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Mechanistic insights on the responses of plant and ecosystem gas exchange to global environmental change: Lessons from Biosphere 2

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ABSTRACT

Scaling up leaf processes to canopy/ecosystem level fluxes is critical for examining feedbacks between vegetation and climate. Collectively, studies from Biosphere 2 Laboratory have provided important insight of leaf-to-ecosystem investigations of multiple environmental parameters that were not before possible in enclosed or field studies. B2L has been a testing lab for the applicability of new technologies such as spectral approaches to detect spatial and temporal changes in photosynthesis within canopies, or for the development of cavity ring-down isotope applications for ecosystem evapotranspiration. Short and long term changes in atmospheric CO_2, drought or temperature allowed for intensive investigation of the interactions between photosynthesis and leaf, soil and ecosystem respiration. Experiments conducted in the rainforest biome have provided some of the most comprehensive dataset to date on the effects of climate change variables on tropical ecosystems. Results from these studies have been later corroborated in natural rainforest ecosystems and have improved the predictive capabilities of models that now show increased resilience of tropics to climate change. Studies of temperature and CO_2 effects on ecosystem respiration and its leaf and soil components have helped reconsider the use of simple first-order kinetics for characterizing respiration in models. The B2L also provided opportunities to quantify the rhizosphere priming effect, or establish the relationships between net primary productivity, atmospheric CO_2 and isoprene emissions.

1. Introduction

Forcing factors of climate change are expected to alter the net carbon balance of terrestrial vegetation causing feedbacks on climate [1,2]. The large global photosynthetic flux from terrestrial vegetation [3,4] has potential to mitigate the rate at which CO_2 accumulates in the atmosphere if carbon gain exceeds respiratory losses. At first, the scientific community engaged in climate change research with emphasis on leaf-level studies that relied on manipulations (by changing air CO_2 or O_3 levels) using mostly growth chambers [5]. In the early 1990s, field studies on effects of climate change forcing factors on ecosystem gas exchange were rare and confined to short stature vegetation [6–8]. The realization that northern forested regions are building up a sustained C sink over several years [9] focused the attention on responses of woody vegetation to elevated CO_2 with the development of Free Air Carbon Enrichment studies (FACE) in forest stands (e.g.[10]). However, teasing apart scalable mechanistic parameters that drive change in ecosystem flux has been problematic (e.g., [11,12]). Issues of physiological acclimation of photosynthesis and respiration [5,13] and interaction between forcing factor variables (e.g., CO_2, precipitation, temperature) have required continuous experimentation in controlled environments with limited applicability to tall and mixed vegetation in the field.

The Biosphere 2 Laboratory (B2L) has been the first facility of its kind to fill the void between experiments in small growth chambers and natural forest stands. The facility has provided the opportunity for ecosystem gas exchange studies, development and testing of plant growth models, and deployment of new spectral techniques and equipment for photosynthesis measurements. The facility was also employed to develop ring-down cavity spectrometry for detecting water isotopes in situ [14] and for the design of Wastewater Gardens, which are being deployed in a number of developing countries [15]. More importantly B2L remains one of the few places (perhaps the only one) where interactive effects of CO_2, temperature and drought have been studied in tropical rainforest vegetation. In this synthesis, we focus on the contributions of B2L to the responses of terrestrial plants and ecosystems to global climate change. The ocean biome has been recently reviewed elsewhere [16], showing interesting parallelisms with

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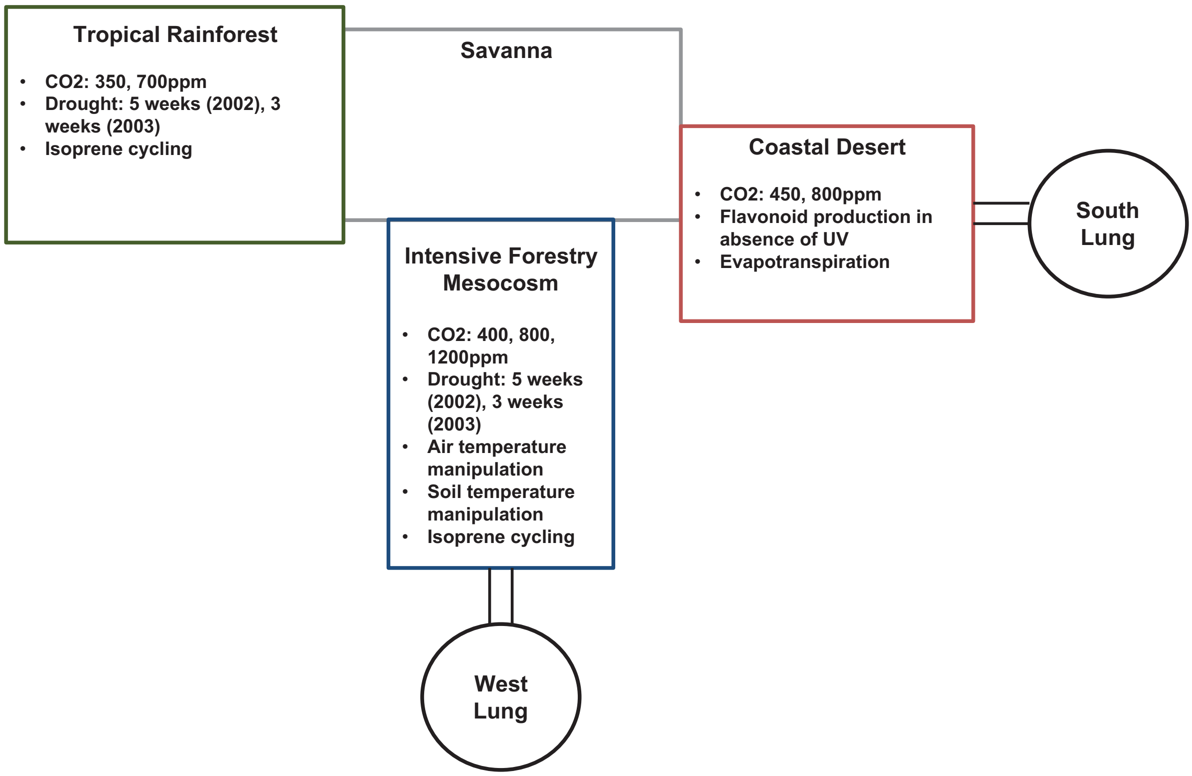

Fig. 1. The climate change manipulations made in the tropical rainforest, desert and intensive forest biome during the operation of B2L.

the responses of terrestrial mesocosms to environmental factors reviewed here.

1.1. The use of Biosphere 2 for climate change research

The B2L site, located in Oracle, Arizona, USA, began in the early 1990s as an investigation of human space colonization in a closed, self-sustainable environment. The first human inhabited mission revealed engineering flaws that resulted in a sharp decline in oxygen concentrations due to soil metabolic activity and CO_2 sorption to concrete surfaces [16,17]. By 1994, the concrete was sealed and the operation of B2L, then led by Columbia University, had a renewed focus on ecosystem responses to climate change. The new research thrust of the 1.25 ha of B2L focused on simulated natural biomes: desert, ocean, tropical rainforest, intensive forestry, savanna and marsh (for system description see [16,18,19]). The B2L included an intensive agricultural biome for food production that was later transformed in a poplar forest plantation (intensive forest biome, IFB) exposed to three levels of atmospheric CO_2. This review focuses on research outcomes from the tropical, desert and forest plantation mesocosms (Fig. 1) that have impacted plant sciences on other systems.

Two technical aspects of B2L proved to be essential for its use in climate change research. First, the facility was designed to be airtight, with volume expansion areas ("lungs") maintaining constant pressure within the facility as temperature varied (Fig. 1). Second the leak rate was known, and found to be approximately 10% volume per year using sulfur hexafluoride (SF_6), about tenfold better than the industrial standards for engineered facilities at the time [18]. Therefore, B2L lent itself to be used as a whole-ecosystem gas exchange cuvette (which could be operated as a closed or semi-open system) enclosing multiple individuals of full grown vegetation. The B2L has the additional benefit to readily manipulate major environmental drivers of ecosystem change such as CO_2, precipitation, or temperature; these manipulations can be repeated over time and across vegetation types (e.g., [20,21]; Fig. 1). These approaches have allowed for scaling-up comparisons of leaf to canopy level processes [22,23], which are essential for determining ecosystem and global carbon fluxes, and their responses to climate change.

Biosphere 2 circumvented some of the problems associated with laboratory experiments. Laboratory experiments unintentionally restrict plant growth, mostly due to space limitations (e.g., plant size, restricted root growth), light or other factors that constrain extrapolation of results [24]. Open top chambers (OTCs) used in field experiments have provided valuable data on ecosystem gas exchange, but OTCs may cause pressure changes, disrupt air flow patterns, suppress soil respiration, reduce precipitation and light availability, or increase temperature within the enclosed vegetation [5,25].

In contrast, Biosphere 2 is essentially a gas exchange cuvette large enough to allow investigation of entire ecosystem dynamics with a precise simulated environment with the exception of a slight reduction in light intensity or photoperiod control. Overall, the biomes at B2L were comprised of hundreds of species, creating dynamic and functioning ecosystems [19]. The sealed environment was used for elevated (and reduced) [CO_2] experiments in multiple mesocosms [14,26,27]. Some of these manipulations were background for secondary manipulations such as progressive drought or temperature [21]. Thus the B2L became an important tool for repeated leaf-to-ecosystem investigations of multiple environmental parameters that were not always possible in enclosed or field studies (Fig. 1).

Biosphere 2 had some shortcomings. Low replication is a major issue in climate manipulation studies, and more so at B2L where only one replicate for each biome or treatment were represented. Soil origin and volume also raises some concerns. Soils were not always representative of the climatic regions represented at B2L. For instance, soils in the tropical biome were a mixture of temperate, subtropical and mix organic substrates as a function of