Blaming the trees: a critique of research on forest responses to high CO_2

Our success in predicting future ecosystem productivity and global carbon balance depends on correctly assessing the role of terrestrial vegetation in global climatic change. Because long-lived woody plants comprise a substantial portion of terrestrial carbon pools and fluxes, the growth and physiological responses of trees are of particular importance. Global-change models demand parameter estimates for these responses. Such estimates will be provided, whether they are rigorously supported by data or are actually only rough 'guesses'. As a research community, we have committed basic errors of method and interpretation that have not been appropriately acknowledged. Here, we attempt to explain how the trees themselves have driven us to such a desperate state.

... because tree growth curves *are* curved

Linear relationships have an ineluctable appeal, and consequently we insist on using simplistic, univariate indices to describe multivariate and nonlinear growth processes. For example, the enhancement ratio is the most widely used index expressing effects of elevated CO_2 on plant growth[1]. When we compute enhancement ratios at several points in time, we usually observe substantial rises and declines in their values and interpret such temporal changes as indicating temporal variation in the CO_2 response. Such a conclusion is incorrect, however, because we forget that growth curves are not linear. It is a simple mathematical truth that a ratio of two nonlinear growth functions will inevitably change with time. For example, any enhancement of the early relative growth rate of a plant will lead to a humped pattern of response in size ratios: they will show a rise (in plants far from their mature size) and then a decline. Consequently, substantial and highly misleading differences can arise between the calculated enhancement ratio at its maximum and the final stimulation of plant growth[2].

... because trees live too long

Enhancement at maturity is more meaningful for the long-term estimation of CO_2 effects, but we have no direct estimates of effects on asymptotic size in long-lived trees. The median duration of our experiments on trees is 195 days (Ref. 3), a very small fraction of the growth curve of a typical tree. Doomed to study seedlings or saplings, we reluctantly learn that the magnitude of such early enhancements overestimates the response of mature individuals. We still do not know how to extrapolate from seedling responses to those of mature trees and yet we parameterize models as if we had good numbers at hand.

... because the calculations are complicated

As empiricists, we have no time for the vagaries of mathematics: we forget that expressing the growth enhancements as ratios directly introduces biases in estimating the magnitude of CO_2 effects. This 'ratio calculation bias' is independent of the 'nonlinearity bias' already described and is exacerbated by small sample sizes, high variance among plants and flawed experimental designs. The third bias in our estimates of growth enhancement is caused by differences in plant variability between treatments, even when there is no CO_2 effect on average plant growth.

... because trees and plots are not identical

We design our experiments without applying the basic rules and regulations of experimental design and then we hope for the best. A survey of the literature from the studies of 70 tree species examined to date[1] yields a grim picture. Among the studies (n = 56) published in refereed journals, 80% presented results of pseudoreplicated experiments, in which CO_2 levels affected unreplicated units (included here are those cases where we felt it was unimportant to inform the reader whether replication at the chamber level was employed or not)! Rotating groups of plants between experimental units, which we frequently do in noble desperation, can commonly make the problem worse. It confounds the CO_2 treatments with a unique sequence in which plants experience growth units of different quality. Consequently, our empirical database suffers from rampant bias resulting from pseudoreplication.

Recently, there have been some valiant attempts at making sense of the diversity of species responses via meta-analysis[4]. However, we forget that even this technique is not immune to the virus of pseudoreplication. Furthermore, the nonlinearity of growth curves for species with different life spans means that there is no single 'correct' point during ontogeny that we can use for comparison across species. These considerations are of critical importance, especially because we often cite or reprint the results of data compilations at face value, without reference to the quality of the original studies. It seems that while CO_2 levels have been rising, our statistical awareness has stood still.

... because we think the errors will average out

We could argue that although any individual species-level measurement might be incorrect, such errors will average out in a large compilation. Unfortunately, because at least three of the four biases described here (resulting from nonlinearity, calculation and variability) result in a systematic and substantial overestimation of CO_2 effects, the average enhancement values themselves are incorrect. In addition, we forget that we should indeed care about the precision and accuracy of individual estimates, because they are needed to set the parameters for various theoretical models of global change. If, as argued a few years ago[5], variation in CO_2 responses among species leads to community change and a 30% additional increase in total forest basal-area in the next century, incorrectly estimated enhancement ratios could lead us astray. The potential for generating 'globally' misleading predictions and badly misguided policies is great.

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