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FIELD CROPS IN A CO₂-ENRICHED
ATMOSPHERE

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PREFACE

The International Institute for Applied Systems Analysis is conducting research to contribute both conceptually and in practice to the management of environmental quality and resources.

This paper is part of the Institute's activities on issues related to the atmospheric environment. It argues that the increase of CO₂ concentration in the atmosphere can enhance crop yield as a result of the response of photosynthetic productivity to CO₂ enrichment.

Janusz Kindler
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ABSTRACT

Every leaf growing in terrestrial ecosystems is now surrounded by air which is subject to increasing CO₂ concentrations. As CO₂ is one of the main substrates for photosynthesis, the increase will inevitably have an impact on the physiological processes of plants. The ecophysiology of CO₂ uptake and transpiration is briefly reviewed, and the possible yield responses are discussed. It is agreed that the yield will be enhanced as a result of the increase in the CO₂ level. However, this improvement may be masked by the same factors that mask the yield improvement obtained through plant breeding. The yield enhancement is therefore difficult to assess by using only historical data. An alternative approach is proposed, which utilizes ecophysiological experiments, tree ring data, and dynamic models of plant ecology.

TABLE OF CONTENTS

1. INTRODUCTION	1
2. ATMOSPHERIC CO ₂ CONCENTRATION, PHYOTOSYNTHESIS AND TRANSPIRATION	2
3. RESPONSE OF PRODUCTIVITY TO CO ₂ BUILD-UP	5
3.1 Formulation	5
3.2 Arguments for Marginal Response	8
3.3 Arguments for Significant Response	11
3.4 Historical Evidence	13
3.5 Masking Factors	14
4. PROPOSED APPROACH FOR FURTHER STUDIES	17
5. CONCLUSIONS	21
REFERENCES	23

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Pekka Kauppi

1. INTRODUCTION

Carbon dioxide has become an intensively studied environmental issue due to its potential for climatic change. The basis for the concern is the so-called greenhouse effect. It implies that an increase in atmospheric CO₂ concentration will be followed by an increase in the earth's surface temperature (Hansen et al. 1981). Changes can also be expected in the world precipitation pattern (Wigley et al. 1980).

The increase detected in the CO₂ level is due to two factors: fossil fuel combustion and the decrease in world biomass (Bolin, 1982). In order to predict future CO₂ levels, studies would be required on (a) CO₂ releases and (b) the reactions of potential carbon sinks: atmosphere, biosphere and the oceans. Both of these problem areas should include consideration of the changes in plant biomass. Prediction of these changes requires information on photosynthesis, dry matter growth, and on cultivation practices and deforestation.

This study deals with the reactions of field crops to a CO₂ enriched atmosphere. The scope is limited to analysis of the response of photosynthetic productivity to CO₂ enrichment, i.e., the impact of the biosphere on CO₂ levels is not discussed. The aim of this study is to draw conclusions with respect to the

crop yields in a CO₂ enriched atmosphere. This goal is, however, at the present stage of the work, merely theoretical. Only the direct impact of CO₂ to photosynthesis is considered. Indirect factors such as the effects of temperature and alterations of growing periods have been deferred, to be dealt with in further studies.

In Section 2, the physiological and ecological background are presented. Section 3 focuses on the quantitative figures of the productivity of field crops. This chapter also deals with masking factors, which are factors that can prevent signals of the potential productivity enhancement from appearing in data records. In the last section, an approach is suggested for further studies on the CO₂/productivity relationships.

2. ATMOSPHERIC CO₂ CONCENTRATION, PHYTOSYNTHESIS AND TRANSPIRATION

Continuous measurements of atmospheric CO₂ concentrations have been available since 1957. These measurements show that there are seasonal variations in CO₂ levels and a clear increasing trend in all parts of the world (WMO/ICSU/UNEP 1981, Figure 1). At present, the annual increase in the CO₂ level is in the order of 1.2 parts per million (ppm by volume). The increase is mainly due to the combustion of fossil fuel, although biospheric factors (Bolin, 1977; Wong, 1978; Woodwell, 1978) and perhaps natural fluctuations (Delmas et al. 1980) are also involved. Despite some uncertainties in the world carbon budget, it is commonly assumed that the increasing trend of the CO₂ level in the atmosphere will continue for the next few decades. The estimated level for the preindustrial CO₂ concentration is 290 ppm (WMO/ICSU/UNEP, 1981). The seasonal average for the year 1981 will be about 340 ppm. It has been estimated that by the year 2050 the level will have reached 400-800 ppm, depending on future energy strategies (Häfele, 1981).

In addition to water, carbon dioxide is the main substrate for photosynthesis. It enters plant leaves by diffusion, along the declining gradient of CO₂ partial pressure from the ambient air to the mesophyll tissue. The photosynthesis, p , can be

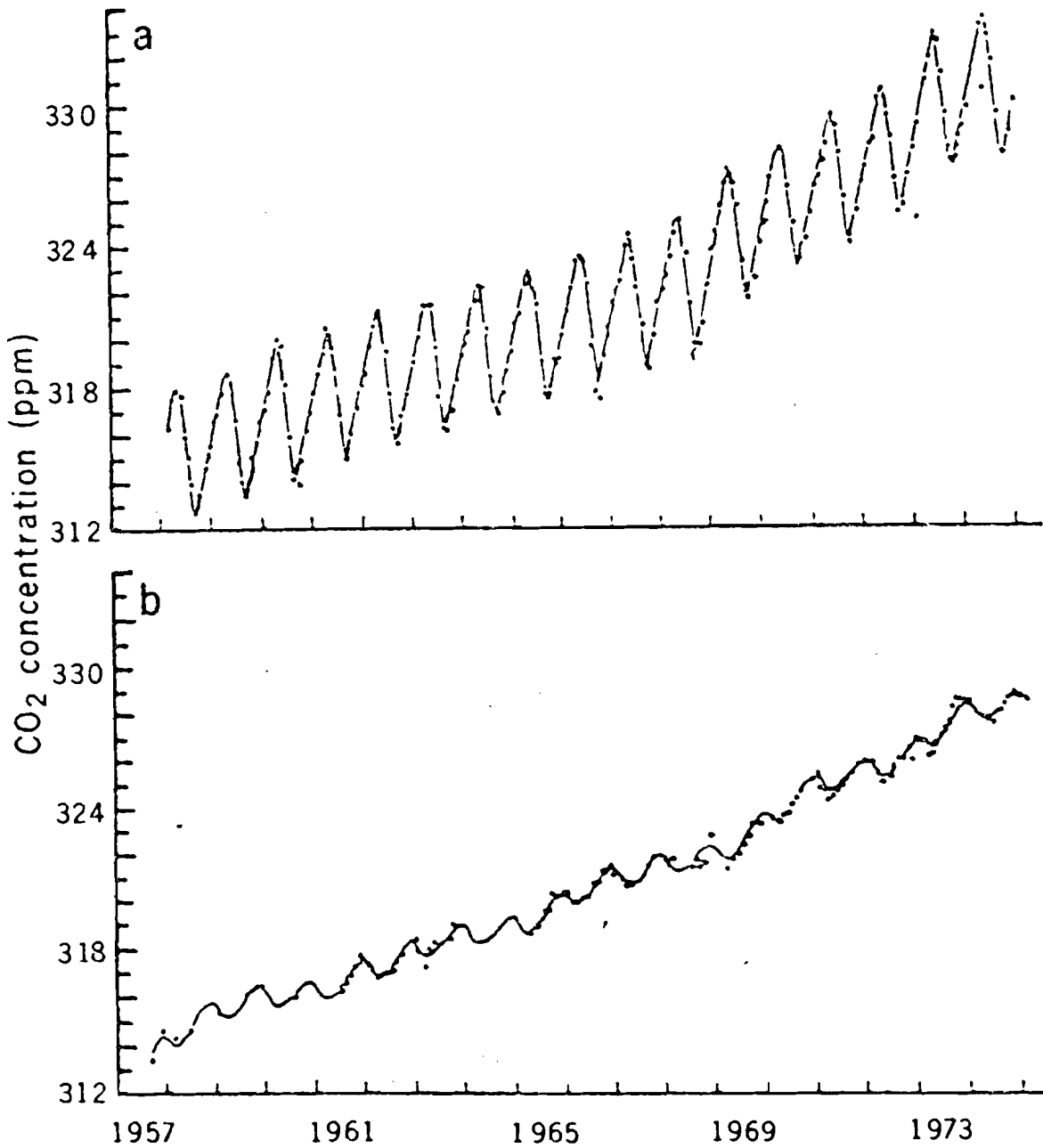


Figure 1. Atmospheric CO₂ concentrations (by volume, dry air)
(a) at the Mauna Loa Observatory, Hawaii, and
(b) at the South Pole (Reproduced by Broecker et al.
1979) from measurements by Keeling and his coworkers

described as a function of ambient and intercellular CO₂ concentrations, C_a and C_i respectively, and the resistance to diffusion, r (e.g., Thornley, 1976):

$$p = \frac{(C_a - C_i)}{r} \quad . \quad (1)$$

This equation is analogous to Ohm's law, which states that electric current is the ratio of potential difference to resistance. When the ambient CO₂ levels increase, the potential difference (C_a - C_i) also tends to increase (e.g., Rosenberg, 1981). This would result in a rapid increase in photosynthesis. However, a quantitative analysis of the photosynthetic response cannot merely be based on Equation (1). Both C_i and r are controlled by acclimatization mechanisms, and the resistance, r, especially, is highly sensitive to CO₂ concentrations.

Membranes in plants are not capable of permitting CO₂ inflow without water outflow. The flows are controlled by mechanisms which regulate the aperture of stomata openings. Other mechanisms are also involved, but are not relevant to the present discussion. The adaptive principle governing stomata causes a compromise between maximal photosynthesis and minimal transpiration. The typical water expenditure for fixing one CO₂ molecule into biomass is 400 molecules of water transpired (de Wit, 1958). The ratio of photosynthesis to transpiration is called the water-use efficiency. A rise in atmospheric CO₂ concentration affects the driving force of CO₂ inflow, but not that of water outflow. Hence we can expect an increase in water-use efficiency. The increase will be either due to the enhancement of photosynthesis or, if the stomata react, to a decrease in transpiration. Such reactions have been observed under certain conditions (Wong et al. 1979). It is assumed that in this way the plant maintains a constant intercellular CO₂ level corresponding to the capacity of the mesophyll tissues to fix carbon.

Short term physiological studies indicate that there is a possibility for an increase in photosynthetic productivity with increasing CO₂ concentrations. Björkman's results (see Osmond et al. 1980) showed that photosynthesis and water-use efficiency

increased in Larrea divaricata by factors of 1.5 and 2.5, respectively, when the CO₂ level was doubled (Figure 2). But can we expect an increase also in harvestable crops? This problem can be analyzed in two steps, by studying (1) a long-term photosynthetic response in field conditions and (2) the growth response corresponding to a given change in long-term photosynthesis (Kramer, 1981). The stem growth in a Scots pine has been found to consume less than 10 percent of its annual carbon budget (Figure 3). Hence, the growth response for a given increase in photosynthesis would probably be very sensitive to the pattern of photosynthate allocation.

3. RESPONSE OF PRODUCTIVITY TO CO₂ BUILD-UP

3.1 Formulation

CO₂ is not known to have toxic effects on plant life at low concentrations. This suggests that the gradual increase in CO₂ levels would not cause declining yield trends. However, if we expect only a marginal yield response, then the problem would not deserve the attention of farmers or foresters. Are there any grounds to expect that the response will be marginal? What is marginal, and what is significant?

Growth data has been analyzed using models with physiologically defined parameters (Charles-Edwards and Fisher, 1980). However, the quantification of important physiological parameters, required for studies on CO₂ responses, is lacking. Therefore, a more simple empirical approach is selected (Bacastow and Keeling, 1973). Denote

time by t ,
ambient CO₂ concentration by $C_a(t)$,
yield corresponding to the ambient CO₂ by $Y_{Ca}(t)$
reference CO₂ concentration by C_o ,
reference yield by Y_o , and
"biotic growth factor" by β .

The yield in a given ambient concentration can be analyzed roughly as

$$Y_{Ca}(t) = Y_o (1 + \beta \ln(C_a(t)/C_o)) \quad . \quad (2)$$

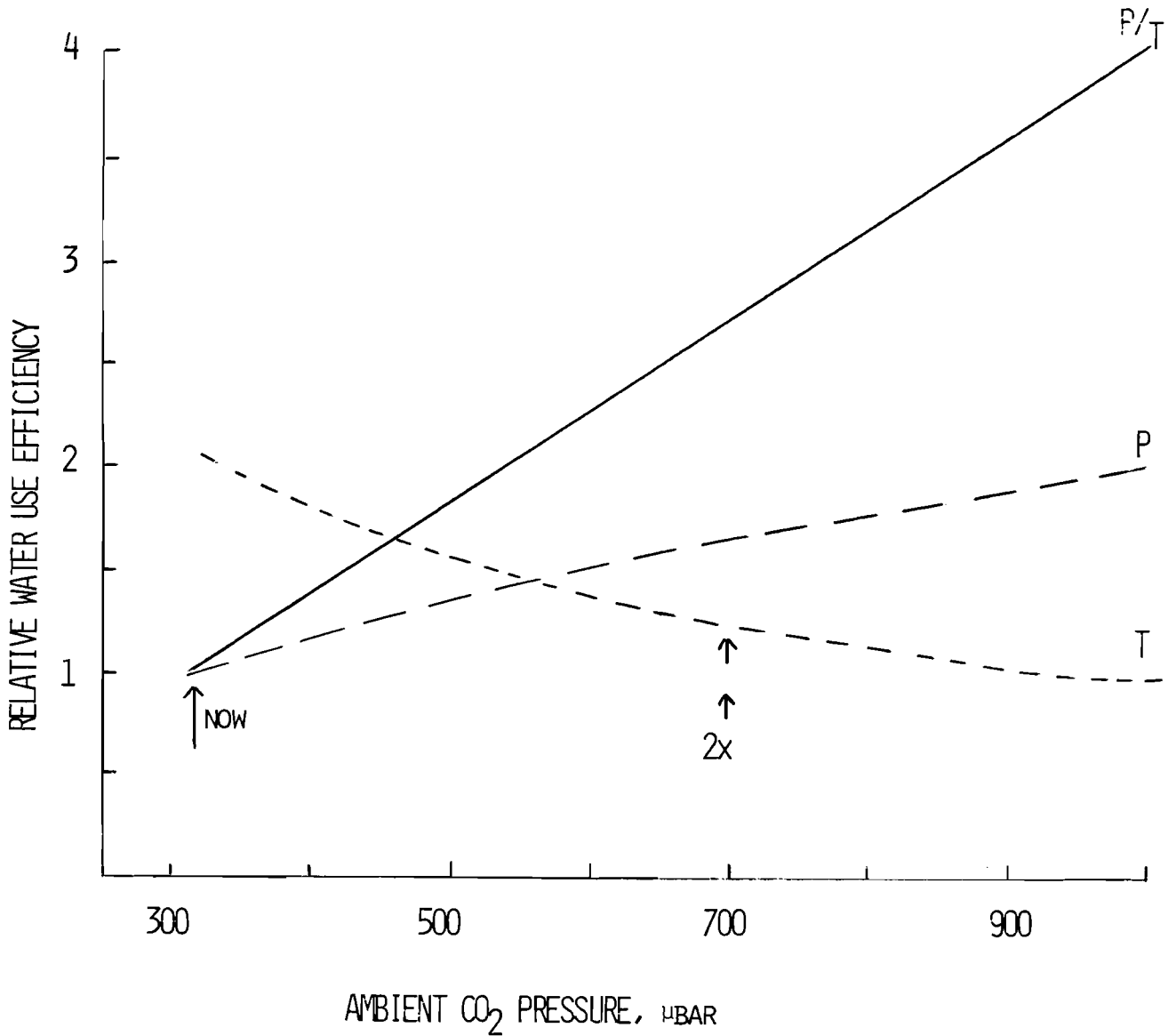


Figure 2. Experimentally determined responses of photosynthesis, transpiration and water use efficiency to short-term increases of ambient CO₂ pressure for the C₃ species *Larrea divaricata*. (From O. Björkman's measurements, Osmond et al. 1980).

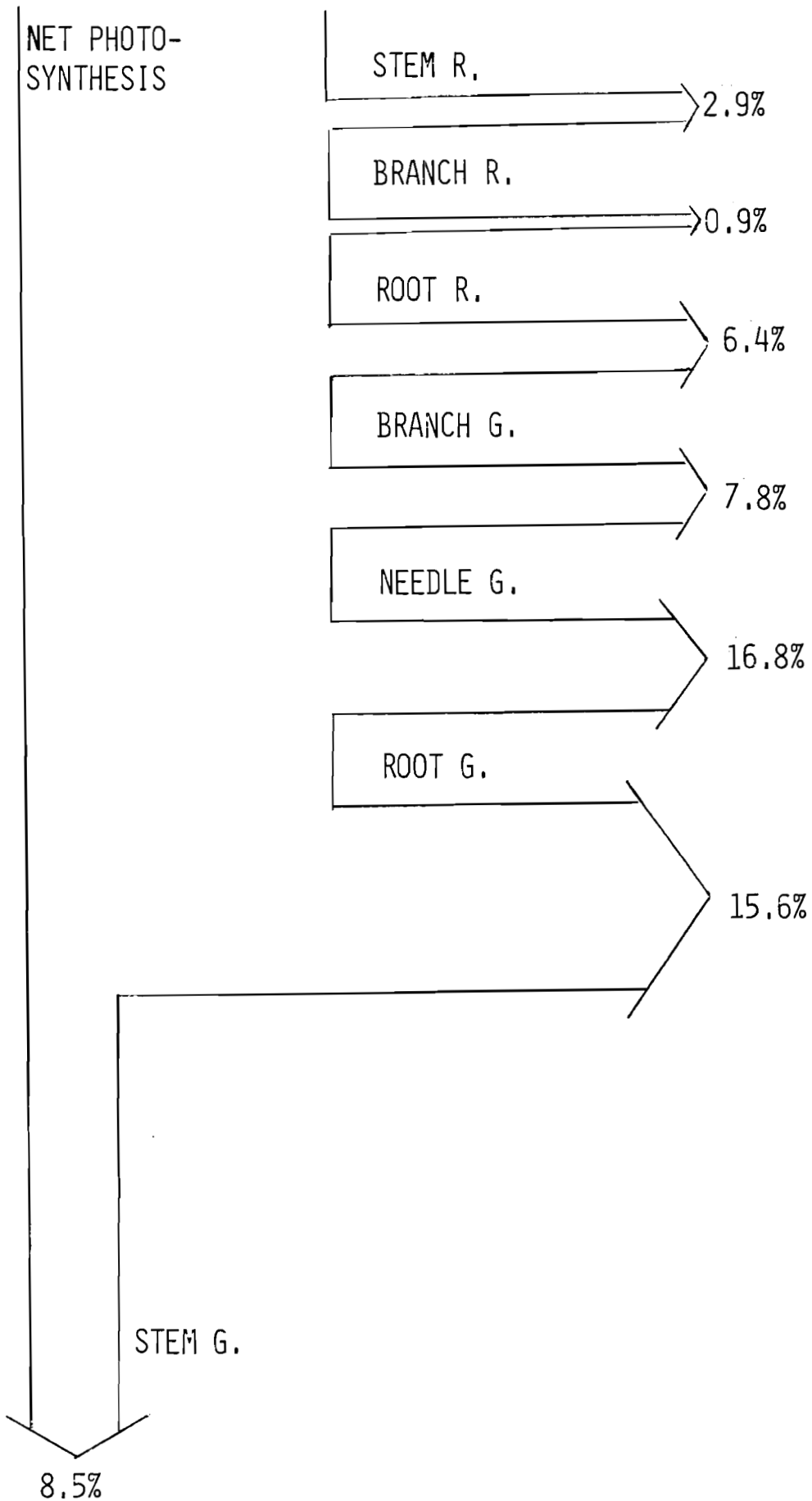


Figure 3. Annual utilization of photosynthates in a 14-year-old Scots pine. R is respiration and G is growth (Ågren et al. 1980).

The biotic growth factor, β , can be interpreted as the percentage increase in yield corresponding to a 1 percent increase in the CO_2 level. The derivative $\frac{dY}{dC} \frac{C_a}{Y}$ decreases slightly with increasing CO_2 concentration within the range 290-1000 ppm (Figure 4).

Equation (2) makes it possible to define that a value for $\beta \gtrsim 0.5$, would result in yield increases comparable to those attained through plant breeding activities. For example, the rather intensive tree breeding program of Finland has been expected to give a 10-15 percent increase in timber yield within one tree generation (Tree breeding committee, 1975).

3.2 Arguments for Marginal Response

There are very few quantitative results on long-term responses of yield to varying CO_2 levels in the literature. Therefore, it is rather difficult to distinguish between the arguments supporting the view $\beta \lesssim 0.1$, and those suggesting that $\beta \gtrsim 0.5$. The judgment made here may sometimes be inaccurate in spite of the fact that the intermediate range $0.1 < \beta < 0.5$ is omitted. It is also worth mentioning that the aim is to present the arguments, and not the conclusions put forward in different publications.

The basic theoretical concept supporting the marginal response is Liebig's law of minimum yield factor. It states that there is always one critical factor limiting plant growth. The yield can, therefore, be improved only by affecting this factor. Since it is obvious that either irradiance, water shortage or one of the 15-20 nutrients necessary normally act as the limiting factor, CO_2 concentration can only affect growth in special cases. The significant response frequently found in greenhouse cultivation (e.g., Hårdh, 1966) is in agreement with this theory, as the other growth factors are maintained at optimum levels. It has also been noted that in greenhouses without CO_2 enrichment, photosynthesis will reduce the CO_2 level down to values as low as 100 ppm (Goudrian and Ajtay, 1979). Under field conditions, where turbulent gas exchange with the atmosphere is effective, the CO_2 concentration is not usually lower than 250 ppm. It

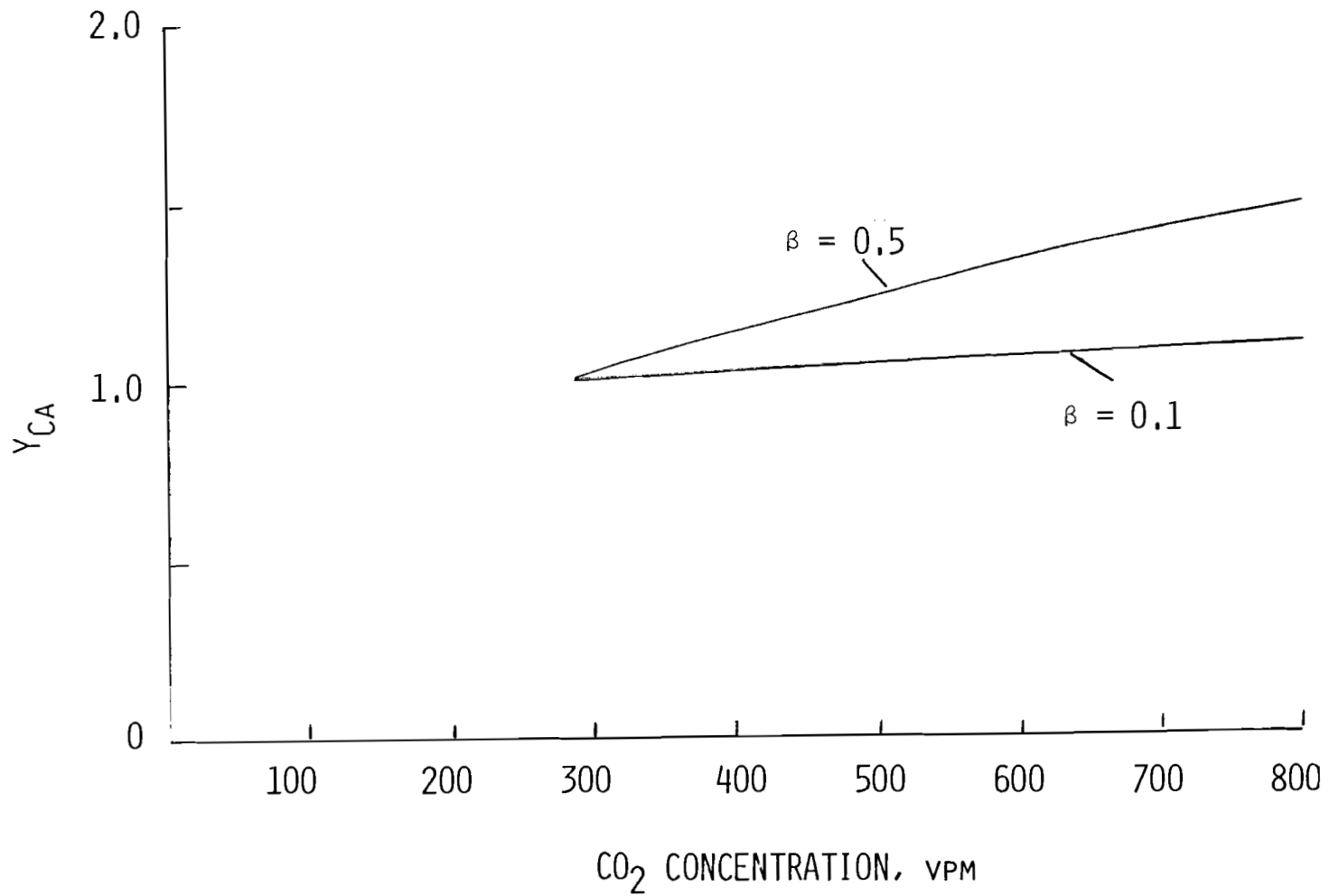


Figure 4. Yield calculated from Eq.(2) at varying CO_2 concentrations. Preindustrial concentration is taken as a reference point with a relative yield value of 1.0

has been argued that the lower concentration in the greenhouse (100 ppm) limits production but the higher field concentration (250 ppm) would not do so.

Neales and Nicholls (1978) report a strong interaction between the CO₂-growth-response and plant age. In this study the growth of 10-day-old wheat plants was increased by 35 percent as the CO₂ level was moved up to 800 ppm. However, with 24-day-old plants the growth was reduced by 44 percent over the same CO₂ range.

Maize and sugarcane are examples of the so-called C₄ plants, which have a different photosynthetic pathway from ordinary C₃ plants (see Black, 1973). The C₄ plants are able to fix carbon efficiently at essentially lower CO₂ levels than the C₃ plants. They will therefore benefit from increasing CO₂ concentrations only as a result of a decline in the water requirements.

Attiwill (1971) has pointed out that an increased rate of assimilation may increase the rate at which a mature stand develops rather than the amount of biomass at the end of a forest succession. In other words, a stand in a CO₂ enriched atmosphere would quickly reach its mature phase but after this quick development there would occur an early growth cessation. If this is true, then the increased assimilation would not yield a net increase in the amount of carbon stored by ecosystems. This is an important point in considering the roles of biosphere, atmosphere and ocean as alternative CO₂ sinks (Woodwell, 1978).

Independently of direct ecological measurements, Hall et al. (1975) studied the problem of yield-CO₂-response by analyzing the seasonal variation in the atmospheric CO₂ concentration. The measurements were taken from the Mauna Loa data (Figure 1(a)). The analysis was based on the reasoning that an enhanced biotic activity should appear as an increase in the seasonal CO₂ variation. No such increase was found.

3.3 Arguments for Significant Response

As an extension of Liebig's law of only one limiting factor, Verduin (1952) pointed out that photosynthesis is a process which is often regulated by numerous factors simultaneously. Furthermore, these colimiting factors tend to influence photosynthesis in an interactive way. Experiments support this view (Koch, 1969; Gross, 1976; Ho, 1977; Green and Wright, 1977; and Enoch and Sachs, 1978), which has also been introduced into the mathematical models for photosynthesis (Thornley, 1976). All these studies deal with short-term photosynthesis. Many factors can suppress this behaviour in long-term growth, since growth is related to short-term photosynthesis in a complicated way (Kramer, 1981). However, in Gifford's experiments (1977, 1979) the relative growth enhancement due to increased CO₂ concentration was found to be the greatest in nonoptimal light and water conditions. In these studies wheat was grown in enriched and depleted CO₂ concentrations with varying light climate or water stress conditions. The experiments lasted for the whole lifetime of the stands and the results were measured in terms of photosynthesis and grain yield (Figure 5).

Gifford (1979) also found interactions between the growth response and the stage of plant development (c.f. Neales and Nicholls, 1978). In this case, young plants exhibited a lower response to CO₂ concentration compared to old plants. The inhibition of growth at the early stage was obvious but it did not govern the response for the whole season. The ability of plants to process photosynthates further may, indeed, occasionally be restricted. This might explain why the response is the greatest in suboptimal conditions. The pool of photosynthates would then tend to remain small due to the moderate photosynthesis and the relatively high respiratory demand.

The biomass storage is of interest as an alternative carbon lock-up (Attiwill, 1971). But from the viewpoint of the forestry sector the key parameter is not the amount of biomass but the rate of biomass production. This rate can increase either with or without an increase in forest biomass. Constant yields with

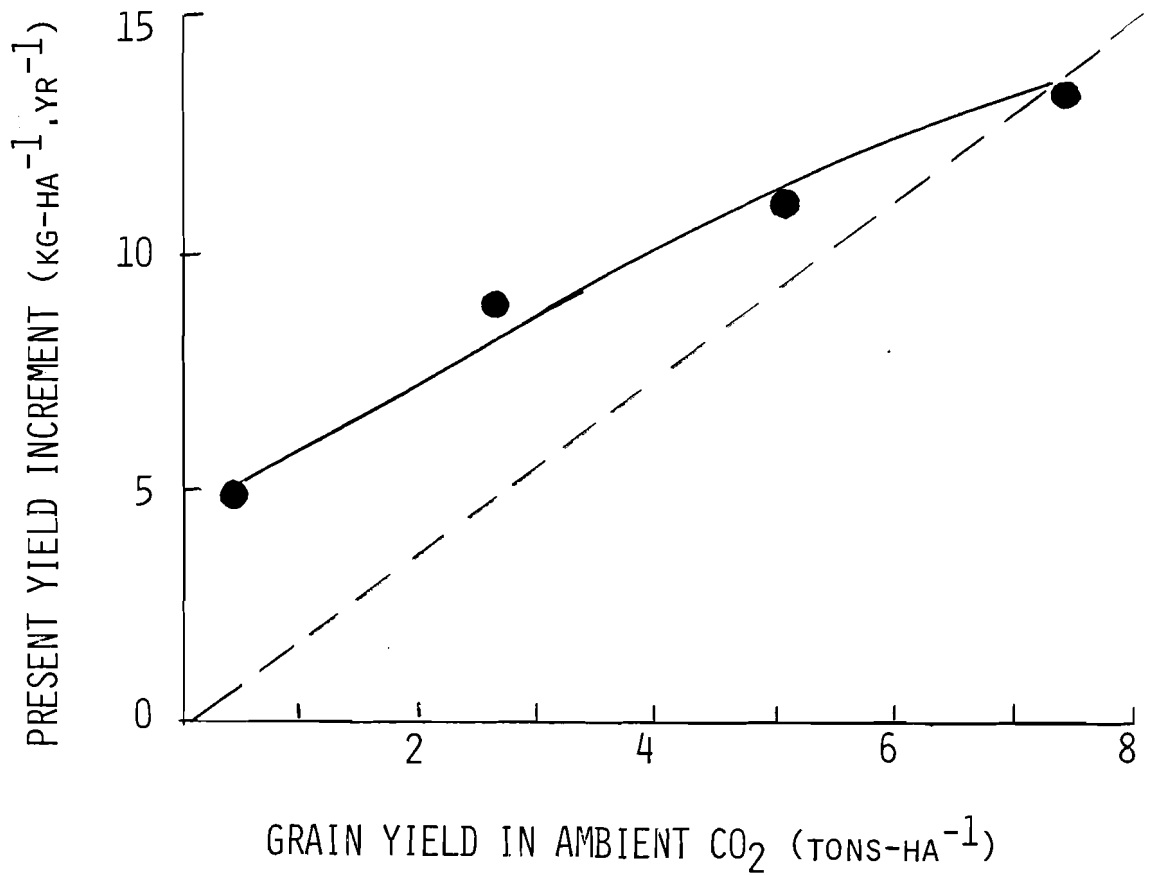


Figure 5. Response of the grain yield of wheat to a 250 ppm enrichment which lasted for the whole growing season. The yield increment is expressed per the current annual CO₂ increase (1.2 ppm). Measured values—solid line, and calculated—dotted line; calculation made with Eq. (2) and β -value of 0.5. (From Gifford, 1979)

shortening rotation periods are just as valuable as increasing yields at constant rotations.

The amplitude of the seasonal variation in the global CO₂ concentration has not increased (Hall et al. 1975). However, this is a fact which is only vaguely connected to productivity. Assuming that there is no enhancement in photosynthesis, the variation should actually be declining due to deforestation (Gifford, 1981). Another approach in studying the response of productivity to the seasonal CO₂ variation has been taken by Rosenberg (1981). His evidence indicates that a depression occurs in the photosynthesis of field-grown alfalfa when the regional ambient CO₂-concentration is at its lowest.

3.4 Historical Evidence

We can consider the preindustrial atmospheric CO₂-concentration, 290 ppm, as the point of reference. With a β -value of 0.5 in Equation (2), the 340 ppm of today would give 7 percent higher yields compared to those at the end of the 19th century. If this is true, one would expect that such a rather high increase would be obvious in historical crop and forest production data. These series, however, contain also other trend-inducing factors. This is illustrated with the following examples.

Annual net growth of the forests of the United States has increased at a surprisingly high rate (Figure 6). On the basis of these data, the total annual timber growth has increased by about 350 percent in the 57 year period from 1920 to 1977. This increase is more than 15 times greater than that expected from the increasing CO₂ levels, using the above assumptions. The main reason for the yield increase is clear. Virgin forests do not have much net growth. Net growth, in the sense it is understood in this article (Clawson, 1979), is possible only after the original stands are opened up by harvesting. Other factors such as a net change in forest area, fertilization and tree breeding are also involved in North American forestry but they are less important. Considering this background it is understandable that a potential enhancement of 7 percent in growth is difficult to detect from forest yield records. This becomes

even more evident when the repeated and serious underestimation of timber growth is considered (Figure 6). The possible effect of CO₂ build-up is easily "hidden", not only within the general increasing trend, but also within any of the five different gaps between predicted and actual timber growth.

Tree growth data for the USA is not exceptional for forests subjected to modern silviculture. Similar patterns have been documented from Finnish forests this century. The growth increase curve will become saturated or at least follow a more gradual slope as soon as the age structure of the stands reaches the optimum. Harvest management is then no longer an overruling factor.

National average wheat yields for Australia over the period 1957-1976 also show an increase, but with a very gradual slope (Figure 7). In these data there is less room for the CO₂ response, especially as plant breeders have continuously produced more efficient strains. It is worth noticing that the average yield is rather low compared to the experimental yields shown in Figure 5. Such a difference frequently occurs during experimentation. In this case, it is not appropriate to expect that the high CO₂ response found by Gifford (1979) at "low" yield levels (Figure 5) should be found in practice. The "low" yield in the experiment was induced by drought which persisted for a long time, while the data set of Figure 7 averages over many factors such as disease and pest damage, local yield losses, nonoptimal timing of operations, etc.

3.5 Masking Factors

Figure 6 showing the net growth of U.S. forests illustrates clearly how management governs the rate at which biomass is produced. It is possible to gain more growth with careful management. It is also possible to decrease growth or even to lose it totally with poor management. The ultimate form of poor management is deforestation. A destroyed ecosystem will in no circumstances gain from enriched CO₂ levels. In the future, factors such as acid rain, and decreased ozone levels will also threaten forest

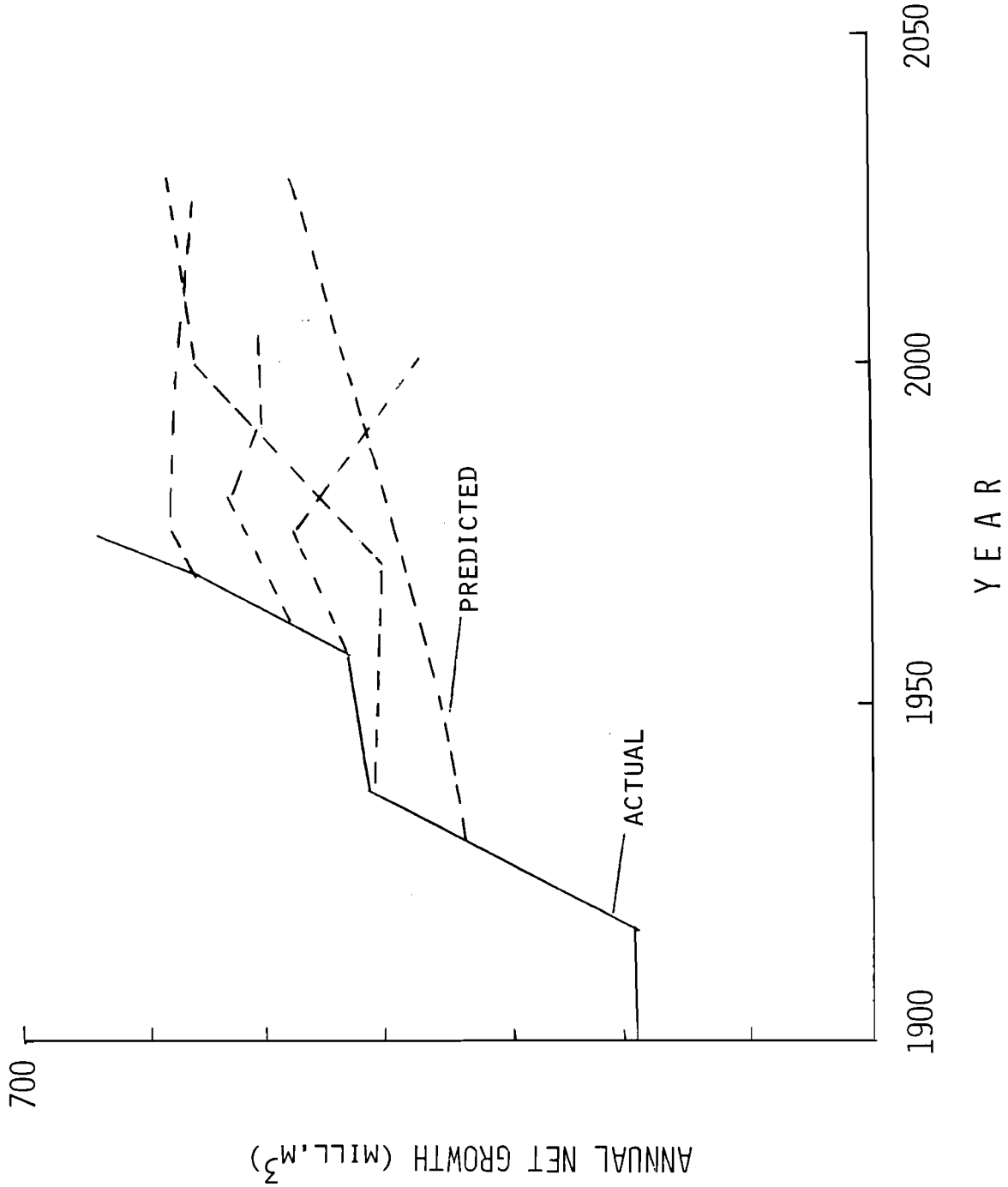


Figure 6. Annual net growth of timber in the United States, 1900 to 1977, and Forest Service projections of future growth made in 1933, 1946, 1952, 1962, and 1970 (Clawson, 1979).

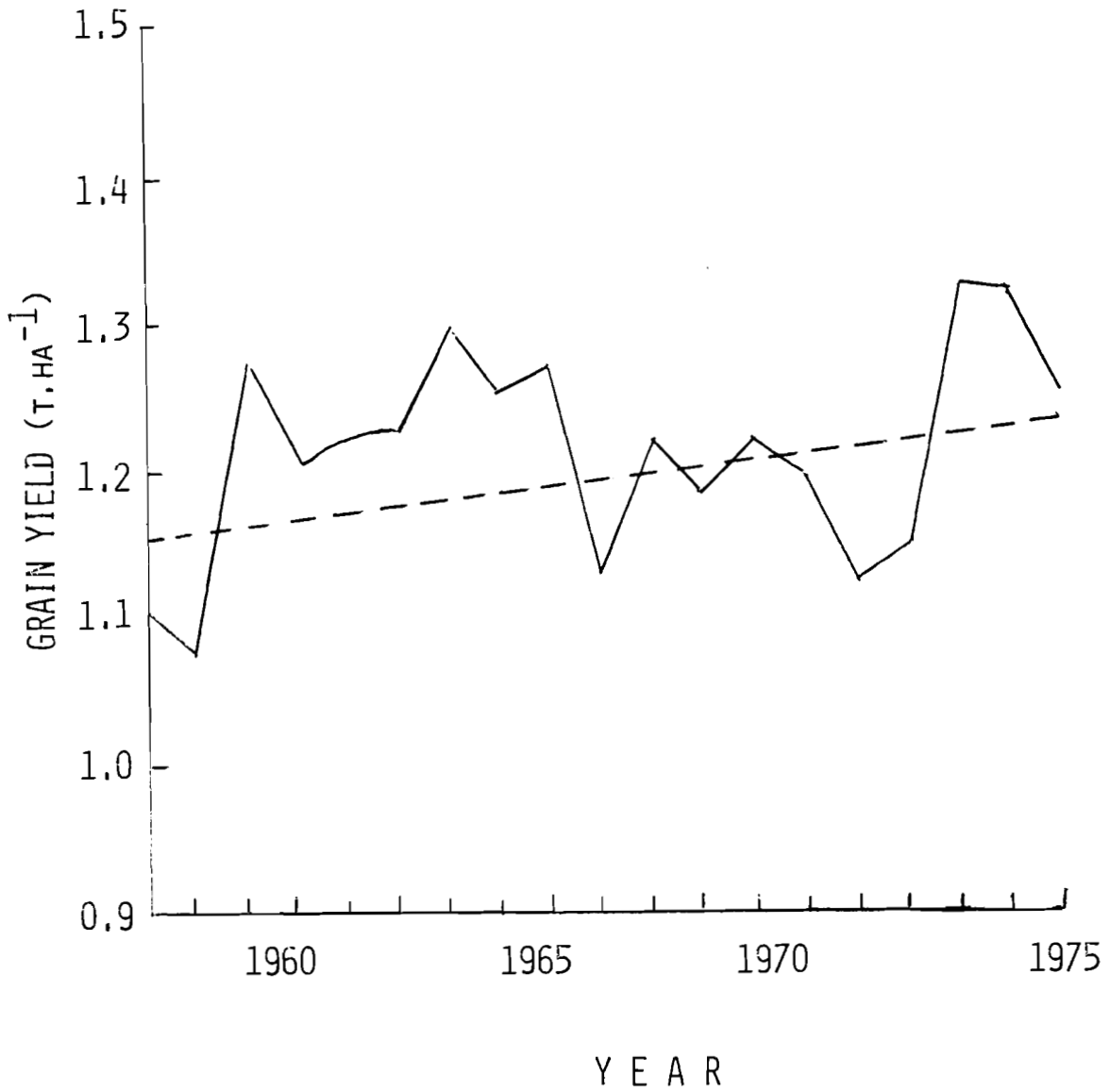


Figure 7. The national average commercial wheat yields in Australia plotted as 3-year running means from 1958 to 1977 (Gifford, 1979)

ecosystems. Irrigation, fertilization and new breeds, on the other hand, have been known to increase yield levels. Hence, they can also mask a CO₂ induced trend in yield records.

In many respects, the potential CO₂-induced trend is similar to the trend achieved by plant breeding. Most of the masking factors listed above can also hide the increased yield potential of the strains bred. Trends from both CO₂ levels and the breeding activity may result in potential increases of the same magnitude. The CO₂ trend deserves increased attention also from plant breeders, especially tree breeders. A tree planted now is likely to spend its most productive years in CO₂-concentrations of 400 to 450 ppm. In one respect, the CO₂-induced trend is potentially more important than the one achieved through tree breeding, as it affects every plant on earth, not only the specially bred strains.

4. PROPOSED APPROACH FOR FURTHER STUDIES

Problem-oriented research on the effect of increasing CO₂ concentration on crop yields should utilize all available materials. This would not be possible without a theoretical framework capable of combining the results from different fields of research. Figure 8 illustrates an approach designed to take into account this consideration.

An analysis of the different growth factors affecting a single crop is already a rather complicated problem (Charles-Edwards and Fisher, 1980). Historical yield records are average values for thousands of crops, which makes such an analysis almost impossible. However, the time series of yields with different species and different climatic regions would serve as one basis for studying the impact of increasing CO₂ level on yields. This kind of data is especially needed for studies on the importance of the potential trend in relation to the different masking factors. Yield records are available from many countries and many species. They should be collected following a carefully designed plan in order to ensure that only reliable time series and interesting regions are included. A wide variety of species should be included from both forests and agricultural ecosystems from cool and warm climates, and from humid as well as arid sites.

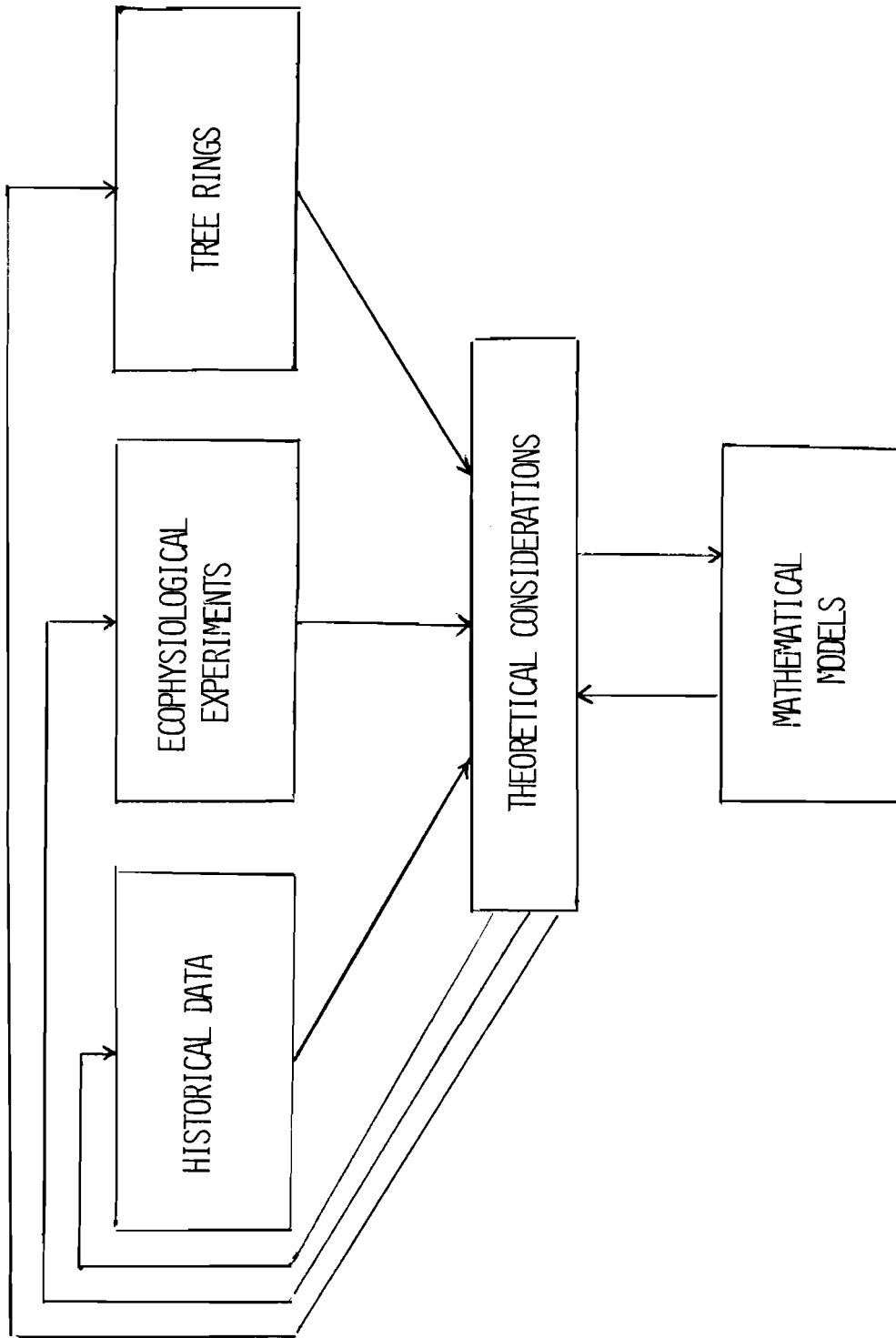


Figure 8. Diagram for an approach suggested for further studies on CO₂-yield relationships

Ecophysiological experiments can be used to test the basic hypothesis. More experiments are required especially in order to study interactive growth responses of the CO₂ concentration on the one hand, and drought, mild climate and nutrients on the other. Key experiments have so far been conducted on wheat. Other species, including woody plants, should be studied as soon as possible. The main emphasis should be laid on experiments lasting longer than 1-2 weeks, otherwise the hypotheses concerning feedback processes cannot be tested.

Tree ring data has so far been used mainly for studying growth fluctuations. The objective in this case has been, for example, to generate missing climatic records for the past centuries (e.g., Garfinkel and Brubaker, 1980), or to understand the mechanisms of fluctuations in order to improve forestry practices (Pohtila, 1980). Less attention has been paid to revealing the potential trends. Sampling will be more difficult when trends are studied instead of fluctuations. A trend is more sensitive to the stand density than is the year-to-year variation (Mikola, 1950). However, there are some possible ways of overcoming this difficulty. One simple way is to select old dominant trees that are known to have grown in a practically constant environment for decades (Francey, 1981). Another method is to extend the data base in order to average out the stand-to-stand variation. In any case, tree ring studies, as well as those analyzing historical data records, are sensitive to biased sampling. It is worth noting that by selecting the data set, a researcher can also select the conclusions. Therefore, special attention is needed in planning an unbiased sampling procedure.

Apart from direct measurements the researcher can also utilize mathematical modelling. The model depicted in Figure 9 can be used, especially for sensitivity analyses. The basic element of the model is one tree; interaction between trees is introduced through changes in the environment (growth-shading, photosynthesis-CO₂ depletion). In this way the tree model is extended to act as a stand model. The model can be identified hierarchically for instantaneous and seasonal time scales. Finally, the model should be extended to cover the whole life cycle of the

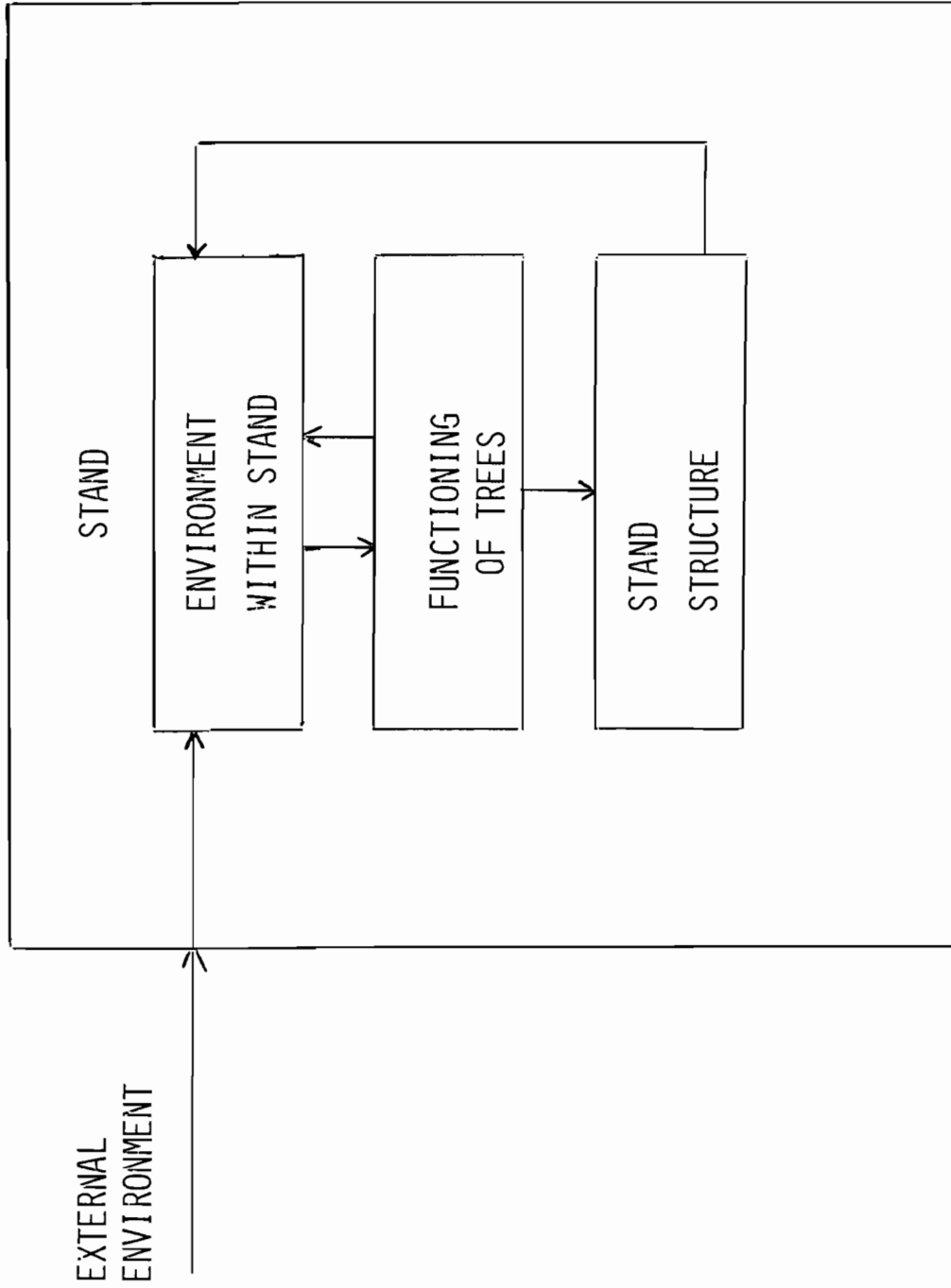


Figure 9. Structure of a model for studies of the plant-environment relationships (Hari et al. 1981)

stand. It must be pointed out that tree processes are not yet known well enough to construct a satisfactory growth model for predictive purposes (cf. Persson, 1980). However, the model is already being used as a tool for defining new hypotheses.

The approach shown in Figure 8 has two important features. The first is the central role of theoretical considerations. Information is collected in order to improve theory: a better theory is required for obtaining better answers to practical questions. Secondly, information is collected from all relevant sources in an interactive way. Many laboratories concentrate on attaining a deep understanding of one of the problem areas. In contrast, this problem-oriented approach does not permit thorough studies to be made in any of the special fields. Here the aim is to synthesize the main results from different fields.

5. CONCLUSIONS

In spite of many uncertainties (Gifford, 1981; Kramer, 1981) the information now available suggests that the CO₂ build-up is possibly causing significant yield responses.

The increase of atmospheric CO₂ concentration has been well documented, and the trend is likely to continue during the next few decades. There are physical and physiological reasons to expect that photosynthesis and water use efficiency of plants are enhanced. These deductions have been confirmed in short-term measurements. Plants can, however, in some developmental phases, even show a negative growth response (Neales and Nicholls, 1978). But there are no results which indicate that such a reaction would continue over prolonged periods.

Complex feedback relations characterize plant processes from instantaneous leaf photosynthesis to the growth of entire crops (Kramer, 1981). Some of these relations can potentially annul the effect of CO₂ build-up on growth. Particular support has been given to the view that, in field conditions, other growth-limiting factors would slow down the CO₂ effect in crop growth. These suggestions, however, have remained unfounded.

Photosynthesis is typically a process which is often limited by many factors simultaneously. This has been founded both theoretically (Verduin, 1952) and empirically. Similar evidence has recently been presented on crop growth. It has been argued that with an increased amount of photosynthates a plant would easily satisfy a nutrient or water deficit. The view of only one limiting growth factor obviously omits this dynamic approach (Luxmoore, 1981; Rosenberg, 1981). It would be relatively easy to test hypotheses concerning the different views empirically, in phytotrons. A rare experiment of this type (Gifford, 1979) suggests that the relative growth increase due to high CO₂ concentrations would be greatest in suboptimal growth conditions. These new views although tested only in wheat experiments, are especially interesting with regard to forests, as most forests grow in suboptimal conditions.

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