BIOMASS AND TOXICITY RESPONSES OF POISON IVY (*TOXICODENDRON RADICANS*) TO ELEVATED ATMOSPHERIC CO_2: COMMENT

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As the earth's environment changes with the alteration of important putative environmental drivers (e.g., CO_2, temperature, nitrogen deposition, biotic invasions, and the frequency and severity of extreme weather events), ecologists and environmental biologists are scrambling to predict what the world may look like under these new conditions. To accomplish this goal, these scientists often use experimental manipulations of the most likely drivers of community and ecosystem change, particularly CO_2, temperature, and nitrogen (e.g., Bergner et al. 2004, Mohan et al. 2006, Reich et al. 2006*a*). But are these relatively small-scale experiments enough to give us an accurate picture of the structure and function of a future world and is there a way to test their predictions?

In a six-year study on the impact of elevated CO_2 on the growth and toxicity of poison ivy (*Toxicodendron radicans*) at the Duke Forest FACE site in North Carolina, USA, Mohan et al. (2006) reported that mean plant biomass of poison ivy increased significantly more in elevated CO_2 than in ambient CO_2 (Fig. 1), and that this increase was far more than in other woody species. They found that elevated atmospheric CO_2 substantially increased poison ivy photosynthesis, water use efficiency, urushiol (the "toxic" compound found in poison ivy), growth, and population biomass. Consequently, Mohan et al. (2006) concluded that poison ivy is likely to become far more abundant (and toxic) with increasing concentrations of atmospheric CO_2. Lianas (woody vines), such as poison ivy, are hypothesized to benefit more from elevated CO_2 than other woody growth forms because lianas allocate a relatively large proportion of their biomass to leaves (a result of low structural tissue

requirements), and thus they should gain more leaf area per total plant biomass with increasing CO_2 and carbon fixation than other growth forms. More leaf area, in turn, would allow lianas to fix even more carbon and thus increase faster in total biomass (size and abundance) with elevated CO_2 (e.g., Körner 2006, Mohan et al. 2006, Zotz et al. 2006). The study by Mohan and colleagues was methodologically sound and their findings and conclusions were consistent with other experimental studies on the effects of elevated CO_2 on liana performance (e.g., Sasek and Strain 1990, 1991, Condon et al. 1992, Granados and Körner 2002, Hättenschwiler and Körner 2003, Zotz et al. 2006). In most cases, however, we have little or no ability to test the validity of predictions based on these types of studies because we lack long-term data on the change in natural plant communities.

In a separate study, Londré and Schnitzer (2006) used empirical observations of temperate liana abundance in the interiors of 14 forests in southern Wisconsin, USA, over a 45-year period (1959–2005) to test whether these long-term data were consistent with the hypothesis that lianas, including poison ivy, have proliferated more than co-occurring trees with global change, which includes the increases in CO_2 (reviewed by Schnitzer and Bongers 2002, Körner 2006). Globally, atmospheric CO_2 levels have risen ~40% over the last 150 years, with nearly 60% of this increase occurring after 1958 (Keeling and Whorf 2005). Thus, if the predictions of experimental studies previously cited are accurate and broadly applicable, both poison ivy and total liana density and biomass should have increased in Wisconsin forests over the past 45 years.

Curiously, the empirical observations of Londré and Schnitzer did not match the predictions of experimental studies. Not only did mean liana abundance and basal area remain constant over the past 45 years in Wisconsin forests (Londré and Schnitzer 2006), but poison ivy was the only species to decrease significantly over this period (Fig. 2). In a separate study in an old-growth maritime forest on Fire Island in New York, USA, Forrester et al. (2006) reported that over a 19-year period (1967–1986) poison ivy ground cover decreased from nearly 10% to <1%. There are a number of potential and non-mutually exclusive explanations to reconcile the disparate findings between the predictions generated from experimental studies and the long-term observational studies.

One likely explanation is that plant growth and proliferation rates are controlled by multiple factors, not just by CO_2 (e.g., Reich et al. 2006*b*). For example, although both mean and low winter temperatures have increased in Wisconsin forests over the last 45 years (Londré and Schnitzer 2006), lianas may still be limited more by freezing winter temperatures and a short growing season than by CO_2. Large vessel elements and relatively thin stems that lack insulation make lianas vulnerable to freezing-induced embolism or possibly the
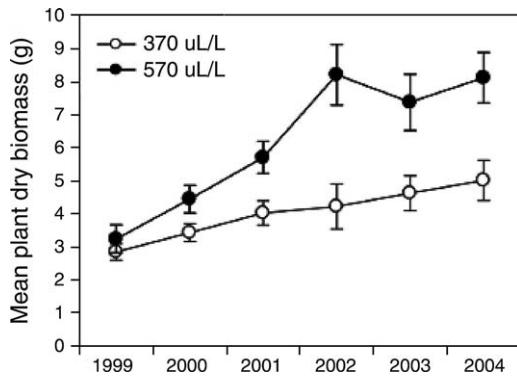
FIG. 1. The change in plant biomass (mean ± SE) from 1999 until 2004 for poison ivy grown in ambient (~370 μL/L) and high (570 μL/L) CO_2 levels at the Duke Face site, North Carolina, USA. This figure is adapted from Mohan et al. (2006) with permission from PNAS (copyright 2006) National Academy of Sciences, USA.

rupturing of vessel elements, which render the vascular system inoperable and ultimately kill the plant (Sperry et al. 1987, Ewers et al. 1991). While many temperate liana species have special adaptations to avoid freezing (e.g., Sperry et al. 1987, Schnitzer 2005), these adaptations come at a cost, which includes an abbreviated growing season compared to many shrubs and trees. For example, many liana species in temperate forests flush their leaves relatively late in the spring and/or drop their leaves early in the autumn, presumably due to their vulnerability to freezing (Schnitzer 2005). Leaves of poison ivy (T. radicans), grape (Vitis spp.), and Virginia creeper (Pathenocissus quinquefolia) typically senesce much earlier than their host trees, resulting in a relatively short growing season (Stiles 1982). Although Stiles (1982) provided compelling evidence that early senescence by the lianas T. radicans and Parthenocissus spp. is an adaptation for seed dispersal (foliar fruit flag hypothesis), early senescence may actually be driven by the vulnerability of lianas to freezing and their need to prepare for winter (e.g., drain their vessel elements in the case of members of the Vitaceae; Schnitzer 2005).

The effect of a shorter growing season may be more detrimental for lianas in northern deciduous forests than in coniferous forests located in a moderate climate, such as the forest at the Duke FACE site. In northern deciduous forests, lianas are unable to take advantage of elevated light regimes in the early or late seasons, before overstory leaf flush and after leaf senescence, whereas competing shrubs and understory trees appear to benefit from early spring and late fall photosynthesis (Harrington et al. 1989). Consequently, if an abbreviated growing season and freezing winters limit lianas but not their competitors (trees and shrubs) in northern deciduous forests, then the potential increases from elevated CO_2 may have little relative benefit to lianas in those forests compared to the pine forest at the Duke FACE site.

Light availability may also be an important determinant of liana distribution within temperate forests (Londré and Schnitzer 2006), and the interaction between elevated CO_2 and light availability may provide an explanation for the discrepancy between the experimental and observational studies. For instance, Hättenschwiler and Körner (2000) reported that light availability in the understory of a mixed broadleaf–coniferous forest in Switzerland strongly determined whether tree seedlings responded to elevated CO_2, with the growth rate of moderately shade-tolerant tree species increasing with elevated CO_2 only under relatively high (4.8% full sun) understory light levels; whereas, deeply shade-tolerant species responded to elevated CO_2 at low understory light levels (0.8% full sun; see also Zotz et al. 2006). Other studies demonstrate that the ability to use enhanced resources other than light is severely constrained in relatively shaded understories (e.g., Walters and Reich 2000). At the Duke FACE site, where Mohan et al. (2006) studied poison ivy, the canopy is dominated by densely planted ~25-year-old shade-intolerant loblolly pines, which, along with a mix of subcanopy hardwood trees, considerably reduce the mean understory light levels to <3% of full sunlight (J. Mohan, personal communication). Nevertheless, this coniferous forest may still allow more

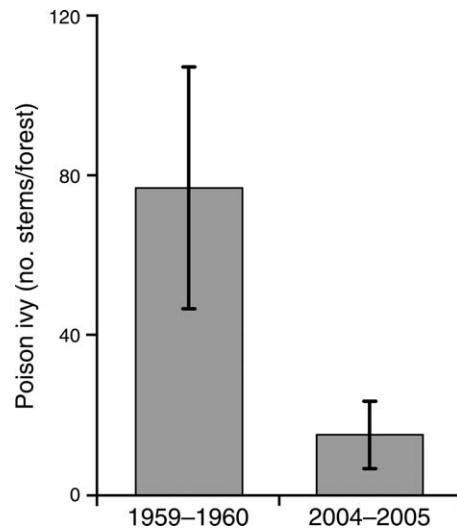FIG. 2. The number of poison ivy vines per forest base (mean ± SE) on 14 deciduous forests in Wisconsin, USA. Lianas were censused in 1959–1960 and in 2004–2005 using 40 point quarter points (160 total measurements). Poison ivy decreased significantly over the 45-year period (Wilcoxon's signed-ranks test, P = 0.02, T_S = 19.5, df = 13). Nearly identical results were found using 40 1-m^2 ground cover plots in these same forests, which generally included smaller poison ivy individuals than in the point quarter method (P = 0.01, T_S = 32.5, df = 13; data from Londré and Schnitzer 2006). Forest size was variable, but all forests were >18 ha in area and had little or no disturbance since the 1960 measurements. Because this is a relative comparison using the same methods in each forest, the actual size of each forest is not as relevant as the comparison between 1960 and 2005.

light penetration into the understory than in the older and relatively dark broadleaf deciduous forests studied by Londré and Schnitzer, which were dominated by mid- and deeply shade-tolerant species (Reich et al. 2003). A light $\times$ CO_2 interaction may have enhanced the response of poison ivy in the pine-dominated stand, but light may have been too limiting for CO_2 to have a strong effect in the shadier broadleaf stand.

The decrease in the abundance and basal area of poison ivy in Wisconsin forests over the past 45 years may be a result of natural successional changes in temperate forests, as these forests grow older and darker. If so, the successional changes in Wisconsin forests may have overwhelmed or prevented the potential increase in poison ivy abundance and biomass from increased CO_2. We note, however, that we lack the data necessary to test whether the understory of these forests has changed over the last half century.

A second possible explanation for the disparate findings between the experimental and observational studies is that top-down trophic control from white-tailed deer and other animals may have overwhelmed the positive effects of CO_2, thereby reducing poison ivy abundance over the past 45 years. Mammals were excluded from the DUKE face study so that the impact of CO_2 on plant growth would not be confounded by herbivory. Deer foraging, however, can substantially alter the structure and composition of temperate forests (Rooney and Waller 2003), and deer populations in southern Wisconsin have increased two- to fivefold over the past 40 years, from 52 to 129 deer/km^2 in the late 1960s to $\sim$259 deer/km^2 in 2004 (WDNR 2004). Poison ivy is a preferred browse species for deer and other animals (Sotala and Kirkpatrick 1973), and thus the large increase in deer abundance over the last 40 years may also account for the decrease in poison ivy in Wisconsin forests. Nevertheless, excluding deer for 16 years on Fire Island (from 1986 to 2002) did not significantly increase poison ivy abundance (mean cover increased from 0.1% to just 0.4% over this period; Forrester et al. 2006), suggesting that deer are not the only factor controlling poison ivy.

A third possible explanation is that the level of CO_2 in the atmosphere is not yet high enough to trigger the increase in liana abundance and basal area. These increases may still be years away. While there is evidence that many species have already responded to environmental changes (e.g., many thousands of species' distributions have shifted poleward or to higher elevation; Parmesan 2006), it is possible that levels of CO_2 will have to be far higher than 380 ppm to allow liana species to overcome such limiting or co-limiting factors as cold winter temperature, length of growing season, light, nutrients, or top-down regulation by mammals. This claim, however, is inconsistent with the findings of Granados and Körner (2002), who reported that lianas grew 48% more at an elevated atmospheric

CO_2 level of 420 ppm compared to 280 ppm, but that the rate of liana biomass increase dropped to 23% at 560 ppm CO_2 (compared to 420 ppm; see also Körner 2004). Furthermore, from a strictly physiological perspective, the effect of increasing CO_2 on plant growth rate may be relatively small compared to the effects of natural microhabitat variability in light or soil nutrients. The latter can lead to 100-fold (or greater) differences in growth of individual plants, whereas a small increase in CO_2 resulted in $\sim$50% increase in liana biomass (Granados and Körner 2002), and more generally, a doubling of CO_2 typically results in a $\sim$1.3-fold increase in plant growth on average (Ainsworth and Long 2005). Thus, variability of resources could mask, limit, or even eliminate the CO_2 effect for poison ivy in many habitats.

A fourth potential explanation may be the artificial nature of elevated CO_2 studies themselves. Klironomos et al. (2005) reported that communities and ecosystems respond very differently to the large, single-step increases in CO_2 implemented by most studies, compared with the more gradual increases in CO_2 that are occurring in the atmosphere. This finding may be due to the ability of plants to acclimate physiologically to gradual increases in CO_2 via plastic responses or microevolutionary changes (e.g., Ward and Kelly 2004, Körner et al. 2005), which would be less likely with a large, single-step increase. If this scenario is true, the lack of change in liana abundance or basal area in Wisconsin forests over the last 45 years may be attributable to the gradual physiological acclimation of plant populations to the increase in atmospheric CO_2, without a net change in the competitive hierarchy among growth forms.

Long-term observational studies, such as that of Londré and Schnitzer (2006), provide information on how communities and ecosystems are changing over time; however, they provide little capacity to explain the mechanisms responsible for that change (or lack thereof). In contrast, controlled experimental studies, such as that of Mohan et al. (2006), can precisely examine the putative factors controlling plant communities. Elevated atmospheric CO_2 may indeed increase poison ivy abundance and biomass in forests, as predicted by Mohan and colleagues, but this increase may become evident only when other overriding factors are removed. Consequently, extrapolating the findings of single-factor experimental studies to predict future community and ecosystem level changes remains exceedingly difficult, and we have yet to determine how broadly to apply predictions from these experiments. While the extent to which the findings of relatively small-scale experimental studies are universal is a common dilemma in ecology, predictions generated from studies on global environmental change differ in that they typically cannot be tested without long-term data, which often do not exist. Furthermore, because we typically test only one to a few factors of environmental

change (e.g., CO_2, N, ozone), we are unable to make accurate predictions beyond those particular factors.

Although far from perfect, controlled global change studies such as those of Mohan and colleagues likely still provide the best available insight for predicting the nature, direction, and magnitude of global change on community dynamics and ecosystem function in a future environment. Factorial approaches that manipulate multiple putative factors that control plant dynamics may further elucidate the relative importance of and interactions among these factors. Nevertheless, the differing results between the experimental and observational studies mentioned here illustrate the difficulty in predicting large-scale, long-term effects from relatively small-scale experimental studies. Long-term observational studies can serve as a guide for controlled experiments, while controlled experiments can serve to test possible mechanisms involved in long-term observed trends, and both approaches combined will provide more accurate predictions of community composition, dynamics, and ecosystem function in a future environment than will either approach alone.

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