

RESEARCH ARTICLE

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Key Points:

- Model simulation accurately captured the seasonality of vegetation activity
- Net ecosystem productivity decreased under reduced summer rainfall and increased temperature scenarios
- Elevated CO₂ scenarios offset the negative impacts of meteorological conditions

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Climate Change Impacts on Net Ecosystem Productivity in a Subtropical Shrubland of Northwestern México

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Abstract The sensitivity of semiarid ecosystems to climate change is not well understood due to competing effects of soil and plant-mediated carbon fluxes. Limited observations of net ecosystem productivity (NEP) under rising air temperature and CO₂ and altered precipitation regimes also hinder climate change assessments. A promising avenue for addressing this challenge is through the application of numerical models. In this work, we combine a mechanistic ecohydrological model and a soil carbon model to simulate soil and plant processes in a subtropical shrubland of northwest México. Due to the influence of the North American monsoon, the site exhibits net carbon losses early in the summer and net carbon gains during the photosynthetically active season. After building confidence in the simulations through comparisons with eddy covariance flux data, we conduct a series of climate change experiments for near-future (2030–2045) scenarios that test the impact of meteorological changes and CO₂ fertilization relative to historical conditions (1990–2005). Results indicate that reductions in NEP arising from warmer conditions are effectively offset by gains in NEP due to the impact of higher CO₂ on water use efficiency. For cases with higher summer rainfall and CO₂ fertilization, climate change impacts lead to an increase of ~25% in NEP relative to historical conditions (mean of 66 g C m⁻²). Net primary production and soil respiration derived from decomposition are shown to be important processes that interact to control NEP and, given the role of semiarid ecosystems in the global carbon budget, deserve attention in future simulation efforts of ecosystem fluxes.

1. Introduction

Although the carbon sink strength of semiarid ecosystems is still under debate (Xiao et al., 2011), recent studies have recognized that these areas have a dominant role, stronger than other biogeographic regions, in regulating the intra-annual and interannual variability of the global carbon cycle (Ahlström et al., 2015; Poulter et al., 2014). A transition to more arid conditions (e.g., increasing temperatures and prolonged drought spells) in these regions (Pachauri et al., 2014; Seager et al., 2007) will have implications on the productivity of semiarid ecosystems. This is the case for most of the North American monsoon (NAM) region, which comprises semiarid areas in the southwestern United States and northwestern México (Douglas et al., 1993; Vivoni et al., 2008). The NAM system is a pronounced increase in precipitation during the warm season (July–September) leading to increased biological activity (Flato et al., 2013; Forzieri et al., 2014). Remote sensing analyses have quantified the spatial and temporal variability of vegetation greening during the NAM (e.g., Tang et al., 2012; Watts et al., 2007). However, ecosystem processes regulating the carbon cycling are not understood well enough to anticipate the implications of climate change on the net carbon balance of these semiarid ecosystems.

The eddy covariance (EC) technique has become a useful approach for measuring water, energy, and carbon fluxes at the ecosystem level (Baldocchi et al., 2001), with several studies conducted in different ecosystems in the NAM region (e.g., Anderson & Vivoni, 2016; Méndez-Barroso et al., 2014; Pérez-Ruiz et al., 2010; Scott et al., 2010, 2015; Yépez et al., 2007). By quantifying carbon dioxide (CO₂) exchanges between ecosystems and the overlying atmosphere (Loescher et al., 2003), net ecosystem productivity (NEP) can be measured via the EC method as a degree of the metabolic activity of a terrestrial ecosystem. Furthermore, traditional flux partitioning models have been applied to estimate NEP components, gross primary productivity (GPP)

and ecosystem respiration (R_{ECO}) (Reichstein et al., 2005; Stoy et al., 2006). Since NEP consists of the difference between GPP and R_{ECO} , its response to hydrometeorological conditions has been difficult to identify (Biederman et al., 2016; Nayak et al., 2015; Scott et al., 2015). This is primarily due to the differential sensitivity of GPP and R_{ECO} to changes in temperature and precipitation (e.g., Euskirchen et al., 2014; Shi et al., 2014). As a result, semiarid ecosystem responses to climate change remain highly uncertain. On the one hand, GPP may be reduced by warming via plant heat stress (Sage & Kubien, 2007) and via stomatal closure from increased evaporative demand and reductions of soil water content (SWC) (Seneviratne et al., 2010; Williams et al., 2013) affecting vegetation productivity (Novick et al., 2016). For instance, Biederman et al. (2017) found that warm temperatures have a negative effect on NEP in semiarid ecosystems of southwestern North America. Stomata respond to transpiration rates in a process known as the apparent “feed forward response”, implying that transpiration strongly decreases at high vapor pressure deficit, particularly during periods of water stress (Duursma et al., 2014; Novick et al., 2016). When stomata close in this manner, carbon assimilation and GPP decrease, thus reducing NEP. Photosynthetic enhancements due to rising CO_2 atmospheric concentrations (Smith et al., 2000) and the lengthening of the growing season (Kunkel, 2016), however, may increase GPP. These changes are known to affect ecosystem water use efficiency ($\text{WUE} = \text{GPP}/\text{evapotranspiration (ET)}$), a measure of the sensitivity of photosynthesis rates to changes in hydroclimatic conditions (Yang et al., 2016). In addition, changes in rainfall timing, intensity, and distribution are also important factors affecting NEP, though the net effect or directionality are unclear (Allard et al., 2008; Gherardi & Sala, 2015; Heisler-White et al., 2008; Miranda et al., 2011; Robertson et al., 2009; Rohr et al., 2013; Ross et al., 2012; Xie et al., 2015).

Similarly, the effects of climate change on R_{ECO} in semiarid ecosystems are uncertain due to complex dynamics occurring during periods of water availability (Collins et al., 2014; Fan et al., 2012). R_{ECO} integrates plant (autotrophic) and microbial (heterotrophic) processes that are coupled (Sacks et al., 2007; Verduzco et al., 2015) and has been shown to increase, decrease, or remain unchanged under warming conditions (Arnone et al., 2008; Lenton & Huntingford, 2003; Luo et al., 2001; Zhou et al., 2007). R_{ECO} is also highly variable under different precipitation conditions (Cable et al., 2008; Harper et al., 2005; Thomey et al., 2011). Some studies have found that warming can substantially increase cellular metabolic maintenance (e.g., Amthor, 1984; Ryan, 1991), which in turn affects autotrophic respiration (R_a). Although studies have shown that plants can acclimate to increasing temperatures (Slot & Kitajima, 2015), the degree of and time to acclimation for different plant functional types is still unknown (Drake et al., 2015; Yamori et al., 2014). Furthermore, heterotrophic respiration has been observed to respond positively to temperature (Lloyd & Taylor, 1994), but its sensitivity has been related to limiting factors such as substrate availability and quality, which are coupled to primary productivity (Sponseller, 2007; Zhou et al., 2013) and SWC (Conant et al., 2004; Davidson et al., 2006; Liu et al., 2009).

Given the uncertainties in quantifying the net carbon response of semiarid ecosystems to climate change, a useful approach for addressing this problem is by combining ecosystem level measurements and numerical modeling. Previous efforts have found misrepresentation in the modeling of semiarid ecosystem carbon fluxes (e.g., Huntzinger et al., 2012; Vargas et al., 2013), net carbon balance (Keenan et al., 2012), and its responses to climate change (Friedlingstein et al., 2014). While simulating water, energy, and carbon fluxes remains challenging in semiarid ecosystems (Fisher et al., 2014; Li et al., 2004; Xu et al., 2013), there has been much progress on coupled water-vegetation model representations in recent years (Faticchi, Pappas, et al., 2016). Included in these advances are more accurate representations of ecosystem processes at shorter temporal scales and the simulation of longer-term phenological variations for different plant functional types (e.g., Ivanov et al., 2008a, 2008b). In addition, finer representations of event-scale and seasonal precipitation effects on vegetation dynamics have been achieved, leading to plant carbon assimilation into a number of pools that are essential for capturing vegetation dynamics (e.g., Faticchi, Pappas, et al., 2016; Ivanov et al., 2008a, 2008b). Given the importance of heterotrophic respiration in semiarid ecosystems (Cable et al., 2008; Verduzco et al., 2015; Yépez et al., 2007), an appropriate representation of this process is necessary for simulating the annual cycle and interannual variability of NEP as well as identifying the impacts of different climate change drivers (e.g., rising CO_2 and changing meteorological conditions).

In this contribution, we combine the mechanistic ecohydrological model of Ivanov et al. (2008a) (TIN-based Real-time Integrated Basin Simulator—Vegetation Generator for Interactive Evolution, *trIBS-VEGGIE*, model)

with the soil carbon model (SCM) of Porporato et al. (2003) to describe ecosystem plant and soil processes (e.g., GPP and autotrophic and heterotrophic respiration) controlling NEP in a subtropical shrubland in northwestern México. In contrast to prior efforts (e.g., terrestrial biosphere models, Huntzinger et al., 2012), the combined tRIBS-VEGGIE and SCM approach tracks energy, water, temperature, and substrate limitations on photosynthesis and respiration from multiple carbon pools using process-level prognostic equations that are tailored to seasonally dry ecosystems. We use a 5 year long record of EC flux and meteorological data (Méndez-Barroso et al., 2014; Villarreal et al., 2016) from a subtropical shrubland as well as remote sensing products to calibrate and test the model simulations for its ability to realistically capture water fluxes, vegetation dynamics, and the components of net ecosystem productivity ($NEP = GPP - R_{ECO}$). After model confirmation, we conduct a series of climate change experiments using long-term forcing generated by the stochastic downscaling of a set of climate projections from Taylor et al. (2012) that represent near-future (2030–2045) meteorological and atmospheric CO₂ conditions as well as a historical forcing data set of equivalent length (1990–2005). We selected the near-future period to avoid the potential for dramatic changes in ecosystem composition due to climate change impacts. Combining tRIBS-VEGGIE and SCM within the climate change experiments allowed us to pose the following questions: (1) What are the mechanisms through which soil-plant processes control NEP in seasonally dry, semiarid ecosystems? (2) What, if any, will be the impacts of climate change on NEP and its components in the subtropical shrubland? and (3) What is the net effect of projected changes in meteorological conditions and atmospheric CO₂ on NEP? As a result, this study aims to understand the potential effects of climate change on ecosystem dynamics and carbon cycling in semiarid areas experiencing strong seasonality.

2. Materials and Methods

2.1. Site Description

The study site is a subtropical shrubland located ~120 km northeast of Hermosillo, Sonora, México (29.74°N, 110.53°W) near the rural town of Rayón at an elevation of 632 m. The local climate is semiarid (Köppen classification BSh) with hot summers and cool winters. The long-term (1961–2009) average annual temperature and precipitation (± 1 standard deviation) are $21.4 \pm 6.4^\circ\text{C}$ and $487 \pm 181 \text{ mm yr}^{-1}$, as obtained from Comisión Nacional del Agua station 00026181 at Rayón, Sonora. Conditions during the study period (2008–2012) were similar to the long-term average, with a mean annual air temperature (TA) of $22.7 \pm 0.6^\circ\text{C}$ and precipitation (P) of $481 \pm 92.8 \text{ mm yr}^{-1}$. Precipitation during the NAM season (July–September) is approximately 76% of the annual total at the site (Vivoni, Rodríguez, et al., 2010) leading to a peak in vegetation greenness in the month of August (Méndez-Barroso et al., 2009). Site vegetation is composed of drought-deciduous trees and shrubs, including torote papelio (*Jatropha cordata*), tree ocotillo (*Fouquieria macdougalii*), acacia (*Acacia cochliacantha*), palo verde (*Parkinsonia praecox*), Mexican mimosa (*Mimosa distachya*), and velvet mesquite (*Prosopis velutina*) as well as organpipe cactus (*Stenocereus thurberi*). Brown (1994) described the vegetation characteristics of subtropical shrublands (or Sinaloan thornscrub) in greater detail. The site topography is relatively flat in proximity to the EC tower (Vivoni, Watts, et al., 2010), while the soils are shallow (~1 m) and classified as regosol-yermosol (INEGI, 2010) with sandy loam (0 to 30 cm) and sandy clay (30 to 100 cm) texture. Prior studies further describe the site properties used here for the model application, including the soil hydraulic properties, the vegetation albedo, and structural properties (e.g., Méndez-Barroso et al., 2014; Vivoni, Rodríguez, et al., 2010; Vivoni, Watts, et al., 2010).

2.2. Site Measurements

Meteorological flux measurements were performed using the EC technique (Baldocchi, 2003, 2008) using a three-dimensional sonic anemometer (CSAT-3, Campbell Sci.) and an open-path infrared gas analyzer (LI-7500, Li-COR Inc.) placed on a 9 m tower over the tree canopy of around 6 m height and oriented with the prevailing southwest wind direction. Vivoni, Watts, et al. (2010) describes the EC installation at the site, including the characteristics of the footprint area. Water vapor and CO₂ concentrations and TA were measured at high frequency (20 Hz), collected with a CR5000 datalogger (Campbell Sci.) and processed to 30 min averaged quantities to obtain latent (LE) and sensible heat flux (H) and net ecosystem exchange (NEE) of CO₂, as described in the following section. By convention, negative NEE values indicate ecosystem

carbon uptake from the atmosphere, which correspond to a positive net ecosystem productivity (i.e., $-NEE = NEP$). Net radiation (R_{net}) was measured using a CNR Lite2 (Kipp and Zonen) radiometer, and incoming solar radiation with a CMP3 radiometer (Campbell Sci.).

For use in the model, incoming solar radiation was partitioned into direct and diffuse components of the visible (VIS, 0.4–0.7 μm) and near-infrared (NIR, 0.7–1.3 μm) bands following the procedures of Spitters et al. (1986), while incoming longwave radiation was estimated as a function of TA (Duarte et al., 2006). A humidity and TA sensor (HMP45D, Vaisala) was used to obtain vapor pressure (VP) and TA. Volumetric SWC was obtained as the average of two reflectometer (CS616-L, Campbell Sci.) measurements at a 10 cm depth over the period 2008–2010 and from a soil moisture sensor (ECH2O probe, Decagon Devices) at the same depth and location for portions of 2012. No additional soil moisture sensors at larger soil depths were available. Local precipitation was measured with a tipping-bucket rain gauge (TB4, Hydrological Services). All meteorological measurements were recorded as 30 min averages within the CR5000 datalogger and averaged to hourly inputs for the model applications. Additional information on measurements is presented by Méndez-Barroso et al. (2014), Villarreal et al. (2016), and Vivoni, Rodríguez, et al. (2010).

Several data gaps occurred during the 2008–2012 period (i.e., 15 to 26% of measurements during all years, except 2008 with 63% missing data since observations started in the summer). We followed the procedure of Robles-Morua et al. (2012) to fill in the necessary meteorological forcing. This process consisted of bias-correcting the surface meteorological data obtained from the North American Land Data Assimilation System (NLDAS) (Mitchell et al., 2004) in the grid pixel (12 km) corresponding to the study site during periods of simultaneous ground data. Linear corrections were applied to hourly variables of atmospheric pressure, incoming solar radiation, and vapor pressure, while TA was corrected using the adiabatic lapse rate ($6.5^\circ\text{C km}^{-1}$) to match the site elevation. A logarithmic profile adjustment was used to modify the 10 m NLDAS wind speed to 2 m height assumed for all forcing variables in the ecohydrological model (tRIBS-VEGGIE). The use of bias-corrected NLDAS products to gap-fill the ground-based data was deemed important to create a continuous series of meteorological forcing.

In addition, we utilized remotely sensed data from the Moderate Resolution Imaging Spectroradiometer (MODIS; ORNL DAAC, 2008) to test the model representation of vegetation dynamics, following Méndez-Barroso et al. (2014). Cloud-free composites of the Normalized Difference Vegetation Index (NDVI, 16 day, 250 m, MOD13Q1) and leaf area index (LAI, 8 day, 1 km, MOD15A2) were linearly interpolated to a daily product for this purpose. Due to its higher temporal resolution, we report the model evaluation against LAI for assessing vegetation dynamics. Previous research in semiarid areas has found good agreement between ground-based vegetation conditions and MODIS (i.e., Fensholt et al., 2004; Jenerette et al., 2010), but it should be noted that there are discrepancies between the site conditions and inferred variables of the remote sensing products due to different spatiotemporal resolutions and sometimes due to scattering and absorption by the atmospheric composition (Nagol et al., 2009).

2.3. Flux Quality Control and Partitioning

Conventional corrections were applied to EC measurements following Scott et al. (2004), including removal of outliers (gas concentrations greater than ± 4 standard deviations, Massman, 2001), a correction for density fluctuations (Webb et al., 1980), and the application of the double-rotation method (Wilczak et al., 2001). In addition, friction velocity (u^*) was calculated according to quantitative methods (Scott et al., 2004), and periods of time with a friction velocity less than $u^* = 0.20 \text{ m s}^{-1}$ were filtered (Aubinet et al., 2000; Xu & Baldocchi, 2004) to reduce nighttime flux underestimation (Barr et al., 2013). The u^* threshold was selected such that there is no dependence between nighttime fluxes and friction velocity. Resulting data gaps were filled in following the procedures of the Eddy Covariance Gap-Filling and Flux-Partitioning Tool available at: <http://www.bgc-jena.mpg.de/~MDIwork/eddyproc/index.php>, following Reichstein et al. (2005). The surface energy balance was evaluated at the study site by Villarreal et al. (2016) over 2008–2010 (a closure of 0.89) and Méndez-Barroso et al. (2014) over summers in 2006–2009 (a closure of 0.75). The partitioning of NEE into its components GPP and R_{ECO} (i.e., $NEE = R_{ECO} - GPP$) was carried out using the sensitivity of R_{ECO} to TA (Flanagan, Wever, & Carlson, 2002; Reichstein et al., 2005). This NEE partitioning approach has been shown to be consistent with other methods (Babst et al., 2014; Desai et al., 2008).

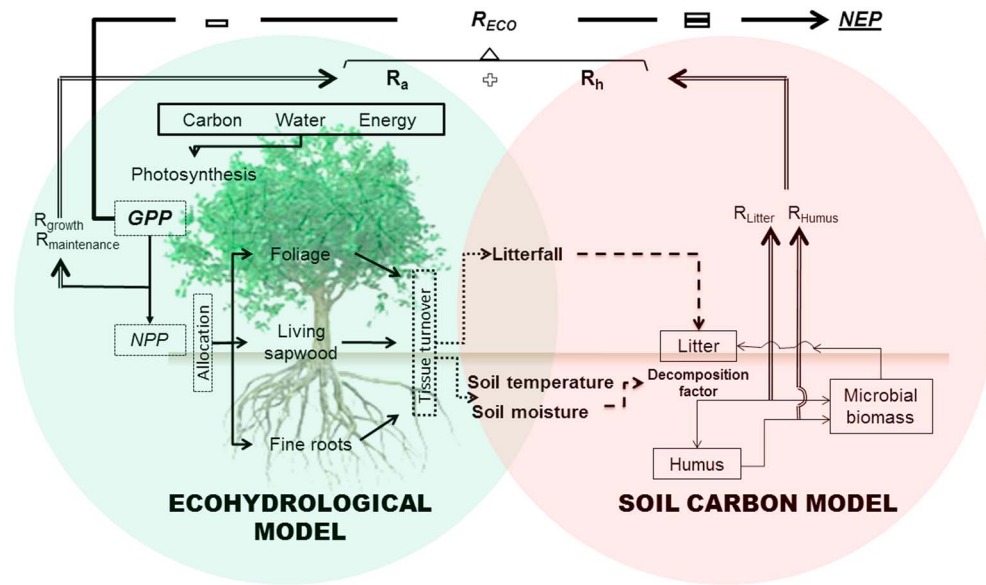


Figure 1. Conceptual diagram of model-based estimation of ecosystem carbon fluxes using tRIBS-VEGGIE and soil carbon model. Dotted lines depict ecohydrological model outputs into the soil carbon model, while double lines specify sources of autotrophic, heterotrophic, and ecosystem respiration ($R_{ECO} = R_a + R_h$). Net ecosystem productivity (NEP) is obtained as $GPP - R_{ECO}$.

2.4. Ecohydrological and Soil Carbon Modeling

Water, energy, and carbon dynamics at the subtropical shrubland were simulated using a combination of an ecohydrological model (tRIBS-VEGGIE, Ivanov et al., 2008a, 2008b) and a SCM (Porporato et al., 2003) coupled through the production of litter and the soil moisture and temperature conditions (Figure 1). Following prior efforts in semiarid regions (Bisht, 2010; Sivandran & Bras, 2012), a drought-deciduous C3 shrub was used as the plant functional type in the one-dimensional simulations using an irregular sub-surface mesh (25 layers over 1 m depth). In addition to vertically resolved soil hydrologic and thermal dynamics, tRIBS-VEGGIE captures a set of biophysical and biochemical plant processes, such as photosynthesis; autotrophic respiration (R_a); carbon allocation to foliage, sapwood, and fine roots; tissue turnover; and vegetation phenology. This allows the estimation of gross and net ($NPP = GPP - R_a$) primary productivity for the plant functional type. The time-evolving plant conditions are directly affected by and provide an influence on the local energy and water budget in an interactive fashion (Ivanov et al., 2008a, 2008b). Simulated SWC, surface energy fluxes (R_{net} , H , and LE), total ET, and LAI, among others, depend on local meteorological conditions, soil properties, and plant functional traits obtained via local measurements or parameterized through a model calibration and validation procedure. Overall, tRIBS-VEGGIE simulates the dynamic feedbacks between vegetation and its surrounding environment at differing time scales, explicitly represented starting at the scale of a few minutes (e.g., resolving canopy leaf temperatures), to hourly resolution (e.g., stomatal dynamics), and up to the daily scale processes (e.g., plant phenology and leaf turnover). Ivanov et al. (2008a, 2008b) provide additional details on the model biophysics and its application in other semiarid settings.

As depicted in Figure 1, tRIBS-VEGGIE does not simulate soil heterotrophic respiration (R_h), limiting its ability to represent net ecosystem productivity ($NEP = GPP - R_a - R_h$). To address this, we implemented a simplified version of the SCM of Porporato et al. (2003) based on three separate carbon pools (litter, humus, and microbial biomass) to track soil organic matter decomposition and heterotrophic respiration (Bolker et al., 1998; Manzoni et al., 2004; Parolari & Porporato, 2016). While this approach does not track nitrogen dynamics, we accounted for C:N effects on decomposition rates through the use of a heuristic factor ϕ described in Rodríguez-Iturbe and Porporato (2004) and based values either on local data or magnitudes reported for the region (Martínez-Yrizar et al., 2007; Núñez et al., 2001). Daily carbon pool dynamics simulated in the SCM were driven by SWC and temperature conditions and the leaf litter production derived from tRIBS-VEGGIE. As a result, the coupling of tRIBS-VEGGIE and SCM allows for the

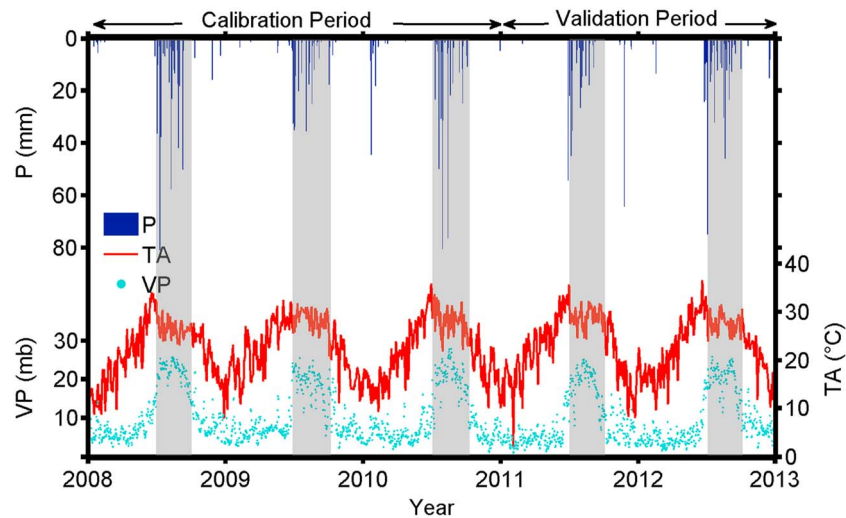


Figure 2. Mean daily meteorological conditions during the study period (2008–2012) consisting of precipitation (P), air temperature (TA), and vapor pressure (VP). Shaded areas represent North American monsoon period (July–September) of each year.

effects of vegetation phenology (i.e., leaf senescence and fall) to impact R_n and NEP when soil moisture and temperature conditions are favorable.

2.5. Model Forcing, Parameterization, and Validation

Gap-filled meteorological observations over the period 2008–2012 were aggregated to hourly resolution as forcing for tRIBS-VEGGIE and consisted of atmospheric pressure, vapor pressure, TA , wind speed, incoming solar and longwave radiation, and precipitation. In addition, direct and diffuse radiation components in the visible and near-infrared bands and the average atmospheric CO_2 concentration during 2008–2012 (390 ppm) were input. Figure 2 presents an example of the meteorological forcing, illustrating the strong seasonality in precipitation and its corresponding effects on TA and vapor pressure during the NAM.

The study period was divided into two subsets for model calibration (2008–2010, 1,096 days) and validation (2011–2012, 731 days) based upon matching the subset length when excluding gap-filled periods. While conditions varied to some extent among the subsets, no trends were noted that would impact model calibration and validation. A similar setup was carried out for the SCM by using leaf litterfall, soil moisture, and soil temperature conditions obtained from tRIBS-VEGGIE as inputs (Figure 1). Following Vivoni et al. (2005), the sequence of tRIBS-VEGGIE and SCM simulations were conducted in a periodic fashion by repeating the same 5 year meteorological forcing six times (i.e., total simulation length of 30 years) and retaining the two subsets in the last 5 year period for model calibration and validation purposes. This initialization approach stabilized SWC, soil temperature, and carbon storage amounts in the vegetation (foliage, sapwood, and fine roots) and soil (litter, microbial biomass, and humus) pools, thus reducing transient errors in the assignment of the initial conditions.

Initial model parameterization was conducted for tRIBS-VEGGIE and SCM based upon prior efforts with each model (e.g., Bisht, 2010; Ivanov et al., 2008a; Parolari & Porporato, 2016; Porporato et al., 2003; Sivandran & Bras, 2012), including applications for the subtropical shrubland (Méndez-Barroso et al., 2014; Vivoni, Rodríguez, et al., 2010). For instance, Table 1 presents the soil hydraulic and thermal properties used in tRIBS-VEGGIE for the sandy loam soils at the site whose initial values were obtained through manual calibration conducted by Méndez-Barroso et al. (2014). As in that work, we simplified the modeling of site conditions by treating the soil profile as a uniform sandy loam. In contrast to Méndez-Barroso et al. (2014), however, we applied the one-dimensional Richards equation using a finite element, backward Euler time stepping numerical approximation for infiltration into the unsaturated soil profile (irregular mesh with 25 layers over 1 m depth), as detailed in Ivanov et al. (2008a). Accordingly, modifications to the soil parameters within feasible ranges based on pedotransfer functions from Rawls et al. (1982) were required to match a larger set of

Table 1
 Soil Parameters

Soil type	Sandy loam
K_s	55
θ_s	0.45
θ_r	0.02
λ_o	0.47
ψ_b	-90
$k_{s,dry}$	0.214
$k_{s,sat}$	2.64
C_s	1,610,586

Note. K_s (mm h^{-1}) = surface hydraulic conductivity; θ_s (-) = saturated moisture content; θ_r (-) = residual moisture content; λ_o (-) = pore size distribution index; ψ_b (mm) = air entry bubbling pressure; $k_{s,dry}$ and $k_{s,sat}$ ($\text{J m}^{-1} \text{s}^{-1} \text{K}^{-1}$) = heat conductivity for dry and saturated soils; C_s ($\text{J m}^{-3} \text{K}^{-1}$) = heat capacity of dry soils.

observations (SWC, R_{net} , H , LE, and LAI) over a longer period (i.e., three continuous years in the calibration period).

An invariant rooting profile extending to 1 m depth and a vegetation fraction ($v_f = 0.6$) were estimated for the study site following Jackson et al. (1996) and Méndez-Barroso et al. (2014). In addition, tRIBS-VEGGIE required a larger set of model parameters to describe biochemical, biophysical, interception, phenological, carbon allocation, and water uptake processes (Ivanov et al., 2008a). Table 2 lists the final parameter values for vegetation processes and indicates their sources as from literature (L), observation (O), or calibration (C).

Manual calibration of vegetation parameters focused on capturing the LAI dynamics during 2008–2010 as observed from MODIS during the NAM growing season. A one-at-a-time sensitivity analysis was conducted to identify the importance of each parameter on the simulation of LAI and limit the sampling necessary for model calibration. Similarly, a

manual calibration approach was used for the SCM parameters (Table 3). We used observations of SCM model parameters or initial conditions when available from the site or nearby areas (e.g., Búrquez et al., 1999; Martínez-Yrizar et al., 1999, 2007; Núñez et al., 2001; Pavón et al., 2005). Though manual calibration was conducted, the combined models are amenable to automated estimation methods (e.g., Duan et al., 1993) due to the low computational demands for single-site applications. The combination of tRIBS-VEGGIE and SCM allowed for simulation of $R_{ECO} = R_a + R_h$ that was compared to R_{ECO} observations derived from the EC method during calibration and subsequently permitted a comparison of NEP between observations and simulations. We validated the model performance using a comparison between simulated and observed values of the aforementioned variables during the 2011–2012 period, which was not used in the model calibration effort.

2.6. Climate Change and CO₂ Fertilization Experiments

We obtained TA (monthly) and precipitation (3 h) projections from the Coupled Model Intercomparison Project version 5 (CMIP5) (Taylor et al., 2012) for three General Circulation Models (GCMs) selected for their ability to represent the NAM system (Geil et al., 2013): CNRM-CM5, HadGEM2-ES, and MIROC5. Single realizations from each model were selected for a near-future period (2030–2045) under the RCP8.5 emissions case (IPCC, 2013), selected to match the 15 year length of a historical forcing period (1990–2005) obtained from NLDAS (labeled as “HIST”). Given the hourly meteorological forcing requirements of tRIBS-VEGGIE, we implemented the stochastic downscaling method of Fatichi et al. (2013) to apply a set of factors of change derived from the individual GCMs and their averaged conditions (referred to hereafter as “AVE”) to the statistical properties obtained from the historical forcing. For each scenario, sets of change factors were calculated separately for the statistical properties of precipitation (e.g., mean, variance, skewness, and frequency of no precipitation at different aggregation periods (1, 6, 24, and 72 h) and mean monthly TA). Since GCM realizations were obtained at a 3 h interval, we followed Fatichi et al. (2011) to extend the statistical properties to a finer hourly resolution for the full set of meteorological forcings (atmospheric pressure, wind speed, incoming solar and longwave radiation, TA, vapor pressure, and precipitation). Since our study periods were relatively short (15 years), we utilized the derived statistical metrics from the method of Fatichi et al. (2013) to generate synthetic (100 years long) hourly forcings for each scenario (HIST, CNRM-CM5, HadGEM2-ES, MIROC5, and AVE). These should be considered as representative realizations of the climate system under stationary historical and near-future conditions, as simulated by these GCMs, allowing statistical sampling to be conducted. Two sets of simulations were performed for each scenario to differentiate the effects of CO₂ fertilization from meteorological changes: (1) No fertilization cases used the average of 365 ppm calculated from historical CO₂ concentrations from 1990–2005 and (2) CO₂ fertilization cases with a constant concentration of 482 ppm, obtained from RCP8.5 from 2030–2045 period (about a 32% increase in CO₂ above historical). Since we are simulating synthetic 100 year long scenarios, it was necessary to use a constant CO₂ concentration that best represents the conditions for each period (i.e., 1990–2005 and 2030–2045).

Table 2
Vegetation Parameters

Parameter	Value	Source
Biochemical processes		
$V_{\max25}$	50	C
K	0.2	C
m	9	L
b	10,000	L
$\epsilon_{3,4}$	0.08	L
r_{sapw}	9.61×10^{-10}	L
r_{root}	1.09×10^{-8}	L
w_{grw}	0.25	L
d_{leaf}	1	L
d_{sapw}	0.04	L
d_{root}	0.33	L
Biophysical and interception processes		
χL	0.01	L
α_{leaf} (VIS, NIR)	0.1, 0.45	L
α_{stem} (VIS, NIR)	0.16, 0.39	L
τ_{leaf} (VIS, NIR)	0.05, 0.25	L
τ_{stem} (VIS, NIR)	0.001, 0.001	L
K_c	0.18	L
g_c	3.9	L
S_{la}	0.011	O
Phenology, allocation, and uptake processes		
γW_{\max}	10	C
b_w	2.5	C
γC_{\max}	7	C
b_c	1	C
T_{cold}	15	C
e_{leaf}	0.25	L
e_{sapw}	0.1	L
e_{root}	0.65	L
ω	0.8	L
ϵ_s	2	L
ζ	1.6	L
T_{soil}	20	C
D_{LH}	10	L
$D_{\text{Tmin,Fav}}$	6	C
$f_{c,\text{init}}$	0.025	L
L_{init}	0.22	L
ψ^*	-0.1	C
ψ_w	-5	C

Note. $V_{\max25}$ ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ leaf s}^{-1}$) is the maximum catalytic capacity of Rubisco at 25°C; K (-) is the time mean Photosynthetically Active Radiation extinction coefficient parameterizing the decay of nitrogen content in the canopy; m (-) is an empirical slope parameter; b ($\text{mmol m}^{-2} \text{ s}^{-1}$) is the minimum stomatal conductance; $\epsilon_{3,4}$ ($\mu\text{mol CO}_2 \mu\text{mol}^{-1}$ photons) is the intrinsic quantum efficiency for CO_2 uptake; r_{sapw} and r_{root} ($\text{g C g C}^{-1} \text{ s}^{-1}$) are the sapwood and fine root respiration coefficients at 10°C; w_{grw} (-) is the fraction of canopy assimilation less maintenance respiration used for tissue growth; d_{leaf} , d_{sapw} , and d_{root} (yr^{-1}) are the turnover rates for leaf, sapwood, and roots; χL (-) is the departure of leaf angles from a random distribution; α_{leaf} and α_{stem} (-) are the leaf and stem reflectances in the visible and near-infrared bands; τ_{leaf} and τ_{stem} (-) are leaf and stem transmittances in the visible and near-infrared bands; K_c (mm h^{-1}) is the canopy drainage coefficient; g_c (mm^{-1}) is the exponential decay parameter of canopy water drainage; S_{la} ($\text{m}^2 \text{ leaf area kg C}^{-1}$) is the specific leaf area; γW_{\max} and γC_{\max} (d^{-1}) are maximum drought and cold-induced foliage loss rates; b_w and b_c (-) are the shape parameters reflecting the sensitivity of canopy to drought and cold; T_{cold} ($^{\circ}\text{C}$) is the temperature threshold below which cold-induced leaf loss begins; e_{leaf} , e_{sapw} , and e_{root} (-) are the base allocation fractions for leaf, sapwood, and roots; ω (-) is the sensitivity parameter of allocation fractions to changes in light and water availability; ϵ_s and ζ (-) are parameters controlling the relation between carbon content in the aboveground and belowground biomass; T_{soil} ($^{\circ}\text{C}$) and D_{LH} (h) are the mean daily soil temperature and day length to be exceeded for the growing season start; $D_{\text{Tmin,Fav}}$ (day) is the minimum duration for which the conditions of transition from/to the dormant season have to be continuously met; $f_{c,\text{init}}$ and L_{init} (-) are the fraction of the structural biomass and leaf area index used to initiate leaf onset; ψ^* and ψ_w (MPa) are the soil matric potentials at which the stomatal closure and plant wilting begins. L = literature; O = observation; C = calibration.

3. Results and Discussion

3.1. Evaluation of Simulated Water, Energy, and Carbon Dynamics

Simulated water, energy, and carbon states and fluxes in the subtropical shrubland were compared to available observations over the calibration, validation, and full study periods using three metrics: correlation

Table 3
Soil Decomposition Parameters

Parameter	Value	Source
C_l	89	L
C_h	895	L
C_b	25	L
C/N_{litter}	23	O
C/N_{humus}	22	L
$C/N_{biomass}$	8	L
r_h	0.003	L/C
r_r	0.65	L
k_b	0.0000988	C
k_h	2.1×10^{-7}	C
k_l	0.00107	C

Note. C_l , C_h , and C_b ($g C m^{-2}$) are initial carbon concentrations in the litter, humus, and biomass pools; C/N_{litter} , C/N_{humus} , and $C/N_{biomass}$ (-) are carbon-nitrogen ratios of litter, humus, and biomass; r_h and r_f (-) are fractions of organic matter undergoing humification and of decomposed organic carbon that is respired; k_l , k_h , and k_b (h^{-1}) are first-order kinetic constants of litter, humus, and biomass. L = literature; O = observation; C = calibration.

coefficient (CC), bias (B), and mean absolute error (MAE) (Vivoni et al., 2006). Table 4 shows the metrics obtained for daily averaged and hourly values, with a CC near 1, a B close to unity, and a low MAE indicating a good match between the observed and simulated variables at both time scales and for all variables. For instance, the simulated surface energy fluxes (R_{net} , H , and LE) exhibit a good correspondence to observations, with high CC (> 0.77), B near unity (within ± 0.16), and an MAE less than $33 W m^{-2}$ for hourly and daily values. Figure 3 illustrates the model performance with respect to the surface energy fluxes by comparing seasonal cycles of R_{net} , H , and LE over the full study period. Note the dramatic change in the partitioning of R_{net} into H and LE upon the onset of the NAM in July, with the arrival of summer storms increasing LE (or ET) substantially. Overall, the ecohydrological model adequately captures monthly variations in the surface energy fluxes, though a consistent underestimation of R_{net} of $14.4 W m^{-2}$ is noted from December through June due to the lack of simulated vegetation (i.e., a decrease in LAI and a corresponding increase in albedo) affecting the absorption of solar radiation, comparable to prior studies

(Ivanov et al., 2008a). In addition, tRIBS-VEGGIE simulation tends to slightly overestimate sensible heat flux from May to August by an average of $12.7 \pm 3.8 W m^{-2}$, despite adequately capturing the latent heat flux, though the difference is within the monthly standard deviation (error bars) obtained across all years. Overall, monthly, daily, and hourly comparisons demonstrate the robust capability of tRIBS-VEGGIE to capture surface energy fluxes, themselves tied to SWC and vegetation conditions.

Figure 4 presents observed and simulated SWC in the top 10 cm, LAI dynamics and litterfall variations during the calibration and validation periods, and simulated soil temperature (T_{soil}) derived from tRIBS-VEGGIE that are critical inputs to the SCM. Note how the summer rainy season during the NAM leads to increases in SWC that were accurately captured by the model, as described in Table 4, with the tRIBS-VEGGIE model serving as an effective tool to interpolate within periods of observed data gaps. Simulated LAI captured well the primary summer growing season (CC ≥ 0.88 , B within 0.06 of unity, MAE ≤ 0.39) and the differences between years.

Table 4
Model Performance Metrics for Daily and Hourly Values

Variable	Calibration period 2008–2010			Validation period 2011–2012			Full period 2008–2012			
	CC	B	MAE	CC	B	MAE	CC	B	MAE	
Daily values	SWC ($m^3 m^{-3}$)	0.86	0.91	0.03	0.93	0.65	0.01	0.86	0.83	0.02
	ET (mm)	0.91	0.81	0.01	0.94	0.89	0.02	0.92	0.84	0.01
	LAI (-)	0.88	1.06	0.39	0.91	1.00	0.36	0.89	1.04	0.38
	R_{net} ($W m^{-2}$)	0.85	0.91	19.46	0.97	0.87	15.05	0.91	0.90	17.70
	LE ($W m^{-2}$)	0.91	0.81	9.22	0.94	0.89	11.2	0.92	0.84	10.01
	H ($W m^{-2}$)	0.76	1.16	16.88	0.82	0.91	18.16	0.77	1.04	17.39
	GPP ($g C m^{-2}$)	0.85	0.92	0.04	0.83	1.16	0.04	0.85	1.05	0.04
	R_{ECO} ($g C m^{-2}$)	0.90	1.09	0.02	0.88	1.16	0.02	0.90	1.12	0.02
	NEP ($g C m^{-2}$)	0.58	0.99	0.03	0.67	0.95	0.03	0.60	0.78	0.03
Hourly values	SWC ($m^3 m^{-3}$)	0.80	0.91	0.03	0.90	0.65	0.01	0.81	0.83	0.02
	ET (mm)	0.86	0.81	0.02	0.79	0.88	0.03	0.83	0.84	0.03
	R_{net} ($W m^{-2}$)	0.96	0.91	28.23	0.97	0.87	31.33	0.96	0.90	29.47
	LE ($W m^{-2}$)	0.86	0.81	15.98	0.79	0.88	22.2	0.83	0.84	18.48
	H ($W m^{-2}$)	0.90	1.16	24.65	0.91	0.91	45.33	0.90	1.04	32.92
	GPP ($g C m^{-2}$)	0.70	1.08	0.07	0.75	1.29	0.05	0.72	1.15	0.06
	R_{ECO} ($g C m^{-2}$)	0.73	1.09	0.04	0.69	1.16	0.04	0.71	1.12	0.04
	NEP ($g C m^{-2}$)	0.58	0.97	0.07	0.63	0.94	0.06	0.60	0.78	0.06

Note. Correlation coefficient (CC), bias (B), and mean absolute error (MAE) are calculated for soil water content (SWC), evapotranspiration (ET), leaf area index (LAI), net radiation (R_{net}), sensible heat flux (H), gross primary productivity (GPP), ecosystem respiration (R_{ECO}), and net ecosystem productivity (NEP) during calibration, validation, and full periods.

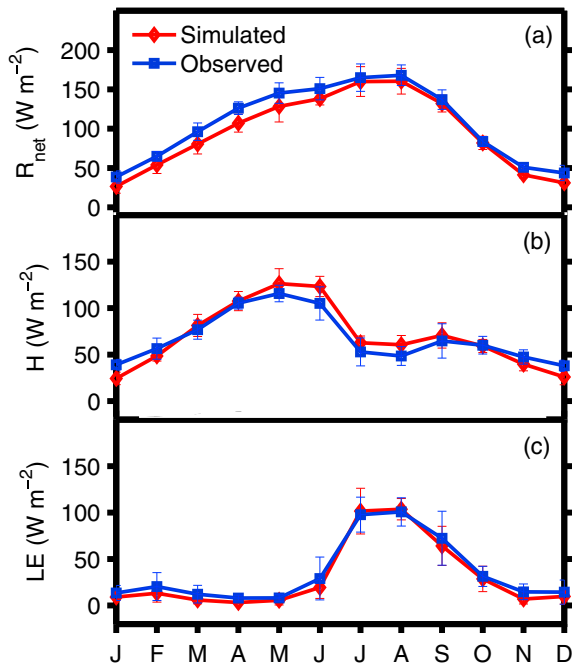


Figure 3. Seasonal cycle of observed versus simulated surface energy fluxes over the study period (2008–2012): (a) net radiation (R_{net}), (b) sensible heat flux (H), and (c) latent heat flux (LE). Symbols are monthly averages and ± 1 standard deviation as error bars.

However, the model did not capture the observed (MODIS-based) LAI variations during the winter period, as noted by Bisht (2010). This is likely due to representing only the drought-deciduous component of the ecosystem (C3 shrubland) and possible issues related to the scale discrepancy between MODIS-based LAI estimates and the model application. Although this might lead to small errors in the estimation of annual biomass, the particularly strong summer season minimizes the role played by the winter in terms of physiological activity, as has been noted with carbon fluxes in the NAM region (e.g., Huxman et al., 2004; Pérez-Ruiz et al., 2010; Scott et al., 2004; Verduzco et al., 2015). Correspondingly, model estimates of GPP were adequate at the hourly resolution as compared to derived values from the EC measurements and improved substantially at the daily resolution (Table 4), though we noted that overestimation during the NAM was typical ($B = 1.23$). Although LAI and the foliage carbon pool appears to have low interannual variations, the simulations of GPP that account for all carbon pools (root, stem, and foliage) correspond well with observations and demonstrate higher values during wetter years, as expected. The few available data on T_{soil} limited the possible tests of the model, though for 2011, tRIBS-VEGGIE matched the observations very well ($CC = 0.97$, $B = 0.99$, and $MAE = 1.9^\circ\text{C}$ for hourly values).

After the NAM ends, soil moisture and temperature conditions become less favorable for the drought-deciduous plants and the subtropical shrubland transitioned into dormancy (low LAI by November) after a complete foliage turnover (Figure 4). Litterfall

was simulated by tRIBS-VEGGIE to account for about 30% of the GPP each year, with values ranging from 120 to 180 $\text{g C m}^{-2} \text{ yr}^{-1}$, consistent with studies in the Sonoran Desert ($\sim 157 \text{ g C m}^{-2} \text{ yr}^{-1}$) (Martínez-Yrizar et al., 1999). Along with the simulated SWC and T_{soil} conditions, litterfall determined inputs to the SCM from which heterotrophic respiration (R_h) fluxes were simulated (Figure 4b). Simulated carbon amounts in the litter and microbial biomass pools ranged from 20 to 200 g C m^{-2} and from 70 to 130 g C m^{-2} , respectively, whereas the carbon amount in the humus pool remained relatively stable at 895–900 g C m^{-2} during

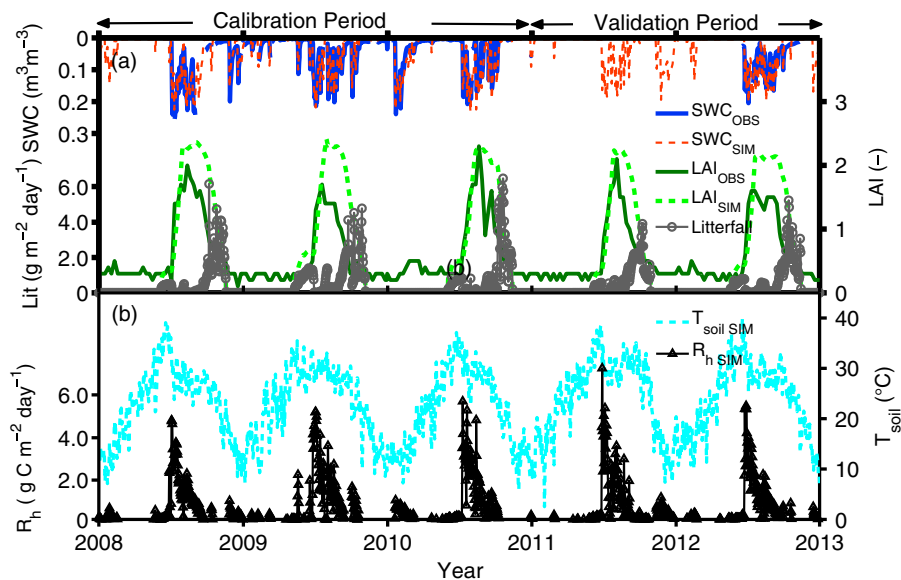


Figure 4. (a) Comparison of daily observed (OBS) and simulated (SIM) soil water content (SWC) and leaf area index (LAI). Simulated litterfall (Lit) in (a), soil temperature (T_{soil}) and heterotrophic respiration (R_h) in (b) from tRIBS-VEGGIE (Litterfall, T_{soil}) and soil carbon model (R_h).

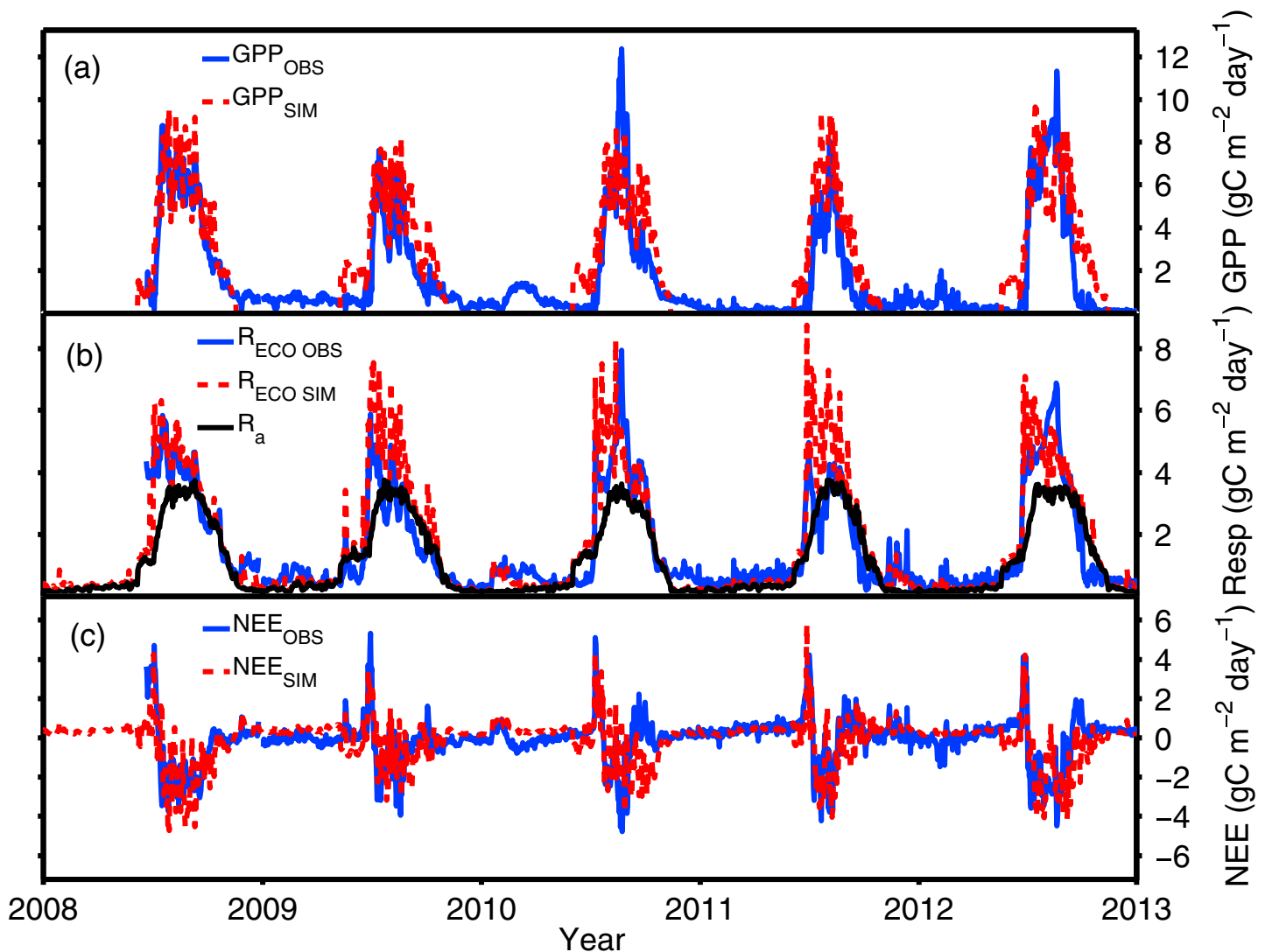


Figure 5. Comparison of observed (OBS) versus simulated (SIM) of (a) gross primary productivity (GPP), (b) ecosystem respiration (R_{ECO}) along with simulated autotrophic respiration (R_a), and (c) net ecosystem exchange (NEE). Simulated R_{ECO} was obtained by combining R_a from the ecohydrological model tRIBS-VEGGIE and R_h from the soil carbon model.

the study period, similar to measured values in semiarid shrublands (e.g., Bolton, Smith, & Link, 1993; Cardoso et al., 2015; Cheng et al., 2015; Goberna et al., 2007). As expected, low amounts of R_h occur during the winter and spring and increase substantially after the first rainfall event during the NAM due to the available SWC and labile substrate, consistent with Verdusco et al. (2015) and Zhang et al. (2014). Simulated litter decomposition decreased as the labile substrate amounts were depleted which leads to a reduction in the microbial biomass pool, similar to observations made in long-term incubation studies (Follett et al., 2007; Steinweg et al., 2008). As a result, the heterotrophic respiration was highly sensitive to the arrival of early storms during the NAM warm season, through its impact on SWC, and to the amount of labile substrate from the previous summer season, via the litterfall occurring at the end of the prior NAM.

By capturing R_h in the SCM, the simulated ecosystem respiration ($R_{\text{ECO}} = R_a + R_h$) was compared to EC measurements in Figure 5. Table 4 indicates a good correspondence between the observed and simulated R_{ECO} ($CC > 0.73$, B within 0.09 of unity, $MAE < 0.04 \text{ gC m}^{-2}$) at hourly and daily resolutions. However, we noted discrepancies in the R_{ECO} for summers with high LAI, suggesting that autotrophic respiration (R_a) for plant growth and maintenance was overestimated to some extent. In addition, simulated R_{ECO} appeared flashier than the observations at the start of the summer season (Figure 5b) due to rapid changes in R_h

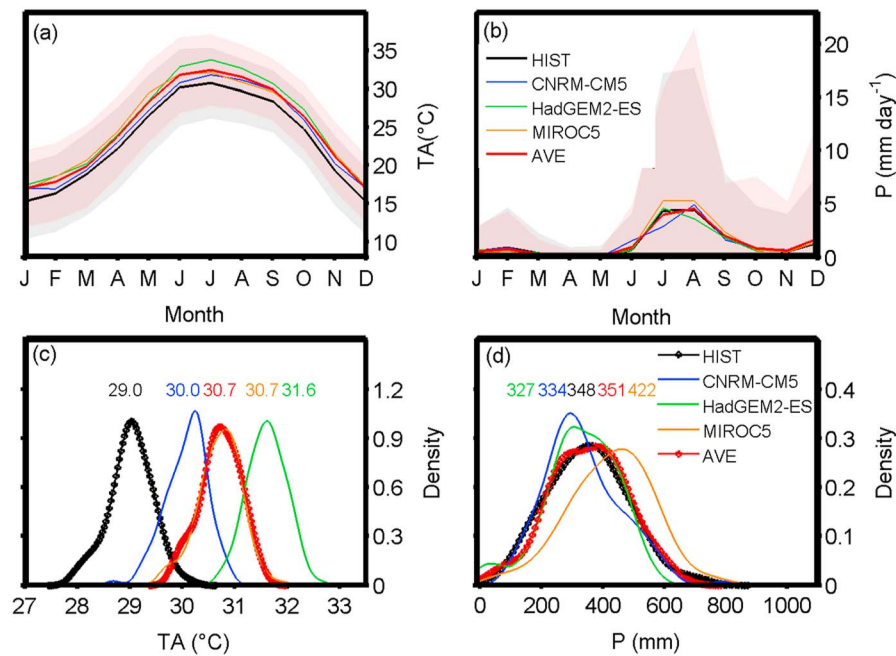


Figure 6. Comparison of meteorological conditions for historical (1990–2005) and climate change experiments (2030–2045) at the study site using representative realizations for HIST, CNRM-CM5, HadGEM2-ES, MIROC5, and AVE. (a, b) Monthly averages of daily air temperature (TA) and precipitation (P) with ± 1 standard deviation shown as a shaded envelope for HIST (gray) and AVE (pink). (c, d) Probability density functions of summer (May–June–July–August–September, MJJAS) average TA and total P. Numbers indicate mean values for each case.

when both labile substrate and water were available and soil temperatures are high. As expected, the contribution of R_h to R_{ECO} decreased while the contribution of R_a increased during the temporal progression of the NAM season, reflecting the reduced role of microbial decomposition and the increased role of plant respiration during the growing period (e.g., Carbone et al., 2016).

Figure 5 and Table 4 also compare observed and simulated GPP, NEE, and NEP, respectively, indicating a reasonable match at hourly and daily scales. Note that the positive NEE (carbon loss) occurring early in the summer would not have been possible to represent without simulating R_h in the SCM, consistent with the metabolic activity of microbial communities when high quality litter inputs were available (Carbone et al., 2011; McCulley et al., 2004; Sponseller, 2007; Thiessen et al., 2013; Unger et al., 2010). Furthermore, the negative NEE (carbon uptake) during the growing season and the stable values of NEE near 0 during the dormant period were accurately captured by the models. Some issues are noted in 2010 which has an observed positive NEE in the late summer season that is not reproduced by the models. Nevertheless, similar patterns of annual NEP were found in the simulations and observations. During the study period, the subtropical shrubland acted as a net sink of carbon during most years (annual NEP from 33 to 105 g C m⁻²), with the exception of 2011, in which both the simulations and observations indicated a net source of carbon (NEP of -53.1 and -98.3 g C m⁻²).

3.2. Meteorological Changes in Historical and Climate Change Experiments

Figure 6 presents the outcomes of the stochastic downscaling procedure applied to historical (1990–2005, NLDAS) and near-future (2030–2045, CNRM-CM5, HadGEM2-ES, MIROC5, and AVE) periods in terms of the seasonal (monthly) cycle of TA and precipitation (Figures 6a and 6b) and the probability density functions (PDFs) of summertime TA and P (Figures 6c and 6d). These metrics were selected to show the range of meteorological changes in the experiments and summarize the model forcing tailored to the study site (i.e., a full set of hourly variables of 100 year duration for each scenario). Due to the model performance and the nature of the seasonal dynamics, a focus is placed on the summer season (May–June–July–August–September, MJJAS) in the analyses, including a distinction between premonsoon (May–June, MJ) and monsoon (July–August–September, JAS) periods. As expected from the RCP8.5 emissions case, a strong warming signal is present in the near future, with increases in mean annual temperature ranging from +1.1 to +2.3°C with respect to the HIST scenario. HadGEM2-ES exhibited the largest increase in mean summer TA

(+2.6°C), whereas CNRM-CM5 had the lowest increase (+1.0°C) relative to HIST. When averaged over the three models, the AVE scenario indicates a warming of +1.7°C in mean summer TA and a shift from a range of 24.4 to 33.6°C in HIST (± 1 standard deviation envelop) to 26.1 to 35.3°C in AVE (Figure 6a). These effects are illustrated nicely through the PDFs of summer (MJJAS) average TA, obtained from hourly values over the 100 year sample size (Figure 6c). Note the increase in summer TA relative to HIST in the following order: CNRM-CM5, MIROC5, and HadGEM2-ES. These estimates are consistent with projections for the NAM (Cook & Seager, 2013; Lee & Wang, 2014; Maloney et al., 2014; Pachauri et al., 2014) suggesting a warming signal of +1.4 and 2.7°C between 2035 and 2065.

A comparison of the seasonal cycle of precipitation from the scenarios (Figure 6b) indicates that the use of factors of change in the stochastic downscaling method preserves rainfall seasonality as compared to the historical period with 60 to 80% of the annual precipitation occurring during summer (MJJAS), while leading to the differences in mean summer precipitation amounts (Figure 6d). Among the GCMs, HadGEM2-ES had lowest mean summer precipitation in the near-future period (327 mm or -21 mm with respect to HIST), whereas MIROC5 exhibited the highest mean summer P (422 mm or +74 mm relative to HIST). When averaged over the three models, the AVE scenario had a nearly identical mean monthly variation of P as HIST (Figure 6b), with a slightly expanded range of variability in August and October and a similar distribution of summer total P (Figure 6d). These comparisons are important since relative precipitation differences among GCMs (i.e., two GCMs have lower P and one has a higher P as compared to HIST) were quite larger than their temperature variations (i.e., all GCMs show rising TA). Precipitation variations in the scenarios might differ from other analysis of the CMIP5 models (Cook & Seager, 2013) or other downscaling approaches applied to the NAM region (Castro et al., 2012; Cerezo-Mota et al., 2011) since the historical seasonality at a monthly resolution was explicitly preserved, rather than allowed to evolve dynamically in the stochastic downscaling approach applied (Faticchi et al., 2013). Nevertheless, the considered scenarios captured a range of plausible near-future precipitation conditions, including increasing, decreasing, or no net change in summer amounts, under a warming trend that is considered realistic for the purposes of identifying climate change impacts.

3.3. Meteorological Change Effects on Simulated Water, Energy, and Carbon Dynamics

Responses to meteorological variations imposed by the climate change experiments were assessed first in the absence of increases in atmospheric CO₂ (365 ppm during 1990–2005). Figure 7 shows the results of the various scenarios (HIST, CNRM-CM5, HadGEM2-ES, MIROC5, and AVE) in terms of the monthly averaged SWC, ET, GPP, and NEP (Figures 7a–7d) during the summer period (MJJAS) as well as the probability density functions of summer season values (Figures 7e–7h), selected to illustrate the rich set of ecohydrological outcomes. The monthly values are obtained as averages over the 100 year periods, while the probability density functions show the full range of total summer season outcomes from each scenario and thus indicate interannual variability represented for historical and near-future conditions. The imposed TA and precipitation changes resulted in substantial summertime variations in the water, energy, and carbon dynamics among the climate change experiments. For instance, scenarios with summer precipitation lower than HIST (HadGEM2-ES and CNRM-CM5, Figure 6d) exhibited decreases in SWC (Figures 7a and 7e) and ET (Figures 7b and 7f), whereas scenarios with summer P at or above HIST (AVE and MIROC5) showed SWC and ET that were similar to or higher than HIST.

The strong correspondence between summer ET and SWC across simulations ($R^2 > 0.88$, $p < 0.05$) is typical of seasonally dry ecosystems (e.g., Scott et al., 2010; Vivoni et al., 2008). Nevertheless, TA differences among the climate change experiments also influenced ET through the sensitivity of plant physiological activity to warming. Specifically, stomatal conductance (g_s) in the simulations was reduced with rising TA for a constant CO₂ value due to increasing vapor pressure deficit and reductions on SWC (Verduzco, 2016). As an example, the HadGEM2-ES scenario with the highest TA (Figure 6c) exhibited increased evaporative demand, which causes complete vegetation failure leading to a reduction in ET due to elimination of the transpiration component. This is consistent with field studies in semiarid ecosystems reporting decreased stomatal conductance and carbon assimilation under warming-induced stress (Hamerlynck et al., 2000; Hamerlynck & Knapp, 1996; Ogle & Reynolds, 2002; Serrat-Capdevila et al., 2011).

Interestingly, differences among the climate change experiments were more pronounced when comparing carbon dynamics through the monthly evolution and summer total GPP (Figures 7c and 7g) and NEP (Figures 7d and 7h). This can be explained through the compensating effects of rising TA and changing P

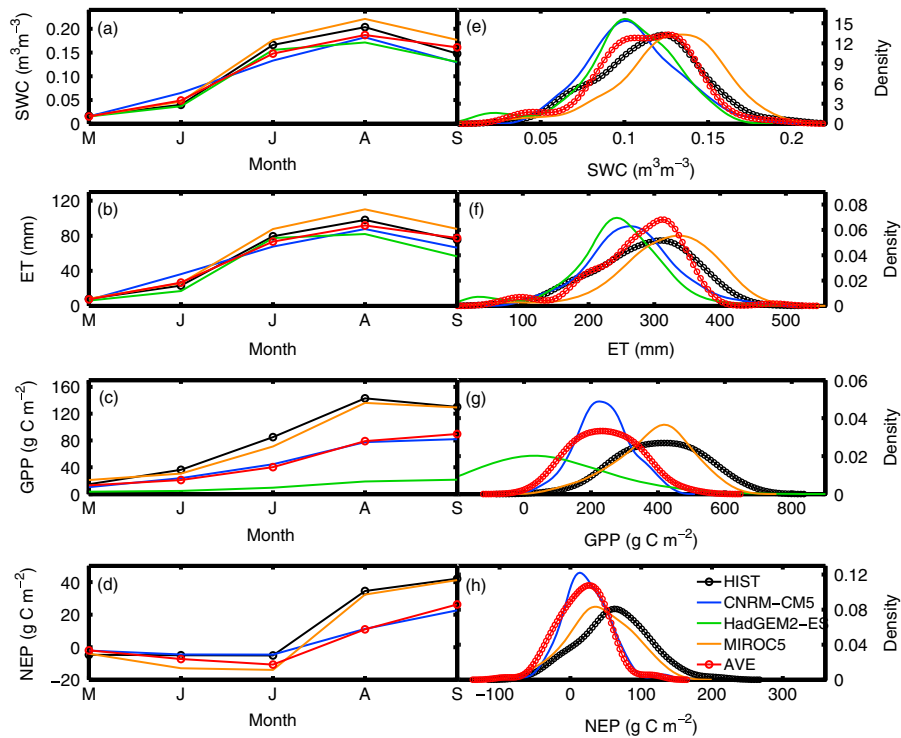


Figure 7. Comparison of water, energy, and carbon dynamics for historical (1990–2005) and climate change experiments (2030–2045) using representative realizations for HIST, CNRM-CM5, HadGEM2-ES, MIROC5, and AVE. Monthly mean values and seasonal probability density functions of (a, e) soil water content (SWC), (b, f) evapotranspiration (ET), (c, g) gross primary productivity (GPP), and (d, h) net ecosystem productivity (NEP) during summer (May–June–July–August–September, MJJAS).

on plant productivity and ecosystem respiration. For instance, MIROC5 and AVE exhibit similar values of TA that were both larger than HIST (Figure 6c), but there is a larger summer P in MIROC5 as compared to both AVE and HIST (which have similar totals, Figure 6d). While rising TA increases evaporative demand, higher P reduces soil moisture stress. The net result is an increase in GPP and NEP in MIROC5 relative to AVE, whereas MIROC5 and HIST are fairly close with respect to summer season carbon fluxes. This suggests that higher summer P has the capacity to compensate for increased summer TA (MIROC5 versus HIST), while maintaining similar precipitation under rising temperature leads to a lower GPP and NEP (AVE versus HIST). This latter case is consistent with experimental studies where increased temperatures have been shown to unfavorably affect productivity under constant precipitation treatments (e.g., Epstein et al., 1997; Mowll et al., 2015; Wu et al., 2011). Moreover, large increases in TA along with decreases in P , like the HadGEM2-ES scenario, significantly decrease GPP in the subtropical shrubland such that there is a collapse in the simulated plant activity. As a result, increased summertime TAs and reduced precipitation could cause large impacts on vegetation productivity that would require further plant adaptations or variations in community composition, as suggested in prior work (Dieleman et al., 2015; Goyal, 2004; Lavee et al., 1998; Moritz & Agudo, 2013; Ponce-Campos et al., 2013; Schwinning & Ehleringer, 2001).

A closer inspection of the summer carbon fluxes in Figure 8 reveals substantial variations between premonsoon (MJ) and monsoon (JAS) periods in the scenarios (HadGEM2-ES is omitted as GPP approached 0 after 35 years of simulation) as well as the relative importance of heterotrophic (R_h) and ecosystem respiration (R_{ECO}) on net ecosystem productivity. For all scenarios, premonsoon magnitudes of R_h and R_{ECO} were smaller than respiration fluxes during the monsoon, consistent with the drier soil conditions and lower microbial biomass (Figures 8a and 8b), as presented in other sites in the NAM region (Barron-Gafford et al., 2012). Furthermore, R_h is a larger fraction of R_{ECO} for the premonsoon period ($R_h/R_{ECO} = 0.53, 0.52, 0.51$ and 0.55 for HIST, CNRM-CM5, MIROC5, and AVE) as compared to monsoon conditions ($R_h/R_{ECO} = 0.32, 0.31, 0.33,$ and 0.34), indicating that R_a increases in importance during the summer. Variations in monsoon values of respiration fluxes across the scenarios follow patterns in GPP (Figure 7g), as shown in prior studies (Gomez-Casanovas et al., 2012; Stoy et al., 2009). For example, R_h was correlated well with GPP ($R^2 > 0.60, p < 0.05$) such that scenarios with a

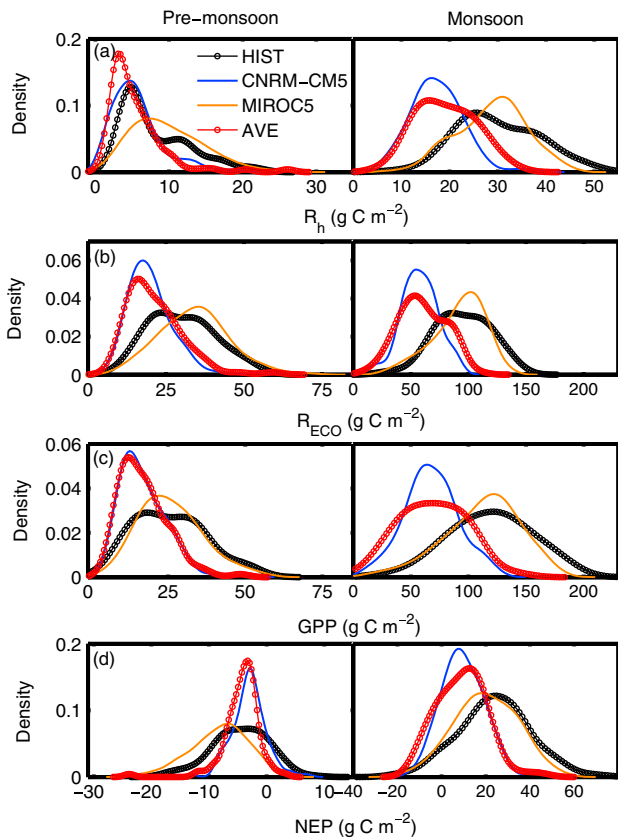


Figure 8. Comparison of carbon dynamics for historical (1990–2005) and climate change experiments (2030–2045) using representative realizations for HIST, CNRM-CM5, MIROC5, and AVE for premonsoon (May–June) and monsoon (July–August–September) periods. Probability density functions of (a) heterotrophic respiration (R_h), (b) ecosystem respiration (R_{ECO}), (c) gross primary productivity (GPP), and (d) net ecosystem productivity (NEP) totals during each period.

higher GPP (HIST and MIROC5) exhibit higher R_h due to the increased availability of litterfall for decomposition (Figures 8b and 8c). In contrast, premonsoon periods showed sensitivity to both GPP and SWC such that MIROC5 with a higher P had substantially larger R_h than those scenarios with similar TA but lower P . This is consistent with other studies indicating that productivity enhancements via water availability are more critical controls on respiration than TA changes in semiarid ecosystems (Janssens et al., 2001; Reichstein et al., 2003). Premonsoon conditions also had substantially lower GPP and NEP as compared to the monsoon period (Figures 8c and 8d), with more negative values of NEP indicating the relative importance of R_{ECO} as compared to GPP prior to the growing season. Furthermore, higher precipitation and rising TAs (MIROC5) promote a more substantial R_h that reduce NEP, whereas a lower P and higher TA (CNRM-CM5 and AVE) resulted in NEP closer to 0. As a result, subtropical shrublands could become a larger net carbon source during premonsoon periods when warming is coupled with increased precipitation.

3.4. CO₂ Fertilization Effects on Simulated Water, Energy, and Carbon Dynamics

Superimposed effects of meteorological changes and increased atmospheric CO₂ concentrations (482 ppm over the 2030–2045 period) were assessed using a second set of simulations for each model scenario (CNRM-CM5, HadGEM2-ES, MIROC5, and AVE). Figure 9 presents the modeling outcomes for the climate change experiments (with and without CO₂ fertilization) relative to the HIST (1990–2005) simulation and the summer (MJJAS) averaged observations (OBS, 2008–2012). Differences between HIST and OBS were only due to the sampling of different time periods since simulations during 2008–2012 were consistent with OBS (Table 4). For the higher CO₂ scenarios, both GPP (+172.1, 188.5, and 210.5 g C m⁻² for CNRM-CM5, MIROC5, and AVE, respectively) and R_{ECO} (+146.9, 147.0, and 153.7 g C m⁻²) show increases when compared to the CO₂ of 365 ppm case (Figures 9a and 9b). Thus, for the same set of imposed meteorological changes, increased atmospheric CO₂ enhances

GPP, as seen in field and remote sensing studies (Ainsworth & Long, 2005; Donohue et al., 2013; Morgan et al., 2004; Wang et al., 2012), and that is consistent with higher observed ecosystem respiration. Larger enhancements in GPP and R_{ECO} were noted for scenarios with more precipitation during the summer (MIROC5 versus CNRM-CM5). However, the increase in GPP due to CO₂ fertilization exceeds that of R_{ECO} due to a reduction of the autotrophic respiration per unit leaf area (e.g., Drake et al., 1997). As a result, NEP from the CO₂ fertilization experiments increased in terms of the median value and the range of values in all scenarios relative to simulations without a rising CO₂ (Figure 9c). Thus, CO₂ fertilization offsets the meteorological impacts on NEP in the near future (2030–2045) at the expense of an increase summer interannual variability. The positive effects of fertilization on the median NEP varied across the scenarios (+34.6, 33.2, and 33.9 g C m⁻²) with a higher increase for AVE with the largest increase in WUE. In addition, the CO₂ fertilization altered NEP at the subtropical shrubland under the HadGEM2-ES scenario permitting ecosystem resilience and a positive carbon balance.

The role of precipitation changes on enhancing NEP was further explored by comparing SWC for the two sets of CO₂ experiments. As expected, higher GPP for scenarios with CO₂ fertilization was linked to a dramatic increase in LAI (+72%, 45%, and 73% for CNRM-CM5, MIROC5, and AVE, respectively) relative to the cases with CO₂ at 365 ppm, which resulted in a higher summertime ET (+18, 13, and 21 mm). While the higher ET under CO₂ fertilization would be expected to deplete soil water, we found no appreciable changes in SWC of the top 10 cm of soil (+0.0013, 0.0007, and 0.0019 m³/m³), even for cases where summertime precipitation decreased or remained similar (CNRM-CM5 and AVE). These results are consistent with Fatichi, Leuzinger, et al. (2016) who showed that increased WUE supports a higher LAI through soil

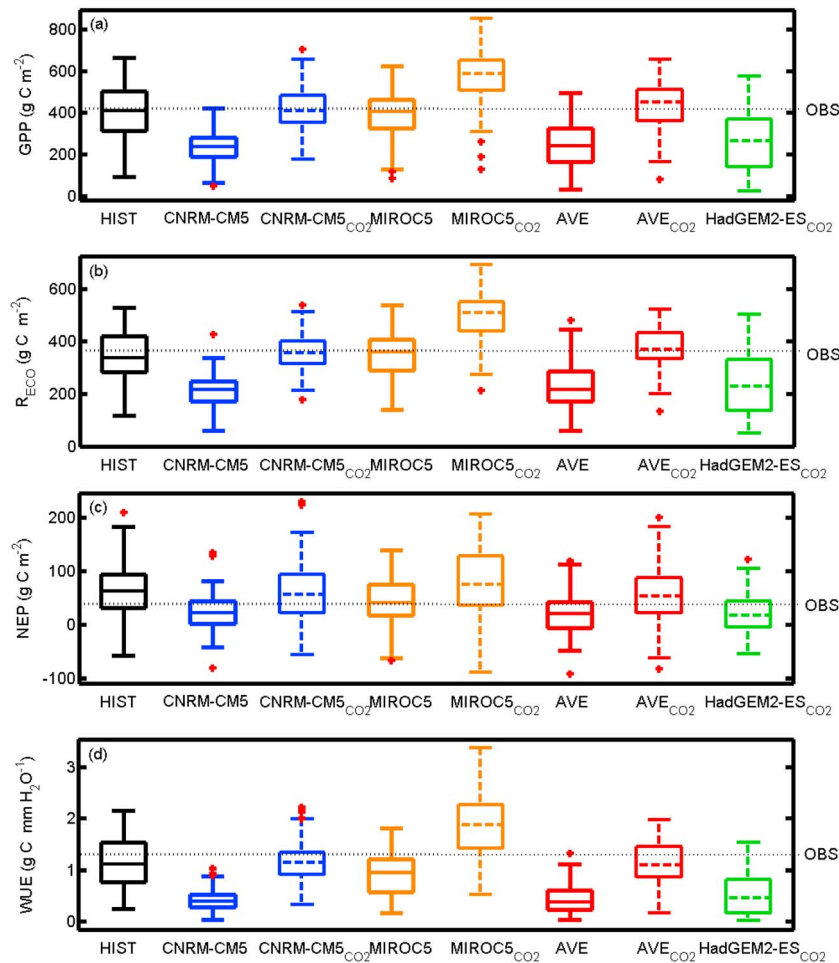


Figure 9. Box-whisker plots of summer (May–June–July–August–September) ecosystem respiration (R_{ECO}), gross primary productivity (GPP), net ecosystem productivity (NEP), and water use efficiency (WUE) for the climate change experiments under meteorological changes and superimposed CO_2 fertilization (labeled with subscript CO_2) using representative realizations for HIST, CNRM-CM5, HadGEM2-ES, MIROC5, and AVE. Dashed horizontal line in each subplot represents summer averages from observations (OBS, 2008–2012).

water savings but leads to a more rapid consumption of SWC due to the increased vegetation. The effects of increased CO_2 on gains in NEP despite a similar SWC when compared to scenarios without fertilization is attributed to ecosystem alterations in water use efficiency ($WUE = GPP/ET$, Figure 9d), which increased substantially (+68%, 42%, and 69%) at the expense of higher summertime interannual variability. Thus, a secondary effect of CO_2 fertilization is to allow more productive summers (i.e., higher NEP), when precipitation is not limiting, through higher WUE. As a result, CO_2 fertilization leads to a more efficient but variable ecosystem in terms of biomass production per amount of water consumed in most of the scenarios. Prior investigations have identified similar CO_2 fertilization effects on WUE, including through experimental studies of semiarid plants (e.g., Leakey et al., 2009; Morgan et al., 2011; Xu et al., 2014) and analyses of remotely sensed data in drylands (e.g., Donohue et al., 2013; Lu et al., 2016). Nevertheless, it has been uncommon to measure WUE directly in semiarid regions with strong vegetation dynamics. As such, there is a need to conduct additional observational analyses in seasonally dry ecosystems to compare with our model-based estimates of the CO_2 fertilization effect on WUE (+40% to 70%), as have been performed in temperate forests (Kauwe et al., 2013). In our study, the increase in WUE was greater in the warmest scenario (HadGEM2-ES) since elevated CO_2 allows plants to decrease stomatal conductance, while maintaining photosynthetic rates (Blumenthal et al., 2013), which resulted in positive NEP under CO_2 fertilization. Similar effects have been observed under experimental CO_2 fertilization (e.g., Cernusak et al., 2013; Conley et al., 2001) and more recently as a trend due to rising CO_2 concentrations (e.g., Lu et al., 2016; Maseyk et al., 2011).

4. Summary and Conclusions

In this work, we combined ecohydrological and soil carbon models to simulate water, energy, and carbon dynamics in a seasonally dry, semiarid ecosystem of northwestern México across temporal resolutions ranging from hourly to interannual variability. Compared to a set of field and remotely sensed observations, the tRIBS-VEGGIE and SCM simulations accurately captured the seasonality of vegetation activity and carbon fluxes of subtropical shrublands (Méndez-Barroso et al., 2014; Villarreal et al., 2016; Vivoni, Rodríguez, et al., 2010). In addition, the simulations represent the main features of net primary productivity in the region, specifically a large respiration pulse early in the summer followed by a gradual switch to carbon fixation during the growing season (Huxman et al., 2004; Verduzco et al., 2015; Yépez et al., 2007). This indicated that the simulation of soil (heterotrophic) respiration is an essential component for reproducing the observed carbon dynamics in this type of ecosystem. Furthermore, simulated R_h was highly sensitive to timing of the first storms during the NAM that increase SWC and to the amount of labile substrate derived from litterfall from the previous summer. Insights gained from the ecohydrological and soil carbon model application could potentially serve to improve terrestrial biosphere models (e.g., Huntzinger et al., 2012) that have been shown to misrepresent carbon dynamics in semiarid shrublands. Nevertheless, the use of the combined models within this ecosystem could be improved by adding a plant functional type, such as winter annuals (Werk et al., 1983) or evergreen shrubs (Biederman et al., 2018), that is active from fall to spring. In this manner, the physiological activity during winters would enhance the representation of vegetation dynamics and impact the generation and decomposition of litterfall, thus affecting the respiratory efflux at the start of the following monsoon. This is consistent with Verduzco et al. (2015) and Zhang et al. (2014), who suggested that the net carbon balance depends on the relative strength of the heterotrophic carbon release versus the primary productivity occurring later in the growing season. Overall, both the observed record and simulations over the studied (2008–2012) and historical (1990–2005) periods showed that the subtropical shrubland was generally a net carbon sink (positive NEP) over both growing season and annual time scales.

Subsequently, we conducted a comparison of historical (1990–2005) and near-future (2030–2045) climate change scenarios obtained from the stochastic downscaling of three GCMs (Fatichi et al., 2011, 2013) tailored for input to the tRIBS-VEGGIE and SCM models. Increased near-future TAs reduced net ecosystem productivity, though a compensation effect was identified for some of GCMs (e.g., MIROC5) exhibiting higher summer precipitation as compared to the historical scenario (HIST). This was attributed to higher plant stress under warmer temperatures and lower precipitation, which limited GPP. Since R_{ECO} was reduced to a lesser degree than GPP, due to warmer temperatures and short-term substrate availability, a lower NEP resulted in all scenarios, with compensation occurring when atmospheric CO_2 concentration was increased. When GCM projections of summer precipitation were substantially lower (HadGEM2-ES), a collapse of the simulated plant activity was observed (i.e., GPP approaching 0). It should be noted, however, that tRIBS-VEGGIE simulations do not currently account for plant thermal acclimation that can prevent “diebacks” due to high temperatures (Hamerlynck et al., 2000; Salvucci & Crafts-Brandner, 2004) or for plant mortality processes induced by cavitation (Fatichi, Pappas, et al., 2016; Plaut et al., 2012), and thus the collapse of plant activity under the HadGEM2-ES scenario is subject to considerable uncertainty.

Our main finding was that reductions in NEP under near-future meteorological changes were significantly offset under the CO_2 fertilization experiments for all considered GCMs. This was mainly attributed to an increase in WUE under elevated CO_2 concentrations via an indirect effect on SWC as identified in other water-limited ecosystems (Fatichi, Pappas, et al., 2016; Lu et al., 2016). As a result of higher SWC, the effects of warming-induced stress can be offset, leading to increases in NEP in the near future for all GCMs relative to the historical period. Increases in WUE under CO_2 fertilization help to explain how seasonally dry ecosystems can recover as a net carbon sink with a strength similar to the historical conditions under the superimposed climate change effects. For the scenario with higher summer precipitation (MIROC5), near-future NEP is larger than HIST, whereas for the case with the highest summer temperature (HadGEM2-ES), CO_2 fertilization prevents the collapse of the simulated plant activity. Nevertheless, these projected changes are also subject to uncertainty since photosynthetic acclimation to elevated CO_2 (Mueller et al., 2016; Newingham et al., 2013; Sage et al., 1989) is not currently considered.

Given the important role of semiarid regions in the terrestrial carbon budget (Ahlström et al., 2015; Poulter et al., 2014), the effects of meteorological changes and CO_2 fertilization on carbon dynamics in seasonally

dry ecosystems could have regional to global consequences. Under warming conditions, lower precipitation and increased atmospheric CO₂, our study suggests that semiarid ecosystems under the influence of the NAM would maintain a similar to actual net carbon balance by the mid-21st century. The offsetting of impacts from meteorological changes in temperature and precipitation and those arising from CO₂ fertilization is an outcome of opposing controls on soil and plant-mediated carbon dynamics. However, changes in the timing, intensity, and distribution of precipitation during the growing season (e.g., Cook & Seager, 2013; Geil et al., 2013), in particular an increase in monsoon rainfall (e.g., Hawkins et al., 2015; Robles-Morua et al., 2015), could lead to ecosystems acting as larger net carbon sinks, due to an increase in WUE under higher CO₂ concentrations, with implications on the global carbon budget. This outcome is consistent with observed biomass trends indicating more efficient productivity in semiarid ecosystems (Donohue et al., 2013), including those in the NAM region (Forzieri et al., 2014). While additional research is necessary to confirm the findings of this study and their implications for terrestrial biosphere models used to capture feedbacks to the climate system (Huntzinger et al., 2012), the combined use of dynamic ecosystem level measurements and numerical modeling is a promising avenue for deciphering the net effect of climate change on the water, energy, and carbon dynamics of seasonally dry, semiarid ecosystems.

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