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PROBLEMS IN PREDICTING THE ECOLOGICAL EFFECTS OF ELEVATED CO_2

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Introduction

The rising level of atmospheric CO_2 is a major global anthropogenic change that we can track and predict with great confidence. We know that atmospheric CO_2 has increased, and we can make relatively good predictions of the levels we can expect to see in the near future. But the ecological effects of this rising CO_2 are not as easy to predict, and this is exactly what scientists are being asked to do by policy makers. Indeed, from the policy makers' point of view, the need for predictions of global change is the *raison d'être* for research on elevated CO_2. How good is our ability to make reasonable predictions, and how can we best improve such predictions? Most would agree that the answer to the first question is "not very good" at this point in time. This makes the second question even more important. The difficulty in making predictions of the ecological effects of rising CO_2 levels stems from two basic problems. First, ecology is a young science which does not have a body of widely-accepted theory which is applicable to the questions of global change. There is no short term solution to this problem, and the longer term solution is to promote the development of the science of ecology. As I will argue later in this chapter, research on the effects of elevated CO_2 can perhaps make a significant contribution to this longer-term goal.

The second major problem in making reliable predictions about the ecological effects of elevated CO_2 is that while scientists are being asked to make predictions at the community, ecosystem and biosphere level, most of the available information available exists at lower levels (Körner, 1993). Fig. 1 shows the traditional hierarchy of the levels of organization in biology, although the point here would apply to alternative hierarchical schemes (e.g. O'Neill et al. 1986) as well. The predictions which are most needed concerning the effects of elevated CO_2 are at the top three levels, but most of our information about the effects of CO_2 are from experiments conducted at lower levels. For example, there are numerous experiments looking at the effects of elevated CO_2 on leaf-level photosynthesis, whole growth and development of individual plants (see reviews by Bazzaz [1990], Mooney, et al. [1991], and Woodward [1991]), but because of costs and logistical constraints, we are just beginning to see longer term experiments on populations and communities in the field.

biosphere ecosystem community population individual organ tissue cell molecule	↑	increasing complexity decreasing understanding

Fig. 1. Levels of organization in biology.

One solution which has been proposed to this problem of making predictions at higher levels of organization is “scaling up” from the lower levels (Ehleringer and Field, 1993). But what exactly does scaling up mean? I find two very different meanings of this term in recent literature:

(1) extrapolation within one level of organization

(2) actual prediction of higher level phenomena using information from a lower level.

I will discuss them both in turn.

Extrapolation

Extrapolation usually means simply extending a quantitative relationship beyond the range of the data on which the relationship is based. Extrapolation is certainly possible and reasonable in many cases. For example, if one could accurately measure NPP in many randomly-placed 1 meter^2 quadrats within a grassland, one can extrapolate to get a good estimate of NPP over a larger area. The issues here are purely practical, not logical. Extrapolating a specific quantitative relationship entails much more risk, as can be seen clearly in a simple example from population growth. Fig. 2 shows a simple computer-generated “logistic” growth curve with random normal noise added.

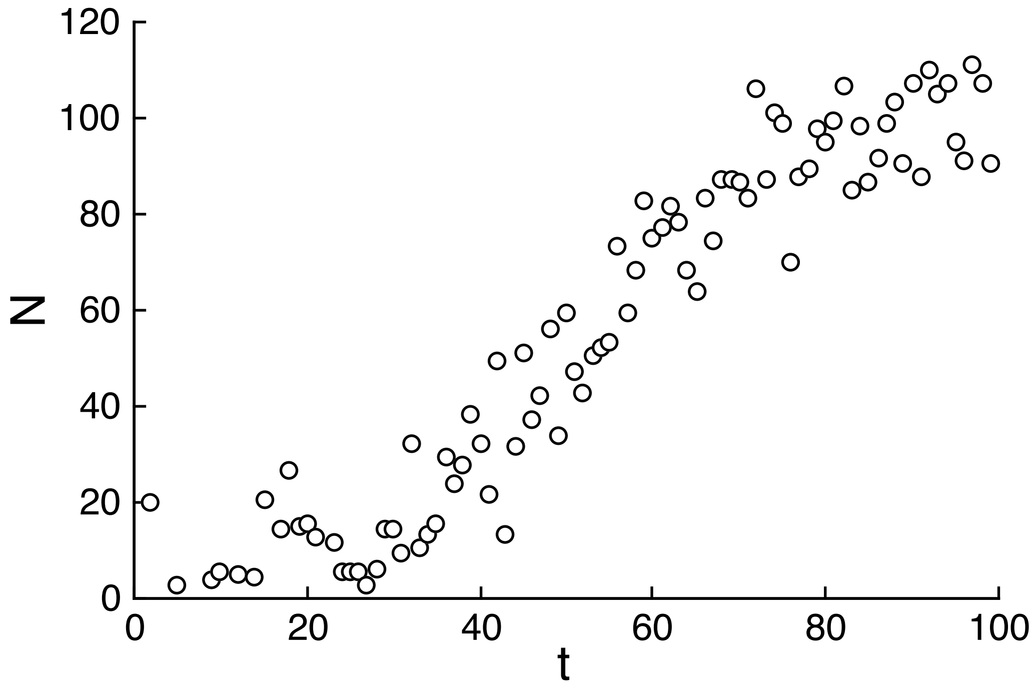

Fig. 2. Logistic growth curve with random normal variation.

If we have data from only one part of the curve, we would not be able to extrapolate very successfully, because we would not have any information on the overall shape of the relationship If we have information only from the beginning of the curve, we would be inclined to conclude that growth is exponential ("geometric growth"). If we have information on the central part of the curve, growth would appear to be approximately linear ("arithmetic growth"). If we have data on the right-hand part of the curve, we would likely conclude that the growth rate is continuously decreasing, such as in a simple saturating function. Extrapolating any of these trends to the other regions of the curve would lead to major errors. One needs either data over the whole range of the relationship, or huge sample sizes to provide the statistical power to see subtle changes in the derivatives over smaller ranges. As another general example of this problem one can point to the development and use of systems analysis models in ecosystem ecology (Patten, 1983). These "black box" models are often developed to predict some specific ecosystem processes, and calibrated using empirical data. Such models are often pretty good at predicting new combinations of variables within the range of the data used to calibrate them, but these same models are often very poor at making predictions outside the range of the data with which they are calibrated. The reason is similar to the example of the logistic growth curve: the characterization of quantitative relationships is usually good enough for interpolating within the range of the calibrating data, but this characterization is not good enough to make predictions far beyond the range of the data. The same issue arises in statistical models.

In conclusion, extrapolation can be dangerous, but it is certainly possible and reasonable in some cases. It is important to note, however, that extrapolation does not usually involve a change in the level of organization in question. Rather, it usually refers to questions of scale within one level of organization.

Reductionism from Below

The second meaning of scaling up I have found in the literature I call “reductionism from below”. This means the actual prediction of higher level phenomena from lower level information. I call it “from below” because reductionism is usually “from above”, i.e. it starts with the higher level phenomenon. In scaling up our starting point is information at the lower level. It is my contention here that this type of scaling up generally fails. For example, there is no basis for assuming that responses of a system to an environmental factor at a higher level of organization will be similar to responses at a lower level, and this has been documented in elevated CO_2 research (Reynolds and Acock, 1985; Reynolds et al., 1993). Short term regulatory responses of leaves to elevated CO_2 (i.e. an increase in the rate of photosynthesis) does not predict whole plant biomass accumulation or acclimatory responses (Mooney and Koch, 1994). On the contrary, acclimatory responses often damp out regulatory response (Bazzaz, 1990). Similarly, the performance of plants grown singly at elevated CO_2 may not be a good predictor of their performance when competing. (Bazzaz and Garbutt, 1988; Bazzaz and McConnaughay, 1992).

Evolutionary responses to elevated CO_2, which we have a strong basis to expect (see other chapters in this volume), present the most difficult problems for prediction. There is no basis for assuming that the plastic response of an organism to an environmental factor will be similar or even in the same general direction as evolutionary responses to that same factor. For example, a plant may respond to shade by etiolating, but natural selection may favor slower growth and shorter stature in the shade (as we see in understory herbs). Similarly, Woodward (1987) presented evidence that plants respond to increasing CO_2 by decreasing the number of stomata (although this conclusion has been disputed [Körner, 1988]). Even if we assume that plants do develop fewer stomata in a CO_2 -enriched environment, I see no *prima facie* reason why we should expect evolutionary responses to be in the same direction. Simply put, evolutionary responses may damp out effects of elevated CO_2 (as populations evolve in an environment of elevated CO_2), or evolutionary responses may amplify short term effects, as competitive relationships are altered and species evolve in different ways. There is no way to predict the long-term outcome at this point.

The problems of scaling up are not limited to evolutionary change. For example, CO_2 is a resource, and there has been significant progress in theories of resource utilization and limitation (Tilman, 1986; Bloom *et al.*, 1985; other chapters in this volume). These theories could provide some reasonable predictions concerning the effects of elevated CO_2 as a resource. Evidence is accumulating, however, that developmental effects of CO_2 on plants (e.g. Reekie and Bazzaz, 1991; Loehle, 1995) may be more important than resource-mediated effects. Since elevated CO_2 is a novel environment, developmental effects will not be predictable. Several species seem to show increased reproductive output in high CO_2 environments, but other species, e.g. *Abutilon*, *Cucumis*, show the opposite response (Bazzaz *et al.*, 1995). There is no way to predict with any confidence the response of reproductive output or allocation to elevated CO_2 in any species under different conditions until we do the appropriate experiments.

As Körner (1993) has pointed out, there is no way that we can now, or will be able in the foreseeable future, to predict ecosystem processes from the physiological properties of organisms. To make the philosophical point that phenomena at any level of organization are “ultimately” reducible to and driven by, phenomena at lower levels, does not mean that we are anywhere near being able to do this. Numerous ecologists (e.g. Allen and Starr; 1982; O'Neill et al., 1986) have argued that pure reductionism in ecology will usually fail. If such reductionism were possible we should all be molecular biologists, or physical chemists, not ecologists. Levin (1993) suggests there may be laws for scaling up, but even if this is so, we are at present very far from discovering and applying them.

The paradigm for scaling up in biology has been the use of biochemistry in medicine: antibiotics are molecules which kill bacteria in a test tube, then scale up to cure disease at whole body level, and then scale up to control epidemics at the population level. However, this type of successful scaling up has proven to be the exception, not the rule. The success of this example of scaling up may be because it takes place mostly within individuals, and the individual is the product of natural selection. Scaling up to supra-organismal levels, such as the community or ecosystem, operates under no such constraints.

Confidence in our ability to scale up depends upon the available data, and our theoretical understanding of the relationships between the levels of organization over which we are scaling (O'Neill *et al.*, 1986). The important argument against scaling up is not philosophical, but depends upon the available data and state of the art. If, in the scores of experiments which have been done on the effect of elevated CO_2, we did observe simple transparent reductionism, it would be quite reasonable to apply this in predicting CO_2 effects. For example, if increased CO_2 almost always resulted in increased photosynthesis at the leaf level, and increased biomass accumulation at the whole plant, population and community levels, we would have a strong basis for applying this prediction generally. But CO_2 research has not yielded such general and simple patterns. As Bazzaz (1990) has pointed out, competitive outcomes will be modified by CO_2 and by the interaction of CO_2 with other environmental factors as different species behave differently in a high CO_2 world, and their response will depend on the identity of the competing species.

We cannot predict the behavior of a system from a lower level without either (1) evidence for such simple patterns across several levels, or (2) a well developed theory which spans the levels in question. The data we have does not support (1), and (2) would require a level of ecological theory far beyond what we have available today or in the foreseeable future. The effects of CO_2 on terrestrial ecosystem will ultimately be reducible to physiology and interactions among individuals and their environments. But when, as in ecology, we don't have a very good understanding of the processes in question, scaling up from a lower level of organizations is much less reliable than predictions based on data from the same level as the phenomena to be predicted.

Two Approaches to Research on Elevated CO_2

In the light of this, we can distinguish two basic types of studies on the effects of elevated CO_2 on plants.

1) reductionist experiments that study the mechanisms of CO_2 effects

2) holistic experiments that look at CO_2 effects on whole systems that are as similar as possible to those about which we are trying to make predictions.

These two classes of experiments represent two legitimate, but in many cases fundamentally different, scientific goals. Scientific understanding is ultimately based on reductionism and mechanism, but the best currently accessible predictions of many phenomena often come from non-mechanistic, holistic “calculation tools” (*sensu* Loehle [1983]; see also Peters [1991]). To argue that one of these two scientific goals is “better” or more important than the other misses the point - they represent different goals, although this is not to say that they do not interact. Both can have integrity and scientific validity (and both can be done poorly). I am suggesting that, over the short term, there is often a tradeoff between these two goals.

As an example of mechanistic research on the effects of CO_2 I refer to an experiment that has been proposed (Bazzaz *et al.*, 1995; Körner, pers. comm.) on the effect of elevated CO_2 on the process of self-thinning (density-dependent mortality) in plant populations. Such an experiment could provide valuable data on the interaction between resource levels and density-dependent mortality. It might even provide insights into the mechanisms of density-dependent mortality beyond questions concerning CO_2. Such an experiment, if done reasonably well, would be very worthwhile scientifically. But I believe such an experiment would be practically useless in the near term in helping us to predict the effects of elevated CO_2 on terrestrial ecosystems that we will be seeing in the coming decades. Similarly, an experiment in which we enrich a whole plant community with CO_2 for as long as possible will probably be much more valuable for predicting what will happen in the coming years, but it will probably not be very useful in showing us the mechanisms by which these changes occur. I call this latter type of experiment “brute-force empiricism”.

Much of modern medicine is based upon such brute-force empiricism. We know a treatment works, but we often do not know the mechanism. Would one be willing to take a drug based purely on the data from *in vitro* studies and chemical theories? No, the principles of public health require that clinical trials be performed. If clinical trials are not possible, we want experiments on animals similar to humans. Similarly, if we’re going to predict effects of elevated CO_2 on terrestrial ecosystems, the best type of data will be from experiments, natural or planned, which are as close to the thing we’re trying to predict as is possible. But the clinical trial of a new medicine whose mechanism of action is not known will probably not provide useful information on the mechanism. It will merely tell us if the medicine works in a specific population.

The only reliable predictions possible for complex phenomena of which we have very limited understanding, come from brute force empiricism and, when necessary, extrapolation. To make a reliable prediction in such a case, one should study the phenomenon itself, or a system as similar to it as possible. In young sciences such as ecology and environmental science, data are more trustworthy than theory in making predictions (Peters, 1991; Weiner, 1995).

How are we able to predict the effects of specific treatments other than elevated CO_2 on terrestrial plant communities? For example, we know from experience that increasing the nutrients in many nutrient-poor plant communities will result in increased biomass and a reduction in species diversity. But we know this from experience - the experiment has been conducted many times. The theories which we have at this point to explain why this occurs are still after-the-fact explanations; they are not really the basis for our prediction that when we add phosphorous to an oligotrophic lake, we will get a huge increase in algal growth and a concurrent decrease in algal diversity. Similarly if we are asked to make a prediction of the effects of building a highway on local populations of plant and animals, the most useful type of information would be the effects of other road building projects on other communities, not deductions from ecological theories. While such "experiments" have been done many times, the "experiment" of elevated CO_2 is being done for the first time.

The challenges presented by global change are before us.

> Predicting and analyzing the structure and function of ecological systems on large spatial and long temporal scales are research challenges of rare potential but daunting difficulty. The potential derives from both *practical need* and *scientific opportunity*. The difficulty reflects the diversity and non linearity of ecological responses. (Field and Ehleringer, 1993; emphasis mine)

The dichotomy I have described fits Field and Ehleringer's eloquent diagnosis.

objective	method
to understand mechanisms of CO_2 effects ("scientific opportunity")	reductionist experiments on single factors and combinations
to make predictions of CO_2 effects as soon as possible ("practical need")	holistic experiments, both natural and planned

Fig. 3. Two basic types of research on effects of elevated CO_2.

Fundamental mechanistic research on effects of elevated CO_2 can and should be justified on its own terms, and it will eventually contribute to our understanding and prediction of global change, but it cannot be justified in terms of predicting global change in the near term. But if the goal is "merely" obtaining the best prediction of change in terrestrial systems as soon as possible, my claim is that an imperfect experiment at the level of organization we want to predict will be better than a perfectly-designed experiment at a much lower level. According to this argument, the following sorts of studies are most likely to yield reasonable predictions in the near future:

1. The study of naturally-occurring communities of high CO_2, e.g. volcanic vents in Italy (Miglietta and Raschi, 1993; Miglietta *et al.*, 1993; Körner and Miglietta, 1994), Java (von Faber, 1925), and California (Koch, 1993). According to the arguments advanced above, despite the limitations of such studies (e.g. possible confounding factors such as other contaminating gases, limited replication, etc.), they probably represent the best available information we have for predicting effects of elevated CO_2 on communities and ecosystems. This is because such studies are perhaps the only ones which are at the appropriate level temporally. I believe the potential value of comparative studies on naturally-occurring high CO_2 communities, in comparison with experimental studies, has been greatly underestimated by researchers.
2. Whole community experiments with elevated CO_2, as realistic and long-term as possible (e.g. open-top chambers, FACE experiments)
3. Microcosm versions of 2.
4. Paleological evidence of community changes correlated with changes in CO_2. If it can be established that CO_2 levels were much higher in the Cretaceous, paleological data on terrestrial plant communities could be of value. Even information on terrestrial systems during periods of lower CO_2 over the past 100,000 years may be useful via extrapolation.

Prediction and Uncertainty

Some of the controversies concerning predictions of global change may result from the two very different uses of the word “prediction” in science. An hypothesis is a prediction: a claim about the behavior of the world based on a theory or model.

Hypotheses are one of our most important research tools. Many of the most exciting and important hypotheses in science are controversial. But the word “prediction” is also used to describe consensus expectations from the scientific and engineering communities on which extra-scientific decisions can and should be based. While the rising levels of CO_2 are predictions in this latter sense, even the best of our predictions about the ecological effects of rising CO_2 are only hypotheses, part of the research program in global change, but not yet firm bases for policy decisions.

It has been said many times that as science progresses we answer questions, but we often raise more questions than we answer. Perhaps one of the most important things we have learned from CO_2 research over the past decade is that things are not as simple as we might have hoped, that we do not know very much, that it will not be easy to make predictions about global effects. Ecology as a science is not yet developed enough to produce the predictions we are being asked to make. We must resist the temptation to confuse the importance of an issue with our ability to understand it. Questions concerning the ecological effects of anthropogenic environmental changes such as elevated CO_2 are perhaps among the most important scientific questions facing the world today, but it does not follow that we have or soon will have the means to answer them. Policy makers want predictions, and they give scientists grants to produce such predictions. I don’t think ecology will be well served if we claim to understand more than we do. Rather we are obliged to communicate to policy makers the concept of uncertainty with which they seem so uncomfortable. But if we can use the opportunity presented by global changes such as elevated CO_2 to do the fundamental ecological research needed to develop a scientific understanding of the processes involved, we can bring scientific opportunity and practical need together in a way that will further both our science and our public responsibility.

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References

Allen, T.F.H. and Starr, T.B. (1982). "Hierarchy: Perspectives for Ecological Complexity." University of Chicago Press, Chicago.

Bazzaz, F.A. (1990). The response of natural ecosystems to the rising global CO_2 levels. *Ann. Rev. Ecol. Syst.* **21**, 167-196.

Bazzaz, F.A., Bassow, S.L., Berntson, G.M. and Thomas, S.C. (1995). Elevated CO_2 and terrestrial vegetation: Implications for and beyond the global carbon budget. *In* "Global Change and Terrestrial Ecosystems" (B. Walker, ed.), Cambridge University Press, Cambridge, in press.

Bazzaz, F.A. and Garbutt, K. (1988). The response of annuals in competitive neighborhoods: Effects of elevated CO_2. *Ecology* **69**, 937-46.

Bazzaz, F.A. and McConnaughay, K.D.M. (1992). Plant-plant interactions in elevated CO_2 environments. *Aust J Bot* **40**, 547-63.

Bloom, A.J., Chapin, F.S. and Mooney, H.A. (1985). Resource limitation in plants - an economic analogy. *Ann. Rev. Ecol. Syst.* **16**, 363-392.

Ehleringer, J.R. and Field, C.B. (eds.). (1993) "Scaling Physiological Processes: Leaf to Globe." Academic Press, San Diego.

Koch, G.W. (1993). The use of natural situations of CO_2 enrichment in studies of vegetation responses to increasing atmospheric CO_2. *In* "Design and Execution of Experiments on CO_2 Enrichment." (E.-D. Schulze and H.A. Mooney, eds.), pp. 381-391. Ecosystem Research Report 6, Commission of the European Community, Brussels.

Körner, C. (1988). Does global increase of CO_2 alter stomatal density? *Flora* **181**, 253-257.

Körner, C. (1993). CO_2 fertilization: the great uncertainty in future vegetation development. *In* "Vegetation Dynamics and Global Change." (A.M. Solomon and H.H. Shugart, eds.), pp. 53-70. Chapman and Hall, London.

Körner, C. and Miglietta, F. (1994). Long term effects of naturally elevated CO_2 on mediterranean grassland and forest trees. *Oecologia* **99**, 343-351.

Levin, S.A. (1993). Concepts of scale at the local level. *In* "Scaling Physiological Processes: Leaf to Globe." (J.R. Ehleringer and C.B. Field, eds.), pp. 7-19. Academic Press, San Diego.

Loehle, C. (1983). Evaluation of theories and calculation tools in ecology. *Ecol. Model.* **19**, 230-247.

Miglietta, F. and Raschi, A. (1993). Studying the effect of elevated CO_2 in the open in a naturally -enriched environment in Central Italy. *Vegetatio* **105**, 391-400.

Miglietta, F., Raschi, A., Bettarini, I., Resti, R. and Selvi, F. (1993). Natural CO_2 springs in Italy: a resource for examining long-term response of vegetation to rising atmospheric CO_2 concentrations. *Plant, Cell Environ.* **16**, 873-878.

Mooney, H.A., Drake, B.G., Luxmoore, R.J., Oechel, W.C. and Pitelka, L.F. (1991). Predicting ecosystem responses to elevated CO_2 concentrations. *BioSci.* **41**, 96-104.

Mooney, H.A. and Koch, G.W. (1994). The impact of rising CO_2 concentrations on the terrestrial biosphere. *Ambio* **23**, 74-76.

O'Neill, R.V., DeAngelis, D.L., Wade, J.B. and Allen, T.F.H. (1986). "A Hierarchical Concept of Ecosystems." Princeton University Press, Princeton.

Patten, B.C. (ed.) (1983) "Systems Analysis and Simulation in Ecology." Academic Press, New York.

Peters, R.H. (1991). "A Critique for Ecology." Cambridge University Press, Cambridge.

Reekie, E.G. and Bazzaz, F.A. (1991). Phenology and growth in four annual species grown in ambient and elevated CO_2. *Can. J. Bot.* **69**, 2475-2481.

Reynolds, J.F. and Acock, B. (1985). Predicting the response of plants to increasing carbon dioxide: A critique of plant growth models. *Ecol. Model.* **29**, 107-129.

Reynolds, J.F., Hilbert, D.W. and Kemp, P.R. (1993). Scaling ecophysiology from the plant to the ecosystem: A conceptual framework. *In* "Scaling Physiological Processes: Leaf to Globe." (J.R. Ehleringer and C.B. Field, eds.), pp. 127-140. Academic Press, San Diego.

Tilman, D.G. (1986). Resources, competition and the dynamics of plant communities. *In* "Plant Ecology." (M.J. Crawley, ed.) pp. 51-75. Blackwell, Oxford.

von Faber, F.C. (1925). Untersuchungen über die Physiologie der javanischen Solfataren-Pflanzen. *Flora N.F.* **18/19**, 89.

Weiner, J. (1995). On the practice of ecology. *J. Ecol.* **83**, 153-158.

Woodward, F.I. (1987). Stomatal numbers are sensitive to increases in CO_2 from pre-industrial levels. *Nature* **327**, 617-618.

Woodward, F.I., Thompson, G.B. and McKee, I.F. (1991). The effects of elevated concentrations of carbon dioxide on individual plants, populations, communities and ecosystems. *Ann. Bot.* **67** (Supplement 1), 23-38.