Blaming the trees: a critique of research on forest responses to high CO₂

O ur success in predicting future eco-
magnitude 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 esti-
mates for these responses. Such estimates will be provided, whether they are rigor-
ously supported by data or are actually only rough ‘guesses’. As a research com-
munity, we have committed basic errors of method and interpretation that have not been appropriately acknowledged. Here, we attempt to explain how the trees them-
selves have driven us to such a desperate state.

… because tree growth curves are curved

Linear relationships have an ineluct-
able appeal, and consequently we insist on using simplistic, univariate indices to de-
scribe multivariate and nonlinear growth processes. For example, the enhancement ratio is the most widely used index ex-
pressing effects of elevated CO₂ on plant growth. When we compute enhancement ratios at several points in time, we usually observe substantial rises and declines in their values and interpret such temporal variation as indicating temporal variation in the CO₂ response. Such a conclusion is incorrect, however, because we forget that growth curves are not linear. It is a sim-
ple mathematical truth that a ratio of two nonlinear growth functions will inevitably change with time. For example, any en-
hancement of the early relative growth rate of a plant will lead to a damped pattern of response in size ratios: they will show a rise (in plants far from their mature size) and then a decline. Consequently, sub-
stantial and highly misleading differences can arise between the calculated enhance-
ment ratio at its maximum and the final stimulation of plant growth.

… because trees live too long

Enhancement at maturity is more mean-
ingful for the long-term estimation of CO₂ effects, but we have no direct estimates of effects on asymptotic size in long-lived trees. The median duration of our experi-
ments 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 param-
eterize 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 esti-
mating the magnitude of CO₂ 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 CO₂ effect on average plant growth.

… because trees and plots are not identical

We design our experiments without applying the basic rules and regulations of the experimental design and then we hope for the best. A survey of the literature from the studies of 70 tree species examined to date yields a grim picture. Among the studies (n = 50) published in refereed journals, 80% presented results of pseudoreplicated experiments, in which CO₂ 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 experi-
mental units, which we frequently do in noble desperation, can commonly make the problem worse. It confounds the CO₂ treatments with a unique sequence in which plants experience growth units of different quality. Consequently, our em-
pirical 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. However, we forget that even this tech-
nique is not immune to the virus of pseudo-
replication. 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 im-
portance, 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 CO₂ levels have been rising, our statistical awareness has stood still.

… because we think the errors will average out

We could argue that although any indi-
vidual species-level measurement might be incorrect, such errors will average out in a large compilation. Unfortunately, be-
cause at least three of the four biases de-
scribed here (resulting from nonlinearity, calculation and variability) result in sys-
tematic and substantial overestimation of CO₂ effects, the average enhancement val-
ues 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, variation in CO₂ responses among species leads to community change and a 30% additional increase in total for-
est basal-area in the next century, incor-
rectly estimated enhancement ratios could lead us astray. The potential for generat-
ing ‘globally’ misleading predictions and badly misguided policies is great.

M. Jasieński
Dept of Organismic and Evolutionary Biology, Harvard University, 16 Divinity Avenue, Cambridge, MA 02138, USA
(jasien@post.harvard.edu)

S.C. Thomas
College of Forest Resources, Univ. of Washington, Seattle, WA 98105, USA

F.A. Bazzaz
Dept of Organismic and Evolutionary Biology, Harvard University, 16 Divinity Avenue, Cambridge, MA 02138, USA

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