. The carbonate system is comprised
of gaseous CO_2, dissolved CO_2, carbonic acid (H_2CO_3),
bicarbonate (HCO_3^-), carbonate ($CO_3^=$), and carbonate-
containing materials. The equilibrium concentrations of
minerals containing Ca, P, Fe, Mn, Cd, Cu, and Pb are
affected by CO_2 partial pressures. The $CaSO_4.2H_2O$
(gypsum)–$CaCo_3$ (calcite) equilibrium is operative in many
dry land soils. The solubility of calcite is decreased as
CO_2 pressures increase.   At 340 ppm CO_2 in the atmos-

phere, calcium sulfate and calcium carbonate coexist at pH
7.8. Increasing the CO_2 concentration lowers the pH at
which the two minerals can coexist. Similarly, the
equilibrium between dolomite [$MgCa(CO_3)_2$] and calcite
($CaCO_3$) is shifted to dolomite by increasing CO_2. It has
recently been postulated that the formation of calcium
carbonates could provide a sink for increased CO_2 because
the inorganic carbonates are in equilibrium with
atmospheric CO_2, provided that exchangeable calcium and
complexes such as gypsum are available in the soil. In
flooded soils, the siderite ($FeCO_3$)–CO_2 equilibrium has a
major buffering effect on soil CO_2 levels.

Because carbonate minerals tend to be relatively
insoluble, an increased CO_2 concentration generally leads
to decreases in the solute concentrations of cations such
as iron and copper, and heavy metals such as lead and
cadmium. The inorganic chemistry of phosphate, however, is
complex; increased pH and increased CO_2 result in greater
solubility of certain phosphate minerals. A 10-fold
increase in CO_2 was said by Lindsay (1979) to shift the
solubility line of octacalcium phosphate upward by 1.3 log
units $H_2PO_4^=$.

Calculations show that CO_2 at 600 ppm in equilibrium
with rain water would decrease the pH 0.15 unit. The
buffering capacity of soil, and the great range in normal
soil and sediment, however, are more important than the
effects of increased CO_2 in the atmosphere. It has
generally been supposed that roots excrete H^+ to the soil
system and render nutrients available. It is now believed
that when plants utilize NO_3^-, the absorption of more
anions than cations results in an excretion of HCO_3^-. This
yields an increase in pH. Roots growing on NH_4^+ and
N_2-fixing organisms should cause a pH drop surrounding the
roots. There are, however, other effects, and higher HCO_3^-
concentrations are said to increase root hair density (Nye
and Tinker, 1977).

1.4 CO_2 and Soil Organic Matter Levels. Erosion plays a
major role in the amount of humus in both cultivated and
forested soils. The majority of organic materials are
usually deposited near their source. Sediments are slowly
decomposed. Addition of nutrients to sediments, rivers and
oceans can cause increases in eutrophication and a net
sequestering of C. Eroded sites present new landscapes and
soil organic matter formation occurs rapidly. This has
been shown in the revegetation of mine spoils, where the
general rise in soil organic matter averages approximately
400 kg/ha/yr over the first 50 years of revegetation.

Climatic alterations due to a "greenhouse effect" could have major influences on soil organic matter levels. Peat lands, taiga forests and sub-alpine tundra exposed to warmer temperatures would have both greater productivity and greater diversity. The amount of potential agricultural land that could be exploited in the northern hemisphere is limited by terrain and by endogenous nutrients. It is known, however, that transformation of northern forested land to agricultural land, and formation of sod Podzolic soils will increase soil organic matter levels.

Soil organic matter comprises approximately 1700 x 10^{15} g of C on a global basis. This is three times the level found in the atmosphere or in the land biota. Movements of C in and out of this source, therefore, can have major impacts on the global CO_2 levels (Bolin et al., 1979). Soil organic matter also plays a major role in soil properties and nutrient dynamics and will be vital to the future response of plants and microorganisms to increased CO_2 levels.

Predictive models of man's influence on soil organic matter (Jenkinson and Rayner, 1977; van Veen and Paul, 1981) have been developed which mimic the effect of past management practices and predict possible future levels. This has been possible since soil humus is composed of a number of constituents which are acted on by a large but generally inactive microbial population. The general concept that soils of the tropics have lower humus levels than those of temperate areas has been disproved (Sanchez et al., 1982a,b). Chemical analyses have shown that all soils have similar components and carbon dating has demonstrated that half of the soil humus is comprised of recalcitrant fractions with mean turnover times of at least 1000 years (van Veen and Paul, 1981).

In aerobic environments, the level of plant C addition has a limited effect on soil humus contents at low plant C/N ratios. Organic matter is stabilized by the reaction of phenol and lignin with inorganic and organic N. The content of these aromatic fractions, their reaction with inorganic particles, and their aggregation leads to long-term stabilization. Green manuring with N-rich legume can have major impacts on the N economy of soil and can relieve much of the fossil fuel requirement for the production of nitrogen fertilizer. Green manures will not, however, lead to major increases in soil organic matter levels unless other management techniques are also incorporated.

Table 2. Effect of Gradual Doubling of Atmospheric CO_2 on Plant Residues, Soil Organic Matter, and Soil Biomass

	Upland Temperate Zone				Upland Tropics				Wetlands		
	Agri. Total	Culti- vated	Forest	Grass- land	Agri. Legume	C_4 Plants	Grass- land	Forest	Paddy	Other*	Tundra
I. Plant matter	1.3	1.25	1.2	1.35	1.4	1.2	1.3	1.10	1.4	1.3	1.3
Soil organic matter	1.1	1.05	1.2	1.2	1.1	1.05	1.15	1.05	1.1	1.4	1.4
Soil nutrients remaining											
N	1.1	1.05	1.1	1.2	1.1	1.05	1.15	1.05	1.1	1.2	1.3
P	0.95	----	.95	.95	----	----	1.0	0.9	0.95	1.1	0.9
Micronutrients		----	.95	.95	----	----	1.0	0.9	0.95	1.0	0.9
Microorganisms		1.05	1.5	1.5	1.1	1.05	1.1	1.05	1.1	1.5	1.00
II. Present soil-C (10^{15}g)	73		210	147			197	90		313-300	30
Estimated new levels (10^{15}g)	80		252	176			226	94		?	42

Area and soil C levels from Bolin et al., 1979.

Values in Part I are ratios of predicted versus present values.

*Includes swamps, marshes and peat bogs.

Crop breeding has been selecting for plants with low
C/N ratios, low root production, and low phenolic contents.
However, in contrast to maize, cotton which has a high C/N
ratio, can yield increased humus levels when grown over a
20-30 year period (Lal and Kang, 1982). The organic matter
model of van Veen and Paul (1981) demonstrated that straw
incorporation over a 50-year period could result in a
stabilization of soil humus levels that were 5-10% higher
than those where straw had not been incorporated.

2. Estimates of the Effect of Doubling Atmospheric CO_2 on
Soil Organic Matter and Biomass. The carbonaceous sub-
strates drive soil microbiological processes ranging from
mineralization-immobilization, through nitrogen fixation,
to denitrification. An understanding of these effects has
to be based on estimates of the changes in available carbon
attributable to plant residue additions, to exudates and
other root derivatives. Table 2 shows the estimates of
some of these variables for a number of representative
plant community types. Those estimates for productivity
are generally lower than values given by Rogers et al.
(1980), Idso (1981), and Idso and Kimball (1982). Idso and
Kimball (1982) have recently reviewed the literature on the
effects of CO_2 on the yield of crops. Of the 355 separate
samples exposed to CO_2 for extended periods, the enrichment
increased yields up to 28%. Goudriaan and Atjay (1979)
concluded that, in the field, plant production is usually
limited by shortages of water and nutrients. Mulching with
plant residues has increased both plant yields (Goswami and
Suri, 1982) and nitrogen fixation in soybeans (Shivashankar
et al., 1976), although the extent to which this is due to
CO_2 or to indirect effects on soil temperature and water
evaporation is not known. Water and temperature were not
considered as limiting factors in calculating productivity
in Table 2. This can in part be rationalized by the fact
that new moisture and temperature regimes will merely
represent a displacement of these zones from their present
locations. To simplify comparisons, values are given as a
ratio of present levels. Thus, a value of 1.25 for plant
matter represents a 25% increase in plant productivity from
present 1982 levels.

This possible displacement of agricultural crops or
ecosystems to different parts of the world would require
slow adjustments in associated soil organic matter levels.
The 100 year time frame involved probably means that this
is possible for agricultural crops. However, forested
areas and wetlands such as peats cannot as easily be
transposed to other portions of the globe without producing
major dislocations on the source-sink relationships.   The

possible utilization of peat lands for agricultural crops
after attendant drainage, would result in significant
increases in atmospheric CO_2 and major mineralization of
sulfur, nitrogen and phosphorus.

Soil organic matter levels are estimated to respond
only slightly to increased productivity. This is in
agreement with the results of long term nutrient
application trials and in model predictions such as those
of van Veen and Paul (1981). It also takes into account
that green manures raise soil fertility, but not long term
soil organic matter levels.

Phosphorus and nitrogen availability will be major
limiting factors for both crop production and soil
organic matter stabilization. The increases in
productivity shown in Table 2 would require a major input
of fertilizers for agricultural lands. In natural
ecosystems where fertilization is not feasible, limitations
of N, P and trace elements will limit plant adaptation to
increased CO_2.

The good response of legumes to CO_2 was considered in
the estimates for cultivated and tropical dryland and for
legume and grassland systems. Rice is also known to
respond well. Temperate cultivation includes a mixture of
legumes and less responsive C_4 crops which should have an
intermediate increase in plant productivity. Tropical C_4
crops are predicted to respond poorly, since some of these
grasses have low nutritive value and grow in soils which
are both deficient in P and contain toxic levels of Al.

Tropical and temperate forests contain a large initial
biomass of nonphotosynthetic tissue so that only a modest
increase in biomass is predicted as the result of increased
atmospheric CO_2. These areas sequester nutrients in
biomass.   Therefore, increased growth will result in major
nutrient stress causing increased C:N ratios of the
substrate and lowering of decomposition rates due to
changes in plant type and composition. For example, beech
leaves (Fagus grundifolia) with a lignin content of 24%,
have a half-life in litter of nine years, while the half-
life for ash leaves (Fraxinus americana) which have 12%
lignin, is 1.4 years (Mellilo et al., 1982). Many
temperate forests have a small proportion of nutrients tied
up in the phytomass.

Kimmins et al. (1979) and Swank and Waide (1980)
summarized studies of thirteen forest sites. The data
show that 10.3% (std. dev. 2.9%) of the nitrogen, and for

seven sites 21.0% (std. dev. 19.2%) of the phosphorus was
associated with the vegetation (roots included). The total
system nutrient levels included the soil chemical content
to a depth of 1 m or less. Sufficient nutrient capital
exists within many temperate forests for a growth response
to elevated CO_2 if mechanisms for increasing nutrient
availability exist. One possible mechanism of increasing
phosphorus supply to trees may result from increased
oxalate excretion by mycorrhizal symbionts. Graustein et
al. (1977) have demonstrated oxalate release by
mycorrhizae, and have outlined feasible reactions by which
oxalate could increase phosphate concentration in soil
solution. The possibility of increased phosphorus,
nitrogen (Section 5.5), and water supply (Section 5.6.4)
led Luxmoore (1981) to hypothesize an increase in phytomass
and nutrient retention of forests with an increase in
atmospheric CO_2. This contrasts with other assessments
(Goudriaan and Atjay, 1979; Kramer, 1981) which suggest
that existing water and nutrient limits on growth may
continue to limit plant response to increased CO_2.

The projected yield increases and organic matter
production will require major nutrient transfers from both
increased N fixation and from mining of presently insoluble
P forms. For example, temperate forests would require a
conversion of one-third of their present inorganic P to
biomass and soil organic matter for the above production
figures to be attained. Mycorrhizal effects and biological
N_2 fixation will have to be even more significant than at
present; mycorrhizal activity will probably be the major
limiting factor in nutrient mobilization.

These data show that microbial soil populations will
be exposed to significantly more available substrate. Most
of the newly produced organic matter is more easily
mineralized than preexisting biomass after the initial
immobilization has been overcome. This will result in
bursts of microbial activity. Thus, the large initial size
of the current soil biomass in all studied ecosystems,
together with increased activity, precludes major changes
in biomass. Pulses of microbial growth will cause larger
short term fluctuations in biomass and nutrient turnover
than the steady state levels indicated in Table 2. The
estimates for increased soil organic matter levels include
changes in management, such as zero tillage. Residue
handling problems, toxic intermediates, and the use of more
of the plant residue for biofuels could alter these
calculations.

The estimated new equilibrium levels for soil organic

matter were obtained by multiplying estimates for present
levels of soil carbon by the expected increase reached
after the soils have attained new steady state levels. The
estimates for carbon in peat and swamplands varies from 300
x 10^{15} g (Atjay et al., 1979) to 900 x 10^{15} g (Bolin et
al., 1979). This represents the largest carbon reservoir,
which has been built up over many years. The method used
for calculating new equilibrium levels cannot be applied to
these soils. The present productivity of these wetlands is
estimated at 4 x 10^{15} g C yr^{-1} out of a total of 63 x 1
10^{15} g C yr^{-1}. The proportion that is stabilized in the
ecosystem is difficult to estimate, but it is much higher
than that for upland sites, indicating that these sites
will continue to be sinks for fixed C as long as climatic
changes do not materially dislocate the lowland areas from
present sites.

3. CO_2 Production and Effects

3.1 Roots. Any increased root growth that may occur under
elevated atmospheric CO_2 will increase the oxygen demand
for root respiration. Root proliferation will be favored
in zones with adequate aeration. However, at very high
root densities the oxygen supply to roots may limit
respiration. Generally, excess CO_2 will not limit root
respiration as much as O_2 deficiency. Also, the apparent
length of the diffusion path in the liquid phase
surrounding roots is more often a factor limiting normal
root respiration than is the gaseous composition of soil
pores (Grable, 1966). This factor could become more
significant at elevated CO_2 if soil water films tend to be
thicker as a result of a slower rate of plant water use.
In fine textured soils and marginally wet soil areas, root
growth may be limited by oxygen supply, and responses to
increased atmospheric CO_2 may not be expected in these
areas.

3.2 Fungi. Changes in the soil atmosphere affect fungal
growth. Soil fungi are relatively insensitive to
reductions in O_2 concentrations to about 4% in the gas
phase. At lower concentrations of O_2, there are some
marked differences among species, and nearly all fungal
growth rates decline at 1% O_2 (Griffin, 1972). In the
presence of 21% O_2, CO_2 has little effect on the growth
rate of most fungi until CO_2 exceeds 10,000 ppm (Smith and
Griffin, 1971). Within the soil, increased partial
pressures of CO_2 are always associated with a reduced
partial pressure of O_2. Therefore, enhanced fungal growth
in gas mixtures containing more CO_2 and less O_2 than the

atmosphere may not be unusual (Griffin, 1972). However, when the CO_2/O_2 ratio exceeds unity, significant changes in the mycoflora occur (Macauley and Griffin, 1969). A significant alteration of the soil atmosphere due to both increased root respiration and to degradation of more soil organic matter could therefore produce unforeseeable changes in the soil mycoflora.

Vesicular Arbuscular Mycorrhiza (VAM) Fungi. These organisms may represent up to 20% of the dry weight of the fungus-root association in some plants (Bethlenfalvay et al., 1982), and total respiration rates in mycorrhizal roots may be twice those in roots not colonized by VAM fungi. If these high respiration rates were to raise the concentration of bicarbonate ion in the soil solution, it could conceivably inhibit VAM fungal growth. Should this be the case, P limitation might lead to diminished symbiotic N_2 fixation. It could also indirectly diminish associative N_2 fixation by decreasing plant growth and root exudation (see Section 5).

3.3 Return of Crop Residues to Soil. With increased above-ground biomass production levels, there will be a greater return of crop residues to the soil, particularly in minimum tillage situations, where straw is not burned. Straw residues of temperate cereals such as wheat can influence development of subsequent crops adversely if there is insufficient time for the residues to be decomposed by microbes. Early in the breakdown process organic acids can accumulate in cool temperate climates, which can inhibit cereal seed germination (Lynch, 1978). To obviate this effect will require attention to such agronomic details as the time and depth of planting of the subsequent crop.

In tropical environments a product of sorghum residue breakdown can severely inhibit the growth of a subsequent crop. Polyphenolic compounds are implicated, and their toxic effect can be ameliorated by allowing a longer period for microbial breakdown of the residues before planting a subsequent crop. It is possible that inoculation of the soil with bacteria can hasten this process.

In semi-arid tropical environments, the growth of annual crops in soils with low nitrogen content may be enhanced by the addition of relatively small amounts (5 t/ha) of organic matter to the soil in the form of farmyard manure. The reason for the beneficial effect does not appear to be the extra supply of plant nutrients. Such

plant growth responses suggest that processes which
increase the rate of return of plant residues to the soil
can have beneficial effects on subsequent crop growth.

4. CO_2 Uptake

4.1 General Observations.
A relatively comprehensive
assessment of the effect of CO_2 concentration factors,
though somewhat outdated and preceding recognition of C_4,
is found in the chapter from "Photosynthesis, Vol. II, Part
1" by Rabinowitch (1951). Additional good discussions are
found in "Prediction and Measurement of Photosynthetic
Activity" (Denmead and Lemon, 1970). While no attempt will
be made to address this aspect in detail, several points
will be made. Given a doubling in atmospheric CO_2, plant
biomass can be expected to increase, although for this to
occur, more combined nitrogen may be required. It is also
possible that more root exudation will occur. This could
stimulate microbial growth in the root zone, especially in
tropical and subtropical soils where carbon sources are
likely to be limiting.

4.2 Microbial Effects.
As the principal and ultimate
degraders of carbonaceous plant and animal litter, detri-
tus, and ejecta, heterotrophic bacteria and fungi would be
affected indirectly by increased CO_2 by having more
oxidizable or fermentable substrate to deal with and more
CO_2 to assimilate. Further, if the mean temperature rises
as a consequence of CO_2 accumulation, rates of hetero-
trophic respiratory and fermentative activity may be
expected to rise significantly. It will be important to
know whether successions of microbial species in various
habitats change from indirect influences such as greater
carbon availability and higher temperatures.

The K_M for cell free fixation of CO_2 by the
autotrophic nitrifying bacteria <u>Nitrobacter</u> has been
calculated to be 5.9×10^{-3} M with respect to bicarbonate
ion. At pH 7.6 and 30°, a CO_2 of approximately 1 vol %
is required to produce this HCO_3^- concentration (Kiesow
et al., 1972). The intercellular CO_2 of <u>Nitrobacter</u>
equilibrated with air was found by the above authors
to be 1.2 vol %, indicating that the CO_2 within the
cells is substantially higher than the partial pressure of
CO_2 in the atmosphere. It is generally considered that
the requirement for CO_2 of autotrophic bacteria such as
nitrifiers is met when biologically produced CO_2 in the
soil must diffuse through approximately one inch of soil.
Soil CO_2 levels are normally not thought to have a

direct effect on nitrification and, subsequently, denitrification.

The increased CO_2 resulting from the microbial degradation of soil organic matter of a rewetted rice soil has been reported to result in a flush of green algae and a depression of the cyanobacteria (Rogers and Kulasooria, 1980). Cyanobacteria, however, have a competitive advantage over green algae at the alkaline pH often found in flooded fields during high photosynthetic periods. The decreased light intensities and N levels associated with the latter periods of rice growth also favor cyanobacteria growth.

Nitrogen-fixing cyanobacteria (blue-green algae) appear to have a ubiquitous distribution on earth. In the free-living state, this distribution seems to be most influenced by the pH of the milieu in which the algae grow. Generally, they are inhibited by acid conditions where the pH is less than pH 5.5-6.0, but particular forms apparently have adapted to more acid conditions. Their considerable growth and nitrogen-fixing activity in estuarine, marine, and inland lake environments is dealt with in Chapter 6. They are also well adapted to growing on the soil surface over a very wide range of environments in forests, on beach and river sands, pastures, and arable fields in both temperate and tropical environments.

Cyanobacteria are often numerous enough to develop a soil crust, usually in association with green algae. The balance between green algae and cyanobacteria in these soil niches is influenced by light intensity with the cyano-bacteria favored at the low-light intensity associated with greater plant canopy closure. Cyanobacteria are also favored by lower soil mineral nitrogen levels, and possibly by the CO_2 levels in the atmosphere surrounding the algae. Temperature and soil moisture conditions, and climatic factors indirectly influenced by atmospheric CO_2 concen-trations, are also likely to influence the growth of cyano-bacteria on the soil surface. Cyanobacteria seem to be adapted to higher soil temperatures and, because they produce resistant spores, to periodic wetting and drying phases. The latter is a situation likely to increase in some parts of the earth as part of the CO_2-induced climatic changes. Thus cyanobacteria distribution is likely to be only modestly affected by increases in atmospheric CO_2, although their occurrence on soils receiving little or no nitrogen fertilizer may increase.

The nitrogen-fixing activity of these cyanobacteria

can have a significant influence on the nitrogen economy of
their habitat. In desert and tundra soils they appear to
be a major current source of nitrogen input to soil. In
agricultural lands, they occur as soil crusts under annual
crops in both temperate and tropical regions, and in rice
they float freely in the paddy water, as well as encrusting
the basal parts of the rice stems. They also occur in
pastures receiving little or no N fertilizer, but their
extent is very much influenced by the canopy development of
the associated plant species. In certain situations, such
as tropical sorghum and grass fields (Dart and Wani, 1982),
the nitrogen-fixing activity can be high, with estimates of
up to 25 Kg N/ha/season. On the Broadbalk long-term wheat
experiment started in 1843, this amount of N would be
sufficient to provide all the nitrogen input necessary to
produce the crop. In tropical soils, the cyanobacterial
nitrogen fixation seems to be mainly limited by surface
soil moisture, and can be reduced to negligible levels
within three days of rain or irrigation because of soil
drying.

Cyanobacteria also occur in symbiotic association with
higher plants, such as mosses, ferns, cycads, and
angiosperms, where their nitrogen fixation contributes
significantly to plant growth. One particular association,
that between the floating fern Azolla, and the cyano-
bacterium, Anabaena azollae, has particular significance in
wet land rice cultivation, and in fresh water ponds, in
both tropical and temperate environments (Moore, 1969;
Peters and Calvert, 1982).

Considering surface soil microbes, specifically
free-living photosynthetic prokaryotes and lichens, it is
necessary to appreciate that CO_2 concentration at the
soil-atmosphere interface is influenced to some extent by
the biota itself (see Section 1 and 2). It should also be
noted that a number of cyanobacteria and unicellular green
algae (eukaryotes) which exhibit C_3 photosynthesis, exhibit
very low CO_2 compensation points and/or no O_2 inhibition of
photosynthesis (Bidwell, 1977; Lloyd et al, 1977) because
they possess a CO_2 concentrating mechanism when grown under
current ambient CO_2 (Berry et al., 1976). This mechanism is
not present at elevated pCO_2 partial pressures (Kaplin et
al, 1982) and it is probable that in organisms possessing
it there will be little effect from increasing CO_2. Higher
CO_2 levels may favor those cyanobacteria and other algae
which lack such a mechanism. Photoheterotrophic growth
and/or heterotrophic growth of such organisms might be
stimulated in nature through an increase in soil organic
matter.

5. Plant Microbial Associations

5.1 Introduction. Microorganism populations are
stimulated many fold in the vicinity of plant roots as a
result of the release of root derived substances as
exudates and as a result of the decay of root cap and
cortical cells. Bacteria live within root tissues and in
specialized root structures such as nodules. This micro-
bial population has a direct effect on plant growth through
its production of plant growth promoters and inhibitors,
through their competition for plant nutrients (immobili-
zation), and through their release of nutrients by break-
down of dead cells (mineralization). Certain bacteria,
such as Azospirillum, can enhance nutrient uptake by crop
plants by a mechanism that is currently not clear. The
activity of rhizosphere microorganisms will be enhanced by
the larger photosynthetic activity of plants at higher CO_2
which will release a greater supply of microbial substrates
through the roots. Current evidence suggests that the
microbial population will be qualitatively similar, and
that the results of their enhanced activity will be, in
general, beneficial for plant growth.

Although more CO_2 is likely to initially increase
immobilization of nutrients into microbial biomass, their
subsequent turnover through mineralization should favor
enhanced nutrient supply under maintenance fertilization
regimes. If nutrients are not supplied as fertilizer, then
immobilization of nutrients is likely to reduce plant
growth, even though plant adaptation features, such as
reduced concentration of nutrients per unit of dry matter,
will work towards maintaining plant growth rates.
Increased plant growth will lead to an increased demand for
plant nutrients such as P and S. The reduced levels of
combined nitrogen in the rhizosphere will favor
nitrogen-fixing bacteria.

Root associated bacteria can also modify the pH of the
immediate root environment, thereby affecting the solubility
of certain plant nutrients. For pastures in South-East
Australia dominated by annual clover plants, one of the
consequences of nitrogen fixation by the root nodules has
been a gradual lowering of soil pH to values which may
limit continued reinfection and nodulation by Rhizobium.
With enhanced N_2 fixation rates predicted as atmospheric
CO_2 rises, this problem could be exacerbated, requiring
new management techniques to maintain the pasture

5.2 Organic Mineralization-Immobilization Reactions. The
mineralization of nutrients in the geocycle of elements can

occur by specific enzymes elaborated during periods of
nutrient deficiencies. It is known that phosphatases and
sulfatases are produced under such conditions. Amidases
are known to occur, but it is generally considered that N
accumulates in the NH_4^+ form only when microorganisms
mineralize more NH_4^+ as a byproduct than is required for
microbial growth.

The current mineralization-immobilization rates of
nutrients such as N, S and P occur at two to three times
the net rates measured by crop uptake or nutrient
accumulation under fallow conditions. The microbial
biomass accounts for 2-5% of the soil carbon and 3-8% of
the N of surface soils (Jenkinson and Ladd, 1980).
Microbial products with fairly rapid turnover rates
comprise an equal fraction. Management of the biomass
and their metabolites through residue management and
timing of cultivation and of fertilizer application could
result in a major decrease in the nitrogen that is lost
from most soil systems. Immobilization should occur
during periods of maximum crop growth. Even a 10%
reduction in the high levels of nitrogen loss, usually
associated with crop growth, would have a major impact on
fertilizer requirements and on nutrient availability.

Increased plant productivity will increase the amounts
of carbon entering the organic pool, first as live biomass
and later as soil organic matter. We have estimated
earlier the soil organic matter build-up from the input of
more live biomass. The large anticipated increase in total
biomass will produce a considerably lower increase in
organic matter.

The increased mineralization of plant material will
increase heterotrophic microbial activity. An increased
demand for the mineral nutrients needed for microbial
decomposition that are not contained in plant material will
further stress the soil resources of nitrogen, phosphorus,
potassium and other essential minerals. The increased
requirement for nitrogen can be partially met by increased
fixation of atmospheric N_2, but the increased requirement
for other nutrients will necessarily be met by either soil
resources, in an unfertilized ecosystem, or by both soil
and fertilizer sources in agricultural systems. Table 2
predicts some depletion in the soil reservoir of these
nutrients. The decreased availability of these plant
nutrients will exert a limiting effect on plant production.

The higher rate of biomass production should stimulate
biological nitrogen fixation, since a widening of the C:N

ratio of the soil stimulates N_2 fixation by both free-living organisms and N_2-fixing organisms. The widening ratios may also encourage increased migration of legumes into grassland. It is unlikely, however, that enough nitrogen will be fixed to maintain the soil C:N ratio and some slight, but permanent, increase in the soil C:N ratio can be predicted to accompany increasing biomass.

For wetlands and poorly aerated uplands, the higher demand for oxygen resulting from increased plant production will cause increased accumulation of plant material, as peat in the wetlands or as increased soil organic matter in the poorly aerated uplands. This organic matter will have a high C:N ratio because of its limited decomposition. The absolute amounts of carbon, nitrogen, sulfur, and other mineral nutrients tied up in this organic material will significantly increase.

A similar effect will occur in those upland areas where the additional plant biomass is difficult to decompose because of its content of inhibitory compounds such as lignins and tannins. This condition will exist in some forests and will result in a higher organic matter accumulation and a wider C:N ratio.

Incomplete oxidation of plant material, especially under conditions of limited soil aeration, will produce organic acids, such as acetate, propionate and butyrate, which are toxic or inhibitory to some biological processes. It is safe to predict an increased concentration of these compounds in oxygen deficient systems. Under current atmospheric CO_2, residues of crop plants such as sorghums and millets produce high amounts of such compounds and the crops must therefore be grown in rotation to avoid such inhibitory effects (Dart, personal communication).

Under seriously limited aeration, the mineralization of increased amounts of biomass produces reduced sulfur compounds such as hydrogen sulfide (H_2S), dimethyl sulfide, and methyl mercaptans which are toxic to both microorganisms and higher plants. Ecosystems that are marginally aerated may be adversely affected by an increased oxygen demand.

Less sulfur and phosphorus will be available under conditions of increased biomass production and the consequent increase in the organic matter pool dilutes what may be an already limited supply. Except for the input of additional sulfur from atmospheric fallout and sulfur and

phosphorus fertilizers, plants are limited to the existing soil supplies.

5.3 Nitrification.

With available moisture and oxygen, and the simultaneously increased availability of CO_2 and NH_3 from mineralization, nitrification by autotrophic bacteria in the surface layer of soil will be stimulated. Nitrite and nitrate, the intermediate and the final products of nitrification, may still serve as plant nutrients, but the nitrogen in these oxidized forms is vulnerable to loss through leaching and/or denitrification by subsurface bacteria. In addition, if oxygen becomes limiting during nitrification so that only the ammonia-oxidizing bacteria function, toxic levels of nitrite may result. Finally, an adventitious result of nitrification is the release of as yet unpredictable amounts of nitric and nitrous oxide (Lipschultz et al., 1981). More NO and N_2O is liberated by denitrifying than by nitrifying organisms. Nitrous oxide moves into the earth's atmosphere and may erode the stratospheric ozone layer. There is currently an equilibrium between loss and replacement of ozone. Increased rate of nitrogen oxide release might decrease the protection afforded by ozone, and increase the penetration of ultraviolet radiation.

5.4 Denitrification.

Denitrifying bacteria are widely distributed in the soil. In an anaerobic environment, these organisms convert nitrate and nitrite to NO, N_2O and N_2. Populations are greatest in the zone reaching from just below the surface to a depth of 15 to 30 cm. Penetration of this zone by nitrate and nitrite added as fertilizer or generated at or near the surface, coupled with increased availability of soil organic matter, will result in increased rates of release of N_2 and a loss of a significant plant nutrient. Smaller but significant quantities of NO and N_2O relative to N_2 will also be released (McKenney et al., 1982) and added as the major source to the stratospheric load described in the previous section.

5.5 Nitrogen Uptake.

Of the essential elements limiting plant growth, N is frequently in notoriously short supply (Subba Rao, 1977). Thus, if CO_2 availability were removed as a limiting factor, increased reliance on N_2 fixation as a source of N would occur. A stimulation of N_2 fixation as a result of atmospheric CO_2 fertilization has been observed (Havelka and Hardy, 1976). This would shift the floristic composition of the vegetation toward legumes and non-legumes capable of symbiotic N_2 fixation (Newton et al., 1977). Plants and bacteria mutually benefiting from

associative N_2 fixation (Vose and Ruschel, 1981) would also flourish.

5.5.1 Symbiotic N_2 Fixation

5.5.1.1 Effects of Higher Atmospheric CO_2 Levels. The major effects of CO_2 enrichment are probably via indirect effects on the symbiotic organisms. Nitrogen-fixing organisms such as Rhizobium and Frankia have major requirements for energy provided as plant photosynthate. They in turn are the major organisms contributing N_2 to agricultural and natural ecosystems, respectively. Highly productive systems cannot be achieved or maintained until a large stock of organic matter is built up during a number of years of N_2 fixation. Early experiments with low light levels and with defoliation indicated that these treatments greatly affected the root-associated symbionts. Quantitative data concerning the effects of CO_2 concentrations are limited. Mulder and van Veen (1960) observed an increase in N_2 fixation when hydroponic culture solution was aerated with 40×10^3 ppm CO_2.

Hardy and Havelka's field experiment (1975) showed that over a nine-week period plants grown with supplemental CO_2 reduced five times as much C_2H_2 and had a greater mass of root nodules than untreated controls. Senescence of the N_2-enriched plants had significantly more nodules than untreated controls. Senescence of the N_2-fixing system was delayed. The work by Phillips et al. (1976) indicated that CO_2-enriched plants had significantly more nodules than the controls. However, CO_2 enrichment had no effect on the number of nodules which developed per unit dry weight of a pea plant and a linear regression existed between the number of root nodules and the dry weight of pea plants. They concluded that CO_2 enrichment resulted in an integrated growth of the entire plant with no special promotion of nodule growth, while Hardy and Havelka (1975) and Rogers et al. (1980) showed preferential fixation of N_2 vs. use of fixed N by CO_2 enrichment.

5.5.1.2 Partitioning of Photosynthates. Nitrogen fixation is a highly energy-intensive process and represents a significant sink for photosynthate (Phillips, 1980). Minchin and Pate (1973), in their classic study of C partitioning in nodulated legumes, found that approximately 10% of the fresh assimilate is used as a substrate for nitrogenase. This figure was later confirmed by Kucey and Paul (1982) in mycorrhizal hosts. Increased N input into the symbiotic association by the microsymbiont in turn stimulates plant growth and photosynthesis. The resulting

autocatalytic cycle (Bethlenfalvay et al., 1978) may
finally be limited by other factors.

5.5.1.3 Productivity. Two major effects on root and soil
processes will be produced by increased plant productivity.
Water and minerals will become even more limiting to
plants. This is especially true for nitrogen, because it
is frequently the most limiting nutrient, and nitrogen from
the mineralization of soil organic nitrogen will not
increase as rapidly as demand for crop production. Thus, the
need for fertilizer will increase more rapidly than
increases in productivity. This will also be expected for
nitrogen-fixing crops such as soybeans.

Thus, nitrogen fixation may increase faster than
productivity, due to the limited ability of the soil to
supply additional nitrogen. Associative and free-living
nitrogen fixers may be stimulated in the same way, but the
effect may be less since they are more dependent on soil
nitrogen concentration rather than plant demand. Mulching,
and increased soil organic matter content, expected to
occur under minimum tillage practices, may also have a
significant effect on N_2 fixation.

5.5.1.4 CO_2 Concentration in the Rhizosphere. The effects
of below-ground CO_2 may be different for host and endo-
phyte. Low concentration of soil CO_2 may be necessary for
optimal root growth, and higher concentrations can be
inhibitory, with peas being inhibited at CO_2 concentrations
as low as 15,000 ppm. At 65,000 ppm of CO_2, beans and
sunflowers are strongly inhibited, while barley and oats
are not (Stolwijk and Thimann, 1957). Under somewhat
different experimental conditions, 80,000 ppm CO_2 was
moderately inhibitory to both peas and barley (Geisler,
1967).

Removal of CO_2 from air is inhibitory to both the
nodulation of legumes and the growth of rhizobia in culture
(Mulder and van Veen, 1960; Lowe and Evans, 1962). The
effect of elevated CO_2 concentration is less clear. It has
been reported that nitrogenase activity, measured by
acetylene reduction, is not measurably different at 0 and
30,000 ppm CO_2 in pea and soybean nodules (Mahon, 1979;
Coker and Schubert, 1981). But in alders, 30,000 ppm CO_2
inhibits nitrogenase activity 20% (Winship and Tjepkema,
1982), while no consistent effect is found in soybean
nodules (Coker and Schubert, 1981). In peas, the
respiration of nodulated root systems is substantially
inhibited by 30,000 ppm CO_2, but this is apparently due to

inhibition of root respiration rather than to nodule
respiration (Mahon, 1979).

Increased CO_2 could lead to more productive rhizobia/
legume associations. In legumes, high concentrations of
CO_2 can increase root and nodule growth due to PEP-carboxy-
lase catalyzed carbon fixation. The fixed carbon serves as
a carbon skeleton for nitrogen fixation, and as an energy-
producing metabolic intermediate. CO_2 at sufficiently high
concentrations can be toxic to plant roots, but good growth
occurs even at 240,000 ppm CO_2, and thus increased
atmospheric CO_2 should not be a significant factor.

5.5.2 Nodulated Non-Legumes. Frankia, an actinomycete,
nodulates a relatively diverse group of wood dicotyledonous
plants including Alnus, Myrica gale, Shepherdia and
Casuarina. These N-fixing symbiotic associations are a
significant source of combined N in various ecosystems.
Since the plants are C_3, it is anticipated that an increase
in atmospheric CO_2 will increase rates of photosynthesis
and photosynthate for the nodule endophyte. This may
enhance total N_2 fixation and N input from these
associations.

5.5.3 Nitrogen-fixing associations. Nitrogen-fixing
bacteria occur in the rhizosphere of many plants, partic-
ularly in the tropics (Dart and Day, 1975; Neyra and
Dobereiner, 1977). Nitrogen balance studies for soil-grown
plants in pots containing measured amounts of combined
nitrogen, show that such bacteria may supply nitrogen for
plant growth. Studies with $^{15}N_2$ for sorghum, sugar cane,
Paspalum notatum, Digitaria decumbans and Setaria
italica confirmed that biologically fixed nitrogen was
transferred to the plant tops (DePolli et al., unpublished;
Wani, Day and Dart, unpublished).

More than 50 plant species from both temperate and
tropical environments, including agriculturally important
crops such as sorghum, pearl millet, setaria, maize, rice,
and wheat are known to stimulate nitrogenase activity in
their rhizospheres as measured by acetylene reduction
assays. For rice, sorghum, millet, setaria and Paspalum
notatum, there appears to be genotypic differences in
activity between lines (Dart and Wani, 1982).

The Broadbalk wilderness experiment at Rothamsted,
started in 1888, suggests that nitrogen fixation associated
with the roots of several weed species resulted in the
build up of soil organic matter, calculated to be 40 kg
N/ha/yr from fixation (Jenkinson and Rayner, 1977).

Other N balance field experiments in Brazil and India
suggest that biological nitrogen fixation contributes
significantly to the plant nitrogen economy. In India a
cross between Pennisetum purpureum and P. americanum
produced 136 tonnes/ha above ground dry matter in a low
fertility alfisol soil. The crop removed 1185 kg N/ha in
30 months, without addition of N fertilizer.

This nitrogen-fixing activity also plays an important
part in the nitrogen economy of estuarine communities and
for Spartina alterniflora in salt marshes, appears to
provide most of their nitrogen requirement (Buresh et al.,
1980). Nitrogen-fixing activity is generally stimulated by
high photosynthetic activity and by high soil moisture
(Dart and Wani, 1982). Both of these are likely to be
enhanced by higher atmospheric CO_2.

If the C to N ratio of the extra plant tissue derived
from increased photosynthetic activity does not change,
then this will create a greater demand for nitrogen, which
must be supplied either by fertilizer or by increased
nitrogen fixation.

5.5.3.1 Inoculation responses. Many different types of
nitrogen-fixing bacteria have been isolated from the
rhizosphere. Some, such as Azotobacter and Azospirillum,
can also influence plant growth by other means (Okon,
1982), perhaps by production of plant growth promoters and
by enrichment of mineral uptake. It is, however, difficult
to quantify the contribution of each process following
inoculation of plants with N_2-fixing bacteria.

Inoculation with N_2-fixing bacteria has increased the
yield of nitrogen and dry matter of a variety of cereal
crops in both pot and field experiements in Israel, India,
and Brazil (Okon, 1982; Dart and Wani, 1982; Boddey and
Dobereiner, 1982). Plants inoculated with Azospirillum
form associations with roots of cereals and forage grasses
which significantly increase mineral uptake (N, P and K) by
the roots and also contribute fixed nitrogen to the plant,
mainly during flowering (Okon, 1982). Significant
increases in yields were obtained in Azospirillum inoc-
ulated fields that received an intermediate level of
nitrogen fertilization at planting. Effects of this type
(N_2 fixation, enhancement of mineral uptake) associated
with rhizosphere bacteria such as Azospirillum, will be
further enhanced by the higher rate of root surface
activity resulting from higher photosynthate supply to the
roots. Furthermore, if the root respiration rates
increase, there may be a selection for bacteria that adapt

and are more efficient under microaerobic conditions, such as Azospirillum.

It is not clear if rhizosphere bacteria are specially active with C_4 plants compared with C_3 plants. Some promising Azospirillum isolates have been obtained from the roots of weeds. It will be important to know if high CO_2 will enhance weed growth more than that of crops. To exploit the potential of root associations with bacteria in agricultural systems will require careful management of any fertilizer additions to obtain maximum benefit under 600 ppm CO_2.

5.5.4 Azolla. Azolla is a floating aquatic fern which contains a cyanobacterium, Anabaena azolla, as a symbiont. Both partners are photosynthetic, and the cyanobacterium can provide the association with its total N requirement. Azolla is a C_3 plant with Calvin cycle intermediates, an O_2 inhibition of photosynthesis and an O_2 dependent CO_2 compensation point. Under optimized laboratory conditions these associations have been shown to double their biomass in 1.6 to 2.0 days and to contain 5-6% N on a dry weight basis. Under good field conditions, doubling times are on the order of 3-5 days with 4-5% N on a dry weight basis. These associations provide an alternative N source for rice. While both rice and Azolla may be expected to respond to CO_2 enrichment of the atmosphere, rice will require additional combined nitrogen if quality is maintained and yields enhanced. Azolla-Anabaena associations may play a significant role in meeting this additional N requirement for rice, and perhaps for other aquatic crops, such as taro.

5.6 Mycorrhiza. Mycorrhizae are symbiotic associations between the host-plant root and a mycorrhizal fungus. The fungi are generally referred to as ecto- or endomycorrhiza. These fungi belong to different classes of the Eumycota. Ectomycorrhizae (ECM) generally colonize woody plant species and are important in forest ecology. Endomycorrhizal fungi are mostly categorized as "vesicular-arbuscular" because of their distinctive morphological characteristics. This latter category colonizes practically all native and agricultural plant species except species belonging to the orders Caryophyllales, Polygonales, and Capparales (Gerdemann, 1968). Ectomycorrhizae are generally biotrophic, but often can be grown in pure culture. Vesicular-arbuscular mycorrhizal (VAM) fungi are obligate biotrophs. They lack host specificity, and some species are world-wide in distribution.

5.6.1 Inoculum. Vesicular-arbuscular mycorrhizal fungi
have not yet been cultured under axenic conditions in the
absence of a host plant, in spite of considerable research
efforts in several laboratories. Efforts are being made to
produce VAM fungi for large-scale inoculation by soil
culture (J. Menge, personal communication) and by a
nutrient-film technique (Rothamsted Report, 1981).

Some data are available which indicate that certain
host-endophyte combinations are more effective than others,
in spite of a general lack of host specificity. The
effectiveness of VAM fungi appears to be more affected by
soil characteristics than by compatibility with any
specific host plant (Mosse, 1975).

Inoculation of field crops with VAM fungi may be
successful when native soil populations are sparse or
consist of relatively ineffective species (Hayman, 1974).
Yield or plant growth increases resulting from field
inoculations have been reported by Black and Tinker (1977).
Inoculation of cowpea with Rhizobium and chopped roots of
a mycorrhizal native grass was carried out in a Brazilian
oxisol by S.M. LaTorraca and T.V. St. John (unpublished
data). Yield of VAM plants in five fertilization
treatments were up to twice those of controls that received
sterilized grass roots and live Rhizobium.

Field inoculations of ectomycorrhizal fungi already
play an important role in establishment of exotic forest
species and reclamation of mine spoils and other unfavor-
able sites (Marx and Krupa, 1978). Thus, techniques
already exist that would allow new ectomycorrhizal fungi to
be introduced as needed to deal with changing conditions
brought about by increasing atmospheric CO_2.

5.6.2 Development. Effects of CO_2 on aerial portions
of the plant (increased photosynthesis) can be expected to
favorably influence the mycorrhizal symbiosis (Hayman,
1974). Competition for carbohydrates by the symbiosis
under limiting light intensity was shown to result in
growth depression of the host plant (Bethlenfalvay et al.,
1982b). The development of host and VAM endophyte appear
to be interrelated ontogenetically with source-sink
relationships as a controlling factor (Bethlenfalvay et
al., 1982a, 1982b). A possible increase in world mean
temperature might influence fungal physiology (Furlan and
Fortin, 1973; Hayman, 1974). Spore germination, infection,
proliferation and sporulation of mycorrhizal fungi all
depend on favorable environmental conditions. Some
environmental factors to which VAM fungi are particularly

sensitive are pH, temperature, and excess water (Mosse et al., 1981).

The presence of decomposing soil organic particles stimulates the proliferation of VAM extra-matrical mycelium (St. John et al., submitted). Since soil hyphae are able to initiate new VAM infection points (Powell, 1976), the presence of increased soil organic matter may encourage more rapid spread of VAM. The direct effects of CO_2 on mycorrhizae have not been studied.

Saif (1981) examined the effect of oxygen concentration on mycorrhizal infection and plant growth response. He found that plants responded better to VAM at CO_2 concentrations of 12 and 16% than at 21%. His artificial atmosphere did not contain even the normal ambient amount of CO_2. His techniques could be used to study CO_2 effects, and work at Rothamsted Experiment Station has apparently shown VAM infection to respond favorably to small increases in CO_2 concentration (B. Mosse, personal communication).

ECM fungi have been studied only slightly more than VAM fungi. Telson et al. (1980) reported that the difference in growth of mycorrhizal and non-mycorrhizal Pinus sylvestris was greater under conditions of higher CO_2 concentration. The growth of the mycorrhizal fungus Pisolithus tinctorius in pure culture was improved by higher than normal CO_2 concentrations.

Read and Armstrong (1972) showed that formation of the mantle of ECM in certain conifers is dependent on transport of oxygen through roots. They noted that oxygen can be very deficient in coniferous humus layers and suggested that mycorrhizal function in the humus environment is dependent on diffusion of O_2 from host roots. If they are correct, ECM establishment and function may be essentially independent of ambient CO_2 levels in nature.

Destruction of native vegetation, the main consumer of CO_2, sometimes has the additional effect of the modification or destruction of mycorrhizal inocula (Reeves et al., 1979). Successional vegetation or agricultural and ornamental species subsequently occupying the site may be strongly influenced by the lack of inocula (Janos, 1980). One consequence is likely to be reduced production on that site, and therefore O_2 production and CO_2 consumption.

5.6.3 Effect on Plant Growth. Most of the P present in mineral soils is precipitated as the aluminum or iron

salt in acid soils and as the calcium salt in alkaline
soils (Focht and Martin, 1979). Only a small fraction of
the total P present in a soil may be available to plants.
As a result, P is one of the major factors which limit
plant growth under natural and cultural conditons.
Mycorrhizal fungi may significantly increase the uptake of
P and other relatively immobile nutrients, such as Zn and
Cu, by their host plants (Hayman, 1978). The mechanism for
this phenomenon is a thorough permeation of the soil volume
availabe to the host by the extra-matrical fungal mycelium,
which can reach soil microsites not exploited by the host
alone (Tinker, 1978). In addition, mycorrhizae release
oxylate which, in turn, causes the release of some
additional nutrients from soil minerals (Graustein et al.,
1977).

5.6.4 Effect on Water Uptake. The effect of mycor-
rhizal fungi on plants when water is the major limiting
factor may be significant, but is not well known (Trappe,
1981). While few crop plants will survive when soil water
potential is below -15×10^5 Pa (Hall et al., 1979), many
fungi and bacteria will thrive at values far below this
(Focht and Martin, 1979). Of particular interest in this
respect are VAM, which appear to be common in desert plants
(Trappe, 1981; Bethlenfalvay, unpublished data).
Modification of plant water status by VAM may result in
increased rates of photosynthesis under intermittent
drought conditions, thus providing a better sink for CO_2.
The mechanism of enhanced water uptake by mycorrhiza is
controversial. Higher rates of P uptake and the improved
nutritional status of mycorrhizal plants have been
implicated as the causal factors (Safir et al., 1972).
More recent work, some of which was reviewed by Hardie and
Leyton (1981), suggests that VAM may help plants acquire
soil water not available to uninfected plants.

5.6.5 Respiratory Cost. Mycorrhizae growth could be
limited by high soil CO_2 concentrations. VAM may represent
up to 20% of the dry weight of the fungus-root association
(Bethlenfalvay et al., 1982d). As respiration by fungi is
2 to 4 times higher than that of vascular plant tissue, and
as CO_2 evolution by mycorrhizae is probably enhanced by
infection respiration (Cooke, 1977), total respiration
rates in mycorrhizae may be up to twice as high as in roots
not colonized by VAM fungi. Increases in above-ground
biomass may therefore be translated into below-ground
respiration rates considerably higher than those found in
experimentation with nonmycorrhizal plants under controlled
conditions.

5.6.6 Effect on N_2 fixation. There are close linkages
between organic C and N accumulation in mature soils and P
contents in the original parent materials. Microbial
growth processes are the principal arena for the adjustment
of N supply to the supply of P (Cole and Heil, 1981). The
availability of P is crucial to N_2 fixation, a process
which has a many-fold higher requirement of P than does
the host plant (Mosse, 1976). Thus the availability of P
is a factor which may determine the rate at which N_2
fixation will be able to accommodate the increased N
requirements of plants growing at a higher CO_2
concentration. Increased uptake of P by mycorrhizal fungi
has been shown to enhance symbiotic N_2 fixation
(Bethlenfalvay and Yoder, 1981) and associative N_2 fixation
(Bagyaraj and Menge, 1978). These processes may therefore
occupy a key position in modifying and controlling the flux
of P and N to plants experiencing enhanced growth due to
CO_2 fertilization.

5.7 Effects on Plant Pathogens

5.7.1 Fungus. Elevation of CO_2 concentration in the
atmosphere and in soil may affect fungal development.
Fungal species such as Sclerotinia minor and Phytophthora
infestans are quite sensitive to CO_2. Species like
Penicillium nigricans, Cochliobolus sativus and many
species of Fusarium are quite tolerant of high CO_2. A
rapid increase in CO_2 may have an adverse effect on some of
the fungi, and changes in the compostion of the fungal
community would be expected. This phenomenon might be
observed in soil pores and microsites which contain a high
concentration of entrapped CO_2 gas. However, given the
adaptative capabilities of microorganisms, a gradual
increase of CO_2 concentration over a long period of time
may cause little overall change to the species present,
and/or their growth.

Extremely high CO_2 concentrations (200,000 ppm or
more) inhibit the hyphal growth of fungi, but sporulation
and development of fruiting bodies (morphogenesis) seems to
be much more sensitive to CO_2. In mushrooms, for instance,
production can be improved by manipulating CO_2. At a high
CO_2, the pathogenicity of Rhizoctonia solani and
Sclerotium rolfsii is reduced. High CO_2 can also
reduce losses by inhibiting the growth of fruit-rotting
fungi on fruits and vegetables.

5.7.2 Bacteria and other plant pathogens. Effects of
doubling the CO_2 in the atmosphere on the growth and
community composition of plant pathogenic bacteria may be

important because bacteria can survive from season to season by living in decaying plant tissues. Hence, the return of extra plant residues to soil may increase the population of pathogens as well as useful organisms.

For other plant pathogens -- virus, mycoplasma, rickettsia, etc. -- that are closely associated with the host system, little direct effect can be expected from increased CO_2 in the atmosphere.

6. Management Options

Direct effects of increased CO_2 levels are not considered to be of major significance on microbial soil activity. This conclusion is based on the assumption that soil CO_2 will not be significantly increased by a doubling of atmospheric CO_2. Photosynthetic microorganisms on the soil surface will be unaffected by increased CO_2 because they already possess a CO_2 pumping system.

Indirect effects of increased atmospheric CO_2 as the result of increased plant productivity will strongly affect microbial soil activity which in turn will control the extent of the crop productivity that is realized. Management of the soil system including the application of existing and yet to be developed technologies will be key to the degree of crop productivity that is realized. Furthermore, some of these technologies, such as minimum tillage, provide models to study the impact of increased crop production.

Techniques such as minimum tillage greatly reduce erosion and the requirements of energy for cultivation. They increase the potential for crop growth and for stabilization of soil organic matter (Phillips et al., 1980). The plant cover and absence of physical disturbance produces a 2°-6°C drop in soil temperature, while soil moisture and aggregate stability are maintained. Minimum tillage in the U.S. is projected to increase from 2.2 Mha in 1974 to 62 Mha, or 45% of the total U.S. cropland, by 2000. At Sydney, Montana, minimum tillage maintained soil organic matter at the level of a virgin grassland site, while conventional tillage reduced organic matter content by 20%. The nitrogen requirement, at least in the short term, is increased, possibly due to increased immobilization and/or losses due to denitrification. Phosphate requirements in minimum tillage may parallel those of nitrogen.

The 1,600 - 2,000 Mha of potentially available land in

the tropics that is subject to rapid decomposition rates
and erosion may benefit from minimum tillage. At present, 60%
of this area is devoted to shifting cultivation. Manage-
ment and maintenance of soil organic matter levels are
essential for erosion control, water penetration, buffering
against acidification, blocking P absorbing sites, and as a
nutrient reservoir. An organic matter increase of 625
kg/ha for annual pastures and 1150 for perennial pastures
has been observed in Australia. Bush fallow produces
similar increases. Residue mulch - minimum tillage has
maintained tropical soil and temperate organic matter
levels 20% above those under conventional tillage.

6.2 Intercropping, Multiple Cropping, Green Manures.
The use of legumes for intercropping, multiple cropping or
as green manures is a management option for nitrogen
provision. Combination of hairy vetch in minimum tillage
maize production is an example. Hairy vetch grown during
the winter periods in Kentucky and other southern states
not only decreases soil erosion and weed growth, but has
the potential for supplying 100-200 kg N/ha to the
following corn crop. The use of a herbicide at the time of
maize growth and the perennial nature of hairy vetch
enables the cycle vetch-maize-vetch.

6.3 Microorganism Addition. Phosphorus limitation
and aluminum toxicity inhibit plant growth in a vast area
of tropical savanna such as the cerrado of Brazil (Sanchez
et al., 1982a). Mycorrhizal fungi, as discussed earlier,
have the potential to cause major increases in P uptake
under tropical conditions of both upland and lowland crops
(Islam et al., 1980; Tinker, 1982). Mycorrhizal
inoculation coupled with their increased activity from
increased crop production will impact positively on these
large areas. Systems for production and inoculation with
preferred mycorrhizal strains are needed. Mycorrhizal
research is needed to provide management options for P
input.

After phosphorus, nitrogen is probably the most
important nutrient for increased crop productivity by
increased CO_2. Several management options exist. In the
case of legumes, inoculation with the most effective
N-fixing microbe will continue to be most important. The
criteria for strain selection are ability to successfully
compete with ineffective indigenous rhizobia, ability to
nodulate the host plant, and ability to efficiently convert
N_2 to ammonia. Similar approaches are being used with
Frankia for the non-legume N_2-fixing trees. Other options
exist for other crops. The Azolla-Anabaena association is

being evaluated as an intercrop with paddy-grown rice.
Some management changes may be needed to optimize nitrogen
input by this system, since in the presence of elevated CO_2
the canopy may close earlier than it does now. The
associative N_2-fixing systems such as between cerial grains
and Azospirillum have been shown to definitely increase
crop yield in at least a few locations (see Section 5.5.3).
Azospirillum inoculation may evolve as a management option
for increasing nitrogen input.

6.4 New Technology Inputs. Manipulation of genetic
materials of both host and microbial symbionts has great
potential to provide new options for increased productiv-
ity. The rate of scientific advances in molecular genetics
has been great relative to the modest rate of increase in
atmospheric CO_2. It is thus reasonably safe to assume that
this evolving technology will obviate many of the limita-
tions of existing technologies.

     A discussion of possible relevant molecular genetic
inputs follows. The time required for most of these
technological advances is longer than many have suggested,
but the advances within the next 25 years should be great.
Molecular genetic manipulations of the N_2 fixation system
pose some of the most difficult challenges in agriculture
because of the high multiplicity of the genes and because
of the sensitivity of nitrogenase to O_2.

     With the above qualifications, the potentials for
genetic manipulation in N_2 fixation and denitrification
will be considerable. Genetic studies have defined many of
the nitrogen fixation genes in blue-green algae, in free-
living organisms, and in Rhizobium, and the genes respon-
sible for nodulation are similarly being characterized.
Improved versions of these genes will be developed and
transferred among strains. Rhizobium which most effic-
iently fix nitrogen may be transformed to become the more
effective nodulators, and, reciprocally, strains which
dominate in the field may be the recipients of improved
nitrogen fixation genes. Nodulation genes could also be
transferred among Rhizobium strains in order to alter their
host specificity. Alternatively, nitrogen fixation genes
could be moved into mycorrhiza or perhaps even plants.

     Following parallel lines of experimentation, nodula-
tion and association genes could be transferred to associa-
tive bacteria. Identification of the plant genes necessary
for these interactions will allow new plant hosts to be
developed through genetic transfer of the plant symbiosis
genes. Of particular interest in this regard would be both

transferring symbiosis genes to crop plants such as corn
and wheat, and transferring stem nodulation genes from
peanuts, Sesbania, or Aeschynemene to new hosts. Stem
nodules might be less susceptible to soil nitrate/ammonia
inhibition and might be more able to take advantage of more
CO_2.

The problem of denitrification may similarly yield to
genetic solutions. The genes that produce N_2O uptake
enzymes could be altered to increase their affinities for
N_2O. They could then scavenge N_2O and reduce it before its
escape to the atmosphere.

Finally, opportunities will arise to create strains
with novel synthetic enzymes. Hybrid genes are now being
created by splicing segments of different genes together,
and we can expect that novel nitrogenase genes will also be
formed through gene synthesis and gene splicing. Such
constructions should yield nitrogen-fixing enzymes that bear
little resemblance to the present enzymes. One purpose for
generating such modified enzymes would be to fix nitrogen
to products other than ammonia. Many more such opportuni-
ties to create novel enzymes will undoubtedly present
themselves. These technologies will greatly expand the
management options in the coming decades.

9. Literature Cited

Atjay, G.L., P. Ketner and P. Duvigneaud. 1979. Terrestrial
    primary production and phytomass. In Scope 13, The
    Global Carbon Cycle, B. Bolin, E.T. Degens, S. Kempe
    and P. Ketner, Eds., John Wiley and Sons, New York,
    pp. 129-181.

Bagyaraj, D.J. and J.A. Menge. 1978. Interaction between a
    VA mycorrhiza and Azotobacter and their effects on
    rhizosphere microflora and plant growth. New Phytol.
    80, 567-573.

Bauer, A. and A.L. Black. 1981. Soil carbon, nitrogen and
    bulk density comparisons in two crop plant tillage
    systems after 25 years and in virgin grasslands. Soil
    Sci. Sco. Am. J. 45, 1166-1170.

Berry, J., J. Boynton, A. Kaplan, and M. Badger. 1976.
    Growth and photosynthesis of Chlamydomonas reinhardii
    as a function of CO_2 concentration. Carnegie Institute
    Year Book. 75, 423-432

Bethlenfalvay, G.J. S.S. Abu-Shakra, and D.A.

Phillips, 1978. Interdependence of nitrogen
and photosynthesis in Pisum Sativum L. II.
Host plant response to nitrogen fixation by
Rhizobium strains. Plant Physiol. 62, 131-133.

Bethlenfalvay, G.J. and J.F. Yoder. 1981. The Glycine-
Glomus-Rhizobium symbiosis. Physiol. Plant. 52,
141-145.

Bethlenfalvay, G.J., M.S. Brown, and R.S. Pacovsky. 1982a.
Relationships between host and endophyte development
in mycorrhizal soybeans. New Phytol. 90, 537-543.

Bethlenfalvay, G.J., R.S. Pacovsky, M.S. Brown, and G.
Fuller. 1982b. Mycotrophic growth and mutualistic
development of host plant and fungal endophyte in an
endomycorrhizal symbiosis. Plant Soil (in press).

Bethlenfalvay, G.J., R.S. Pacovsky, H.M. Bayne, and A.
Stafford. 1982c. Interactions between N_2 fixation
mycorrhizal colonization and host plant growth in the
Phaseolus-Rhizobium-Glomus symbiosis. Plant Physiol.
(in press).

Bethlenfalvay, G.J., R.S. Pacovsky, and M.S. Brown. 1982d.
Parasitic and mutualistic associations between a
mycorrhizal fungus and soybean: development of the
endophyte. Phytopathology. 72, 894-897.

Bidwell, R.G.S. 1977. Photosynthesis and light and dark
respiration in fresh water algae. Can. J. Bot.
55, 809-818.

Black, R.L.B. and P.B. Tinker. 1977. Interaction between
effects of vesicular-arbuscular mycorrhiza and
fertilizer phosphorus on yields of potatoes in the
field. Nature 267, 510-511.

Boddey, R.M. and G. Dobereiner. 1982. Association of
Azospirillum: Other diazotrophs with tropical
Gramineae. 12th Intl. Congress of Soil Science. New
Delhi, India, Feb. 8-16, 1982. Symposia Papers pp.
23-47.

Bolin, B., E.T. Degen, S. Kempe and P. Ketner, Eds. 1979.
The Global Carbon Cycle. John Wiley and Sons, New
York.

Buresch, P.J., M.E Casselman and W.H. Patrick, Jr. 1980.

Nitrogen fixation in flooded soil systems, a review. Adv. Agron. 33, 149-192.

Coker, G.T. and K. Schubert. 1981. Carbon dioxide fixation in soybean roots and nodules. Plant Physiol. 67, 691-696.

Cole, C. V. and R. D. Heil. 1981. Phosphorus effect on terrestrial nitrogen cycling. In F. E. Clark and T. Rosswell, Eds, Terrestrial N-Cycles Ecological Bulletin. Vol. 3. Stockholm, pp. 363-374.

Coleman, D.C. 1973. Compartmental analysis of "total soil respiration": an exploratory study. Oikos 24, 361-366.

Cooke, R. 1977. The Biology of Symbiotic Fungi. John Wiley and Sons, London.

Dart, P.J. and J.M. Day. 1975. In Non-symbiotic Nitrogen Fixation, N. Walker, Ed. John Wiley and Sons, New York, pp. 225-252.

Dart, P.J. and S.D. Wani. 1982. Nonsymbiotic nitrogen fixation and soil fertility. In The Tropics Trans. 12th Intl. Congress of Soil Science 1, 3-27.

de Jong, E. and E.A. Paul. 1979. The composition of the soil atomsphere and its relationship to soil aeration and respiration. In Encyclopedia of Earth Science Series. Vol. VI. Soil Science and Applied Geology. O.W. Finkle, Jr., Ed. Reinhold Book Corp., New York.

de Jong, E., H.J.V. Schappert and K.B. MacDonald. 1974. Carbon dioxide evolution from virgin and cultivated soil as affected by management practices and climate. Canadian J. Soil Sci. 54, 299-307.

Denmead, O.T. and E.R. Lemon. 1970. Prediction and measurement of photosynthetic activity. Wageningen Center for Agricultural Publishing and Documentation, pp. 149-164 and 199-205.

De-Polli, H., M. Eiichi and J. Dobereiner. 1977. Confirmation of nitrogen fixation in two tropical grasses by molecular nitrogen 15 incorporation. Soil Biol. Biochem. 9, 119-123.

Dreyfus, B.L. and J.R. Dommergue. 1981. Nitrogen fixing nodules induced by Rhizobium on the stem of tropical legume Sesbania rostrata. FEMS Lett. 10, 313-317.

Focht, D.D. and J.P. Martin. 1979. Microbiological and biochemical aspects of semi-arid agricultural soils. In Agriculture in Semi-Arid Environments, A.E. Hall, G.H. Cannel and H.W. Lawton, Eds. Springer-Verlag, Berlin, pp. 119-147.

Furlan, V. and J.A. Fortin. 1973. Formation of endomycorrhizae by Endogone calospora on Allium cepa under three temperature regimes. Nat. Can. 100, 467-477.

Garrett, S.D. 1981. Soil Fungi and Soil Fertility. Pergamon Press, Oxford.

Geisler, G. 1967. Interactive effects of CO_2 and O_2 in soil on root and top growth of barley and peas. Plant Physiol. 42, 305-307.

Gerdemann, J.W. 1968. Vesicular-arbuscular mycorrhiza and plant growth. Ann. Rev. Phytopathol. 6, 397-418.

Goswami, K. and V.K. Suri. 1982. Carbon fertilization: Influence of simulated field soil respiration on soybean crop. Proc. 12th ISSS Congress, Delhi.

Goudriaan, J. and G.L. Ajtay. 1979. The possible effects of increased CO_2 on photosynthesis. In The Global Carbon Cycle, B. Bolin, E.T. Degens, S. Kempe and P. Ketner, Eds. John Wiley and Sons, New York, pp. 237-250.

Grable, A.R. 1966. Soil aeration and plant growth. Adv. Agron. 18, 57-106.

Graustein, W.C., K. Cromack and P. Sollins. 1977. Calcium oxalate: Occurrence in soils and effect on nutrient and geochemical cycles. Science. 198, 1252-1254.

Greenwood, D.J. 1970. Distribution of carbon dioxide in the aqueous phase of aerobic soils. J. Soil Sci. 21, 314-329.

Griffin, D.M. 1972. Ecology of Soil Fungi. Syracuse Univ. Press., Syracuse, N.Y.

Hall, A.E., K.W. Foster and J.G. Waines. 1979. Crop adaptation to semi-arid environments. In Agriculture in Semi-Arid Environments, A.E. Hall, G.H. Cannell and H.W. Lawton, Eds. Springer-Verlag, Berlin, pp. 148-179.

Hardie, K. and L. Leyton. 1981. The influence of
vesicular-arbuscular mycorrhiza on growth and water
relations of red clover. I. In phosphate deficient
soil. New Phytol. 89, 599-608.

Hardy, R.W.F. and U.D. Havelka. 1975. Photosynthate
as a major factor limiting N_2 fixation by field grown
legumes with emphasis on soybeans. In Symbiotic
Nitrogen Fixation in Plants, R.S. Nutman, Ed.,
Cambridge University Press, London, pp. 421-439.

Havelka, U.D. and R.W.F. Hardy. 1976. Legume N_2 fixation
as a problem in carbon nutrition. In Nitrogen
Fixation, W.E. Newton and C.J. Nyman, Eds., Vol. 2.,
Washington State Univ. Press, pp. 456-475.

Hayman, D.S. 1974. Plant growth responses to vesicular-
arbuscular mycorrhiza. VI. Effect of light and
temperature. New Phytol. 73, 71-80.

Idso, S.B. 1981. Carbon dioxide – an alternative view. New
Scientist 92, 444-446.

Idso, S.B. and B.A. Kimball. 1982. Man, carbon dioxide,
climate and food: A global perspective. Symposium on
Plant Production Under Drought Conditions. Tulsa, OK.

Islam, R., A. Ayanaba and F.E. Sander. 1980. Response of
cowpea (Vigna unguiculata) to inoculation with VA
mycorrhizal fungi and to rock phosphate fertilization
in some unsterilized Nigerian soils. Plant and Soil
54, 107-117.

Janos, D.P. 1980. Mycorrhizae influence tropical
succession. Biotropica 12 (Supplement), 56-64.

Jenkinson, D.S. and J.H. Rayner. 1977. The turnover of soil
organic matter in some of the Rothamsted classical
experiments. Soil Sci. 123, 298.

Jenkinson, D.S. and J.W. Ladd. 1980. In Soil Biochemistry,
Vol. 5, E.A. Paul and J.W. Ladd, Eds., Marcel Dekker,
New York.

Johnen, B.G. 1974. Bildung, Menge und Umsetzung von
Pflanzenwurzein im Boden. Agrikulturchemischen
Institut der Rheinishchen Friedrich-Wilhelms-
Universitat, Bonn.

Kaplan, A., D. Zenvirth, L. Reinhold and J.A. Berry. 1982.

Involvement of a primary electrogenic pump in the mechanism for HCO_3^- uptake by the cyanobacterium Anabaena variablis. Plant Physiol. 69, 978–982.

Karagouni, A.D. and J.H. Slater. 1978. Growth of the blue-green alga Anacystis nidulans during washout from light- and carbon dioxide-limited chemostats. FEMS Microbiol. Lett. 4, 295–299.

Kimmins, J.P., J. de Catanzaro and D. Binkley. 1979. Tabular summary of data from the literature on the biogeochemistry of temperate forest ecoystems. ENFOR Project P-8 Report, Faculty of Forestry, Univ. of British Columbia, Vancouver, British Columbia, p. 104.

Kramer, P.J. 1981. Carbon dioxide concentration, photosynthesis, and dry matter production. BioScience 31, 29–33.

Kucey, R.M.N. and E.A. Paul. 1982. Carbon flow, photosynthesis and N_2 fixation in mycorrhizal and nodulated faba beans (Vicea faba L.). Soil Biol. Biochem., in press.

Lal, R. and B.T. Kang. 1982. Management of organic matter in soils of the tropics and subtropics. Proc. 12th ISSS Congress, Delhi. 1, 152.

Lindsay, W.L. 1979. Chemical Equilibria in Soil. John Wiley and Sons, New York.

Lipschultz, F., O.C. Zafiriou, S.C. Wofsy, M.B. McElroy, F.W. Valoris and S.W. Watson. 1981. Production of NO and N_2O by soil nitrifying bacteria. Nature 294, 641–643.

Lloyd, N.D.H., D.J. Canvin and D.A. Culver. 1977. Photosynthesis and photorespiration in algae. Plant Physiol. 59, 936–940.

Lowe, R.H. and H.J. Evans. 1962. Soil Science 94, 351–356.

Luxmoore, R.J. 1981. CO_2 and phytomass. BioScience 31, 626.

Lynch, J.N. 1978. Productivity and phytotoxicity of acetic acid in anaerobic soil and plant residues. Soil Biol. Biochem. 10, 131–135.

Macauley, B.J. and D.M. Griffin. 1969. Effects of carbon dioxide and oxygen on the activity of some soil fungi. Trans. Brit. Mycol. Soc. 53, 53–62.

Mahon, J.D. 1979. Plant Physiol. 63, 892-897.

Marx, D.H. and S.V. Krupa. 1978. Mycorrhizae. A. Ectomy-
    corrhizae. In Interactions between Non-pathogenic Soil
    Microorganisms and Plants. Y.R. Dommergues and S.V.
    Krupa, Eds. Elsivier Scientific Publishing Co.,
    Amsterdam, pp. 373-400.

McKenney, D.J., K.F. Shuttleworth, J.R. Vriesacker and
    W.I. Findlay. 1982. Production and loss of nitric
    oxide from denitrification in anaerobic Brookston
    clay. Appl. Environ. Microbiol. 43, 534-541.

Melillo, J.N., J.D. Aber and J.F. Muratore. 1982. Nitrogen
    and lignin control of hardwood leaf litter
    decomposition dynamics ecology (in press).

Minchin, F.R. and J.S. Pate. 1973. The carbon balance of a
    legume and the functional economy of its nodules.
    J. Exp. Bot. 24, 259-271.

Moore, A.W. 1969. Azolla: biology and agronomic
    significance. Bot. Rev. 35, 17-34.

Mosse, B. 1975. Specificity in VA mycorrhizas. In
    Endomycorrhizas, F.E. Sanders, B. Mosse and P.B.
    Tinker, Eds., Academic Press, London. pp. 469-484.

Mosse, B. 1976. The role of mycorrhiza in legume nutrition
    on marginal soils. In Exploiting the Legume-
    Rhizobium Symbiosis in Tropical Agriculture, J.M.
    Vincent, A.S. Whitney and J. Vose, Eds., Coll. Trop.
    Agri. Misc. Publ. 145. Univ. Hawaii, pp. 275-292.

Mosse, B., D.P. Stribley and F. Le Tacon. 1981. Ecology
    of mycorrhizae and mycorrhizal fungi. Advances in
    Microbial Ecology 5, 137-210.

Mulder, E.G. and W.L. van Veen. 1960. The influence of
    carbon dioxide on symbiotic nitrogen fixation. Plant
    and Soil 13, 265-278.

Newton, W., J.R. Postgate, and C. Rodriguez-Barrueco. 1977.
    Recent Developments in Nitrogen Fixation. Academic
    Press, London.

Neyra, C.A. and J. Dobreiner. 1977. Nitrogen fixation
    in grasses. Adv. Agron. 29, 1028.

Nye, P.H. and P.B. Tinker. 1977. Solute movement in the

soil-root system. University of California Press,
Berkeley.

Okon, Y. 1982. Azospirillum: Physiological properties,
    mode of association with roots and its application
    for the benefit of cereal and forage grass crops.
    Special volume on Nitrogen Fixation. Israel Journal
    of Botany, in press.

Patrick, W.H. 1977. Oxygen content of soil air by a field
    method. Soil Sci. Soc. Am. J. 41, 651-652.

Payne, W.J. 1981. Denitrification. Wiley-Interscience, New
    York.

Peters, G.A. and H.E. Calvert. 1982. The Azolla-Anabaena
    Symbiosis, Chapter in Algal Symbiosis: A Continuum
    of Interaction Strategies. Sponsored by the
    Phytological Society of America, Cambridge
    University Press (in press).

Phillips, D.A., K.D. Newell, S.A. Hassell, and C.E.
    Felling. 1976. The effect of CO_2 enrichment on root
    nodule development and symbiotic N_2 reduction in
    Pisum sativan L. Amer. J. Bot. 63, 356-362.

Phillips, R.E., R.E. Blevins, G.W. Thomas, W.W. Frye and
    S.G. Phillips. 1980. No tillage agriculture. Science
    208, 1108-1113.

Phillips, D.A. 1980. Efficiency of nitrogen fixation in
    legumes. Ann. Rev. Plant Physiol. 31, 29-49.

Powell, C.L.I. 1976. Development of mycorrhizal infections
    from Endogone spores and infected root segments.
    Trans. Brit. Mycol. Soc. 66, 439-445.

Rabinowitch, E.I. 1951. Photosynthesis, Vol.
    II, Part I.   Interscience Publishers Inc.,
    New York, p. 886.

Read, D.J. and W. Armstrong. 1972. A relationship between
    oxygen transport and the formation of the ectotrophic
    mycorrhizal sheath in conifer seedlings. New Phytol.
    71, 49-53.

Reeves, F.B., D. Wagner, T. Moorman and J. Kiel. 1979.
    The role of endomycorrhizae in revegetation practices
    in the semi-arid West. I. A comparison of incidence
    of mycorrhizae in severely disturbed vs. natural
    environments. Am. J. Bot. 66, 6-13.

Reichle, D.E., B.E. Dinger, N.T. Edwards, W.F. Harris
     and P. Sollins. 1973. Carbon flow and storage in a
     forest ecosystem. In G.M. Woodwell and E.V. Pecan
     Eds., Proc. of the Symposium in Biology, Upton, New
     York.

Rogers, P.A. and S.A. Kulasooriya. 1980. Blue-green algae
     and rice. The International Rice Research Institute,
     Los Banos, Laguna, Phillipines.

Rogers, H.H., G.E. Bingham, J.D. Cure, W.W. Heck, A.S.
     Heagle, D.W. Israel, J.M. Smith, K.A. Surano, and
     J.F. Thomas. 1980. Response of vegetation to carbon
     dioxide. U.S. Department of Energy and U.S.
     Department of Agriculture Joint Publication.

Russell, E.W. 1973. Soil conditions and plant growth.
     10th ed. Longmans, London, Chapter 18.

Safir, G., J.S. Boyer and J.W. Gerdemann. 1972. Nutrient
     status and mycorrhizal enhancement of water transport
     in soybean. Plant Physiol. 49, 700-703.

Saif, S.R. 1981. The influence of soil aeration on the
     efficiency of vesicular-arbuscular mycorrhizae.
     I. Effect of soil oxygen on the growth and mineral
     uptake of Eupatorim odoratum L. innoculated with
     Glomus macrocarpus. New Phytol. 88, 649-659.

Sanchez, P.A., D.E. Bandy, J.F. Villachica and J.J.
     Nicholaides. 1982a. Amazon basin soils: Management for
     continuous crop production. Science 216, 821-827.

Sanchez, P.A., M.P. Gichuru and L.B. Katz. 1982b. Organic
     matter in major soils of the tropical and temperate
     regions. Proc. 12th ISSS Congress, Delhi. 1, 99.

Schwartz, D.M. and F.A. Bazzaz. 1973. In situ measurements
     of carbon dioxide gradients in a soil-plant-
     atmosphere system. Oecologia 12, 161-167.

Shivashankar, K., K. Vlassak and J. Livens. 1976. A
     comparison of the effect of straw incorporation and
     carbon dioxide enrichment on the growth, nitrogen
     fixation and yield of soybeans. J. Agric. Sci. 87,
     81-85.

Smith, A.M. and D.M. Griffin. 1971. Oxygen and the ecology
     of Armillariella elegans Heim. Austr. J. Biol. Sci.
     24, 231-262.

Stewart, W.D.P. 1975. Nitrogen fixation by free-living
    organisms. Cambridge Univ. Press.

Stolwijk, J.A. and K.V. Thimann. 1957. On the uptake of
    carbon dioxide and bicarbonate by roots, and its
    influence on growth. Plant Physiol. 32, 513-520.

Subba Rao, N.S. 1977. Nitrogen deficiency as a world-wide
    problem. In A Treatise on Nitrogen Fixation,
    R.W.F. Hardy and A.H. Gibson, Eds. John Wiley and
    Sons, New York, pp. 3-32.

Swank, W.T. and J.B. Waide. 1980. Interpretations of
    nutrient cycling research in a management context:
    Evaluating potential effects of alternative
    management strategies on site productivity. In
    Forests: Fresh Perspectives from Ecosystem Analysis,
    R.W. Waring, Ed. Oregon State University Press,
    Corvallis, pp. 137-158.

Telson, M., I.A. Leone and F.B. Flower. 1980. The role of
    an ectomycorrhizal fungus Pisolthus tinctorius in
    the survival and growth of scots pine subjected to
    landfill conditions. (Abstr.) Phytopathology 70, 470.

Tinker, P.B. 1978. Effects of vesicular-arbuscular
    mycorrhizae on plant nutrition and plant growth.
    Physiol. Veg. 16, 743-751.

Tinker, P.B. 1982. Mycorrhizas: The present position. In
    Whither Soil Research. Trans. 12th Intl Congress of
    Soil Science. New Delhi. 5, 140-166.

Trappe, J.M. 1981. Mycorrhizae and productivity of arid
    and semi-arid rangelands. In Advances in Food
    Producing Systems for Arid and Semi-Arid Lands. Acad.
    Press, London, pp. 581-599.

van Veen, J.A. and E.A. Paul. 1981. Organic carbon
    dynamics in grassland soils. I. Background
    information and computer simulation. Can. J. Soil
    Sci. 61, 185-201.

Vose, P.B. and A.P. Ruschel. 1981. Associative N_2
    fixation, Vols. 1 and 2. CRC Press, Boca Raton.

Winship, L.J. and J.D. Tjepkema. 1982. Plant Physiol.
    (accepted).