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Effects of Urbanization-Induced Environmental Changes on Ecosystem Functioning in the Phoenix Metropolitan Region, USA

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ABSTRACT

Urban ecosystems are profoundly modified by human activities and thereby provide a unique "natural laboratory" to study potential ecosystem responses to anthropogenic environmental changes. Because urban environments are now affected by urban heat islands, carbon dioxide domes, and high-level nitrogen deposition, to some extent they portend the future of the global ecosystem. Urbanization in the metropolitan region of Phoenix, Arizona (USA) has resulted in pronounced changes in air temperature (T_{air}), atmospheric CO_2 concentration, and nitrogen deposition (N_{dep}). In this study, we used a process-based ecosystem model to explore how the *Larrea tridentata* dominated Sonoran Desert ecosystem may respond to these urbanization-induced environmental changes. We found that water availability controls the magnitude and pattern of responses of the desert ecosystem to elevated CO_2, air temperature, N deposition and their combinations. Urbanization effects were much stronger in wet years than normal and dry years. At the ecosystem level, aboveground net primary productivity (ANPP) and soil organic matter (SOM) both increased with increasing CO_2 and N_{dep} individually and in combinations with changes in T_{air}. Soil N (N_{soil}) responded positively to increased N deposition and air temperature, but negatively to elevated CO_2. Correspondingly, ANPP and SOM of the *Larrea* ecosystem decreased along the urban–suburban–wildland gradient, whereas N_{soil} peaked in the suburban area. At the plant functional type (FT) level, ANPP generally responded positively to elevated CO_2 and N_{dep}, but negatively to increased T_{air}. C_3 winter annuals showed a greater ANPP response to higher CO_2 levels (>420 ppm) than shrubs, which could lead over the long term to changes in species composition, because competition among functional groups is strong for resources such as soil water and nutrients. Overall, the combined effects of the three environmental factors depended on rainfall variability and nonlinear interactions within and between plant functional types and environmental factors. We intend to use these simulation results as working hypotheses to guide our field experiments and observations. Experimental testing of these hypotheses through this process should improve our understanding of urban ecosystems under increasing environmental stresses.

Key words: Urbanization; environment changes; desert; PALS–FT model; urban-wildland gradients; *Larrea*; simulation experiments.

INTRODUCTION

Urbanization is accelerating worldwide, with about 50% of the human population now living in urban areas, and this figure is projected to increase to 60% by 2025 (Pickett and others 2001). Urbanization directly transforms landscapes and affects biodiversity, ecosystem productivity, watershed discharge characteristics, and biogeochemical cycles (McDonnell and others 1997; Grimm and others 2000; Jenerette and Wu 2001; Pickett and others 2001; McKinney 2002; Kaye and others 2006). Urbanization also indirectly influences ecosystems across various scales by altering abiotic environmental conditions, including atmospheric chemistry, climate, and soil properties (Idso and others 1998; Lovett and others 2000; Pouyat and others 2002; Kalnay and Cai 2003; Hope and others 2005; Pataki and others 2006) and biotic components, such as introduced exotic species (Airola and Buchholz 1984; Hope and others 2003). Yet, urban areas have been largely ignored in general ecological studies and are among the least understood of all ecosystems (Pickett and others 2001; Grimm and others 2000).

Urban areas are known to be sources of greenhouse gases (CO_2, CH_4, N_2O), air pollutants (O_3, NO_x gases, NO_3^-, NH_4^+), and heat that are driving environmental change regionally and globally. Numerous studies have shown that air temperature (Karl and others 1988; Jones and others 1990), atmospheric CO_2 concentration (Grimmond and others 2002; Idso and others 2001, 2002; Pataki and others 2003), and nitrogen (N) deposition (Lovett and others 2000; Fenn and others 2003; Carreiro and Tripler 2005), are all higher in urban areas than their rural surroundings. These factors are also known to be major global change drivers. Therefore, remnant ecosystem patches along an urban-to-rural environmental gradient may be treated as a ''natural laboratory'' for studying plant and ecosystem responses to environmental changes (Carreiro and Tripler 2005). Several ecosystem processes have been found to vary significantly along an urban-to-wildland gradient, such as primary productivity (Gregg and others 2003), soil carbon dynamics and gas exchange (Pouyat and others 2002; Koerner and Klopatek 2002), and litter decomposition and soil N dynamics (Groffman and others 1995; Pouyat and others 1997; Hope and others 2005). However, it remains difficult to isolate the relative contributions of the different environmental driving variables which simultaneously and interactively affect ecosystem responses. To address such problems, simulation

modeling has become a powerful approach in ecosystem and global change studies (Melillo and others 1993; Canham and others 2003; Reynolds and others 2004; Wu and others 2006).

Deserts have received little attention in the study of ecosystem responses to global environmental changes, especially with respect to elevated atmospheric [CO_2] (Naumberg and others 2003). Studies on other ecosystems have shown that elevated CO_2 often stimulates photosynthesis and decreases stomatal conductance, thereby enhancing water-use efficiency (Drake and others 1997), which is particularly relevant for water-limited desert plants (Noy-Meir 1973; Smith and others 1997). Therefore deserts have been said to be the most responsive of all ecosystem types to elevated CO_2 (Strain and Bazzaz 1983; Melillo and others 1993). However, recent FACE (free air CO_2 enrichment experiment) studies in the Mojave Desert showed that there was no long-term reduction in stomatal conductance (Huxman and others 1998; Naumburg and others 2003), no decrease in plant water loss for shrubs (Pataki and others 2000), and no enhancement of soil moisture (Nowak and others 2004a). These studies suggest that the responses of desert plants and ecosystems to elevated CO_2 are influenced not only by water but also by nitrogen availability (Smith and others 1997), and that more research is needed to uncover the interactive effects of multiple environmental factors on desert ecosystems.

The major objective of this study was, therefore, to explore through simulation modeling the interactive effects of urbanization-induced environmental changes on a desert ecosystem in the Phoenix metropolitan region of the southwestern USA. By so doing, we intend to generate a series of working hypotheses that can be used to guide our ongoing empirical studies. Our simulation modeling addressed the following questions: (1) How do air temperature, ambient CO_2, and N deposition individually and interactively affect the annual net primary productivity (ANPP), soil organic matter (SOM), and soil N dynamics of the *desert* ecosystem? (2) How do different plant functional types (FTs) within the ecosystem respond to these environmental changes? (3) How do variations in precipitation influence the response patterns of the desert ecosystem? (4) What are the model predictions on the variations in ANPP, SOM, and N_{soil} across the urban-wildland environmental gradients in the Phoenix area?

The Phoenix metropolitan area, home to the Central Arizona-Phoenix Long-Term Ecological Research (CAP LTER) project, provides a unique
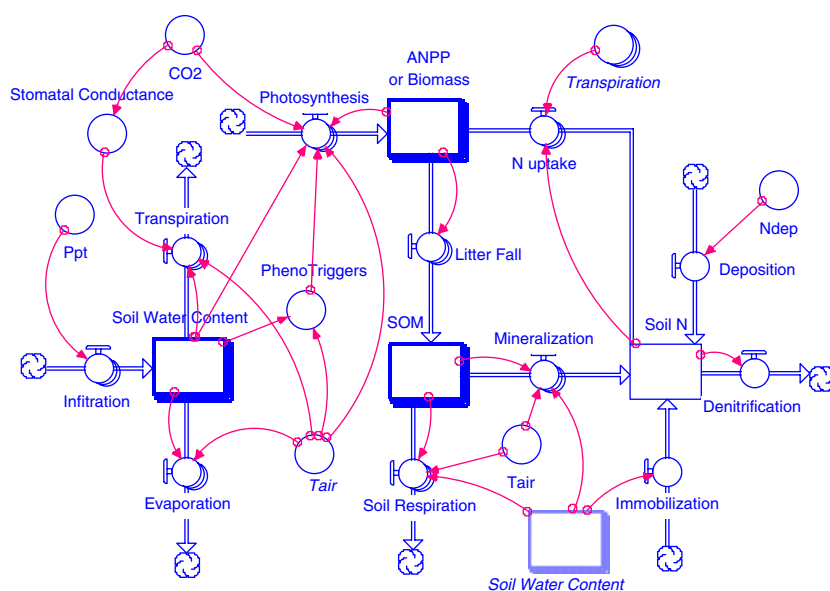
Figure 1. A schematic conceptual diagram showing how major environmental factors (*circles*) influence the ecosystem processes (*pipe lines* with *arrows*) that control the ecosystem properties (*boxes*) of interest in this study. *Thin lines* with *arrows* show direct connections between environmental factors and ecosystem processes and between the processes and ecosystem properties. This diagram shows only those key components and functional relationships in the PALS–PHX model that are most closely related to the topics of this study. For detailed descriptions of the model structure, see Shen and others (2005).

Abbreviation	Description	Unit
CO_2	Atmospheric CO_2 concentration	ppm
ANPP	Aboveground annual primary productivity	g DM m^{-2} y^{-1}
SOM	Soil organic matter	g C m^{-2}
Ppt	Precipitation	mm
T_{air}	Air temperature	°C
N_{dep}	Nitrogen deposition	kg N ha^{-1} y^{-1}
PhenoTriggers	Phenologic triggers	0 or 1

opportunity for studying the interactive effects of anthropogenic environmental changes on desert ecosystem processes because of the existence of pronounced urban-wildland gradients of air temperature (T_{air}), near surface [CO_2], and N deposition (N_{dep}). Specifically, air temperature is approximately 7.5°C higher in the urban center of Phoenix than in its desert surroundings due to the effect of ''urban heat island'' (Balling and Brazel 1987; Brazel and others 2000). Furthermore, a ''CO_2 dome'' has formed over the cityscape, with ambient CO_2 concentration near the urban center nearly double the global mean concentration (Idso and others 1998, 2001). Finally, a SW–NE gradient of N deposition rate also exists, ranging from less than five to a maximum of approximately 30 kg ha^{-1} y^{-1} against the mountains to the northeast (Fenn and others 2003). *Larrea tridentata*-dominated communities are the most widely distributed native ecosystem type in the Sonoran Desert, and are found along these environmental gradients.

Taking advantage of these existing data sets, this study integrates ecosystem modeling with urban-to-wildland gradient analysis to investigate how increases in CO_2, N deposition and air temperature may interactively affect ecosystem processes in the Phoenix metropolitan region. Here we report on the design and results of our simulation study, and discuss the major findings and their implications for understanding ecosystem responses to multiplicative environmental changes in urban regions and beyond.

MATERIALS AND METHODS

The Ecosystem Model

The process-based ecosystem model, PALS–PHX, was a modified version of PALS–FT (Patch Arid Land Simulator–Functional Types), originally developed for the Chihuahuan Desert (Reynolds and others 1997, 2000; Kemp and others 1997, 2003). The original PALS–FT simulates daily dynamics of carbon (C), N, and water (H_2O) in a representative patch of a desert ecosystem (Reynolds and others 1997, 2000, 2004; Kemp and others 1997, 2003), explicitly considering six plant functional types: shrub, subshrub, C_3 winter annuals, C_4 summer annuals, perennial grasses, and forbs that may compete for soil water and N as defined by their unique rooting distribution char-

acteristics (see Shen and others 2005). The model consists of four interacting modules: (1) atmospheric driving variables and surface energy budget, (2) soil-water distribution and water cycling, (3) phenology, physiology, and growth of plant functional types, and (4) nutrient (C, N) cycling. Figure 1 shows how the key components and functional relationships are linked in the PALS–PHX model, highlighting the pathways through which the major ecosystem variables (ANPP, SOM, N_{soil}, and soil water content) and processes (for example, photosynthesis, transpiration, evaporation, litter fall, SOM decomposition, N mineralization, and N uptake) of interest are affected by the four environmental factors (that is, CO_2, T_{air}, precipitation, N_{dep}). PALS–FT has been used extensively to study ecosystem responses to climate change and rainfall variability in the Chihuahuan Desert (Reynolds and others 1997, 2000, 2004; Gao and Reynolds 2003).

Shen and others (2005) incorporated several changes into PALS–FT to better represent the Sonoran Desert, and validated the adapted version (PALS–PHX) based on empirical observations of *Larrea*-dominated communities in the Phoenix area. Specifically, our direct comparison between the observed and predicted ANPP under current Sonoran Desert climate conditions showed a relative error of ±2.4% at the ecosystem level. The prediction error was larger at the functional type level, but all fell within ±25% for the six functional types (Shen and others 2005), with 4.5% for the dominant shrub functional type that included *Larrea*. Parton and others (1993) suggested a relative error of 25% as a threshold for the acceptability of model predictions. Because our goal for this study was to explore the patterns of ecosystem responses to changing environmental conditions, instead of making point predictions, we consider this relative error acceptable. Because the details of PALS–PHX can be found in Shen and others (2005), here we only briefly describe some of the major features of the model that are most relevant to this particular study.

PALS–PHX computes the ecosystem-level ANPP by integrating the daily plant growth of all functional types based on the following equation:

$$G_j = X_{lvs} \cdot SLA_j \cdot A_{max,j} \cdot (12/0.46) \cdot (1 - R_{loss,j}) \cdot F_c \cdot F_t \cdot S_j^N \quad (1)$$

where G_j is the amount of daily plant growth (g dry mass m^{-2}) for functional type j, X_{lvs} is the leaf dry mass (g), SLA is the specific leaf area (m^2 g^{-1}), $A_{max,j}$ is the maximum potential net photosynthetic rate (mol CO_2 m^{-2} s^{-1}), 12 (g) is the mass of C per mol CO_2, 0.46 is the average C content (46%) in plant tissues, R_{loss} is the respiratory loss of photosynthetic production per day, F_t is the temperature influence factor (for forbs and grasses, not for shrubs and annuals), F_c ($2/\pi \times$ photoperiod $\times$ 3,600) is a conversion factor (changing time unit from second to day), and S_j^N is a linear scalar accounting for the effect of leaf N on $A_{max,j}$ (see Eq. 13 in Shen and others 2005).

Atmospheric CO_2 is a crucial input for computing the maximum potential net photosynthetic rate ($A_{max,j}$, mol CO_2 m^{-2} s^{-1}), which is estimated using the following equation:

$$A_{max,j} = \frac{g_j}{1.6} \times \frac{C_a - C_i}{P} \quad (2)$$

where g_j is the stomatal conductance of plant functional type j (mol H_2O m^{-2} s^{-1}; see Reynolds and others 2000; Shen and others 2005), C_a is the partial pressure of atmospheric CO_2 (kPa), and C_i is the partial pressure of intercellular CO_2 (kPa, see Eq. 12 in Shen and others 2005), 1.6 is the ratio of diffusivity of H_2O (21.2×10^{-6}) to CO_2 (12.9×10^{-6}), and P is the atmospheric vapor pressure (kPa).
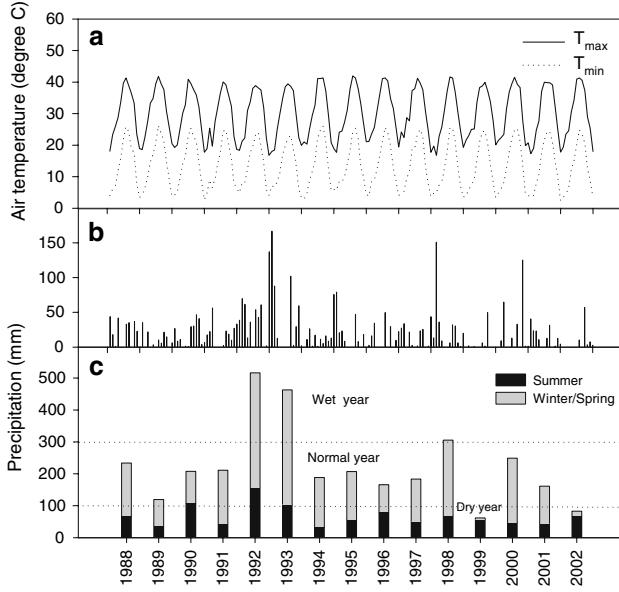
Stomatal conductance g_j is calculated as an exponential function of functional-type leaf water potential (ψ_j), with a linear relationship to decreasing atmospheric vapor deficit (VPD in kPa) and a CO_2 modifying factor (M_{CO_2}):

$$g_j = a \cdot e^{(b \cdot \psi_j)} \cdot (1 - 0.1 \cdot VPD) \cdot M_{CO_2} \quad (3)$$

where a and b are functional type-specific parameters defining the exponential decline in g_j with decreasing ψ_j (Table A2 in Shen and others 2005). A daily value for leaf water potential of each functional type (j) is calculated from the water potential of all soil layers weighted by the fraction of roots of each functional type in each specific soil layer (see Kemp and others 1997). M_{CO_2} is a modifier that takes into account down-regulation of g_j in response to elevated CO_2 (Thornley 1998):

$$M_{CO_2} = \frac{1 + c_{CO_2}}{1 + c_{CO_2} \cdot \frac{C_a}{0.036}} \quad (4)$$

where C_a is the atmospheric [CO_2], c_{CO_2} is a parameter that determines the degree of g_j down-regulation. The factor c_{CO_2} takes values of 0.73, 3.17, −10.4, 1, −10.4, and 0.9 for *Larrea*, subshrub, C_4 perennial grasses, C_3 annuals, C_4 annuals, and forbs, respectively (Nowak and others 2001; Naumberg and others 2003; Ainsworth and Long 2005).

Figure 2. Seasonal and interannual variations in **A** maximum (T_{max}) and minimum (T_{min}) air temperatures, **B** monthly precipitation, and **C** seasonal/annual precipitation that were used to drive the PALS–PHX model. These values were used as control conditions for all simulation experiments in this study. The dataset was obtained from the Wadell Weather station (northwest of Phoenix) operated by the Arizona Meteorological Network (AZMET; http://www.ag.arizona.edu/azmet/azdata.htm).

The dynamics of SOM pools are defined by the following differential equation (Parton and others 1993; Kemp and others 2003):

$$\frac{dC_i}{dt} = K_i \cdot A \cdot T_m \cdot C_i \qquad (5)$$

where C_i is the amount of carbon in different SOM pools, K_i is the maximum decomposition rate (day^{-1}) for the ith pool, T_m is the effect of soil texture on SOM turnover, and A is the combined abiotic impact of soil moisture and soil temperature on decomposition. Soil temperatures at different layers are calculated from air temperatures, thus changes in air temperature also influence SOM decomposition and N mineralization that is closely coupled with SOM decay.

Soil N (N_{soil}) content is determined by six processes: mineralization (N_{min}), deposition (N_{dep}), fixation (N_{fix}), volatilization (N_{vol}), immobilization (N_{imb}), and plant uptake (N_{upt}), that is,

$$N_{soil} = N_{min} + N_{dep} + N_{fix} - N_{upt} - N_{vol} - N_{imb}. \qquad (6)$$

The N mineralization process involves decomposition of plant residuals (leaf, stem, and root) and SOM (see Shen and others 2005 for details). N deposition includes both dry and wet deposition. The model assumes that the N dry deposition is directly added to the soil N pool and fully available for plant uptake. Wet deposition is a function of precipitation (Parton and others 1988):

$$N_{wet, dep} = 0.1 \times (0.0001 + 0.096 \times Ppt) \qquad (7)$$

N_{vol} is estimated to be 5% of N_{min}, and N_{fix} and N_{imb} were set to zero in this study. N taken up by plants is closely related to daily canopy-water transpiration, that is, N_{upt} is a product of daily canopy transpiration (Tr_{daily}) and N concentration of soil solution:

$$N_{upt} = Tr_{daily} \times \frac{N_{soil}}{W_{soil}}. \qquad (8)$$

The total daily N_{upt} is further allocated to different plant organs (that is, leaf, stem, and root) based on the daily new growth (in DM m^{-2} day^{-1}) and fixed average N fractions of different plant organs (see Table A2 in Shen and others 2005). The real-time leaf N content (%) is calculated as absolute N content in leaves (g N m^{-2}) divided by leaf biomass (g DM m^{-2}), and it determines the magnitude of the N scalar that is used to modify $A_{max,j}$ therefore ANPP (see Eq. 13 in Shen and others 2005).

Inputs to PALS–PHX include data on climatic conditions, soil physical properties, plant and soil C and N storage, and plant ecophysiological parameters. Major model outputs include ANPP, evapotranspiration, canopy cover, SOM, soil-water recharge, and soil C and N mineralization. Climatic data, including T_{max} and T_{min}, precipitation, solar radiation, and relative humidity, were obtained from the Wadell Weather Station near Phoenix for a 15-year period from 1988 to 2002. Figure 2 shows the seasonal and interannual variations of the three major climatic driving variables (T_{max}, T_{min}, and precipitation). We can see that air temperatures vary noticeably in season and precipitation varies dramatically among the 15 years. Other model parameter values were derived from a CAP LTER field survey dataset and the literature (see details in Shen and others 2005).

Table 1. Values of the Three Urbanization-Induced Environmental Factors used in Simulations

	Temperature change (δT; °C)		CO_2 concentration (CO_2; ppm)	N deposition rate (N_{dep}; kg N ha^{-1} y^{-1})
	δT_{max}	δT_{min}		
Maximum	3.0	7.5	520	26.0
Medium	1	5.5	440	14.0
Minimum	−1	3.5	370	4.0
Simulation interval	0.50	0.50	10	1
Control	Observed	Observed	360	2.0

Temperature differences were derived from Balling and Brazel (1987) and Brazel and others (2000); CO_2 concentrations from Idso and others (1998) and Wentz and others (2002); and N deposition from Fenn and others (2003). A full factorial experimental design yielded 27 treatment combinations[1].
[1]Three factors (air temperature, CO_2 concentration, and N deposition) and three levels (maximum, middle, and minimum) for each factor for a total of 27 combinations: NminCminTmax, NminCminTmid, NminCminTmin, NminCmidTmax, NminCmidTmid, NminCmidTmin, NminCmaxTmax, NminCmaxTmid, NminCmaxTmin, NmidCminTmax, NmidCminTmid, NmidCminTmin, NmidCmidTmax, NmidCmidTmid, NmidCmidTmin, NmidCmaxTmax, NmidCmaxTmid, NmidCmaxTmin, NmaxCminTmax, NmaxCminTmid, NmaxCminTmin, NmaxCmidTmax, NmaxCmidTmid, NmaxCmidTmin, NmaxCmaxTmax, NmaxCmaxTmid, NmaxCmaxTmin. N = N deposition, C = CO_2 concentration, T = temperature, max = maximum level, mid = middle level, and min = minimum level.

Urban-Wildland Gradients of Environmental Factors

To obtain a set of values for environmental factors that are reasonable for our simulation study, we followed the urban-rural gradient approach (McDonnell and others 1997; Luck and Wu 2002; Carreiro and Tripler 2005; here referred to as the urban-wildland gradient). That is, the ranges of environmental changes of interest were estimated through space-for-time substitution.

CO_2 Gradient. Idso and others (1998) described an ''urban CO_2 dome'' in the Phoenix metropolitan area with pre-dawn CO_2 concentration as high as 555 ppm in the city center, decreasing to approximately 370 ppm on the city outskirts. The mid-afternoon urban-wildland CO_2 gradient was shallower, decreasing from 470 ppm in the urban center to 345 ppm in the exurban area. Additional studies showed that the ''urban CO_2 dome'' is a year-round phenomenon in Phoenix (Idso and others 2001, 2002). The urban-wildland difference in CO_2 in Phoenix was higher than that found in other American cities, such as St Louis, New Orleans, and Cincinnati (Idso and others 1998). Considering that the urban-wildland difference in CO_2 concentration differs depending on time of day, day of week, and season, we used the CO_2 levels ranging from 370 to 520 ppm as our model inputs for the urban and suburban area. A CO_2 concentration of 360 ppm was used as the control condition for the desert wildland (Table 1).

Temperature Gradient. Studies of urban heat islands in Phoenix (Balling and Brazel 1987; Brazel and others 2000) showed that the urban-wildland temperature difference ranged from −1.0 to 3.0°C

for maximum air temperature (T_{max}) and from 3.5 to 7.5°C for minimum air temperature (T_{min}) between 1988 and 2002. We used these values in our simulation experiments to define the bounds of changes in air temperature (Table 1). These urban-wildland temperature differences vary in time, and the largest differences usually occur in summertime (June–August), with consistently higher temperature increase in nighttime than daytime (Balling and Brazel 1987). Overall, the heat island effect in Phoenix is statistically significant for all months and all hours of the day (Hsu 1984). In our simulation design, for simplicity we did not explicitly consider the temporal variability in T_{max} and T_{min}. We also assumed that changes in T_{max} and T_{min} occurred in concert with one another, as indicated by field observations (Brazel and others 2000).

N Deposition Gradient. Dry deposition is usually the largest component of total atmospheric N input in the arid southwestern US (Baker and others 2001; Fenn and others 2003). Baker and others (2001) estimated dry N deposition of 18.5 kg N ha^{-1} y^{-1} and wet N deposition of 2.4 kg ha^{-1} y^{-1} for the Phoenix area. Fenn and others (2003) reported that the simulated N deposition rate varied from 7 to 26 kg N ha^{-1} y^{-1} across the central Arizona–Phoenix area, with upwind desert having the lowest rate, downwind desert the highest rate, and urban core in between. The dry N deposition rate varies seasonally, peaking during the winter months (October to March) and declining during the summer. We used the maximum of 26 kg N ha^{-1} y^{-1} and the minimum of 4 kg N ha^{-1} y^{-1} as the N_{dep} input for our simulation study (Table 1). The control value of N_{dep} rate in the Sonoran Desert was assigned as 2 kg ha^{-1} y^{-1} (Fenn and others

2003). When used for this simulation study, these annual rates were downscaled to daily input values.

Experimental Simulation Design and Data Organization

From the model equations above, the three environmental factors of interest may influence ecosystem processes through multiple pathways. For example, CO_2 concentration can influence SOM and N_{soil} by affecting plant growth and litter production (more growth results in greater litterfall). Temperature can influence SOM and N_{soil} not only by affecting decomposition rate, but also through its effect on canopy transpiration and soil evaporation (Figure 1). Thus, we conducted two groups of simulation experiments using PALS–PHX: single-factor analyses to address how ecosystem processes respond to changes in each of the three environmental factors, and multiple-factor analyses to address the combined influences of the three factors on ecosystem processes (ANPP, SOM, and N_{soil}).

For the single-factor analyses, only one factor (for example, CO_2) was manipulated in each simulation experiment (or model run), the other two factors (that is, temperature and N deposition) were held at the control levels shown in Table 1. Specifically, CO_2 concentration was varied from 360 to 520 ppm with the interval of 10 ppm; N_{dep} was changed from 2 to 26 kg N ha^{-1} y^{-1} with the interval of 1 kg N ha^{-1} y^{-1}; T_{max} and T_{min} were first altered at the same time, with T_{max} varying from +3.5 to +7.5°C and T_{min} from −1 to +3.0°C on the basis of the observed ambient temperatures (that is, control temperatures indicated in Table 1 and shown in Figure 2), then to further explore the relative importance of the influence of T_{max} and T_{min}, one was altered while holding another at its control condition. In summary, there were 17 CO_2 levels, 25 N_{dep} levels, and 9 temperature levels. Because the PALS–PHX is a deterministic model there is only one possible outcome for each treatment level, thus only one model run was conducted for each treatment level, resulting in 69 total model runs (27 for the temperature treatments).

For the multi-factor combinational analyses, each of the three environmental factors was manipulated at three levels—maximum, medium, and minimum—yielding 27 combinations (=3 levels powered by 3 factors) (Table 1). We conducted each simulation/model run for each of the combinations independently. Relative to all the above stated treatment levels, the control condition had

CO_2 level of 360 ppm, N_{dep} of 2 kg ha^{-1} y^{-1}, and ambient observed temperatures and precipitation (Table 1), which also represented the wildland conditions.

For all simulation experiments, ANPP, SOM, and N_{soil} were simulated for a time span of 15 years, with a daily time step. In addition, effects of precipitation variability were examined by categorizing the 15 years into 3 year types: wet years with a mean annual precipitation of 490.0 mm, dry years with 72.4 mm, and normal years with 207.6 mm (Figure 2). Daily model outputs for ANPP, SOM and soil N were aggregated to annual ANPP, SOM accumulation and average soil N content. These annual data were further averaged for each of the three precipitation categories (normal, dry, and wet years), and standard errors were calculated to represent variability within each category.

RESULTS

Ecosystem-Level Response to Urbanization-Induced Environmental Changes

Aboveground Net Primary Productivity (ANPP). The responses of ecosystem ANPP to changes in T_{air}, N_{dep}, and CO_2 and their combinations differed markedly in different types of years with contrasting mean annual rainfall. In general, ANPP responded strongly in wet years, moderately in normal years, and only minimally in dry years (Figure 3). Ecosystem ANPP showed a nonlinear response to elevated CO_2 and T_{air} in wet years, but linear responses in normal and dry years (Figure 3A, C, D). The responses of ANPP to increasing N_{dep} were linear in all type of years (Figure 3B). Increased CO_2 and N_{dep} stimulated ANPP of the *Larrea* ecosystem whereas increased T_{air} depressed it. Comparing the separate manipulations of T_{max} and T_{min} suggests that the temperature effect on ANPP was attributed mainly to changes in T_{max} (Figure 3D).

Comparing the response of ANPP to changes in the three environmental factors, effects of elevated N_{dep} and CO_2 on ecosystem ANPP were similar, but larger than that of T_{air} (Figure 3). For example, in response to the largest increases in N_{dep} (24 kg ha^{-1} y^{-1}), CO_2 (160 ppm), and T_{air} (4.0°C) in the Phoenix urban area (see Table 1), the mean ANPP for the 15 simulation years increased by 42.7, 52.5, and −7.8 g DM m^{-2} y^{-1} compared to the mean ANPP under control conditions (76.3 g DM m^{-2} y^{-1}), respectively. The dominance of N_{dep} and CO_2 over temperature in affecting ecosystem ANPP be-
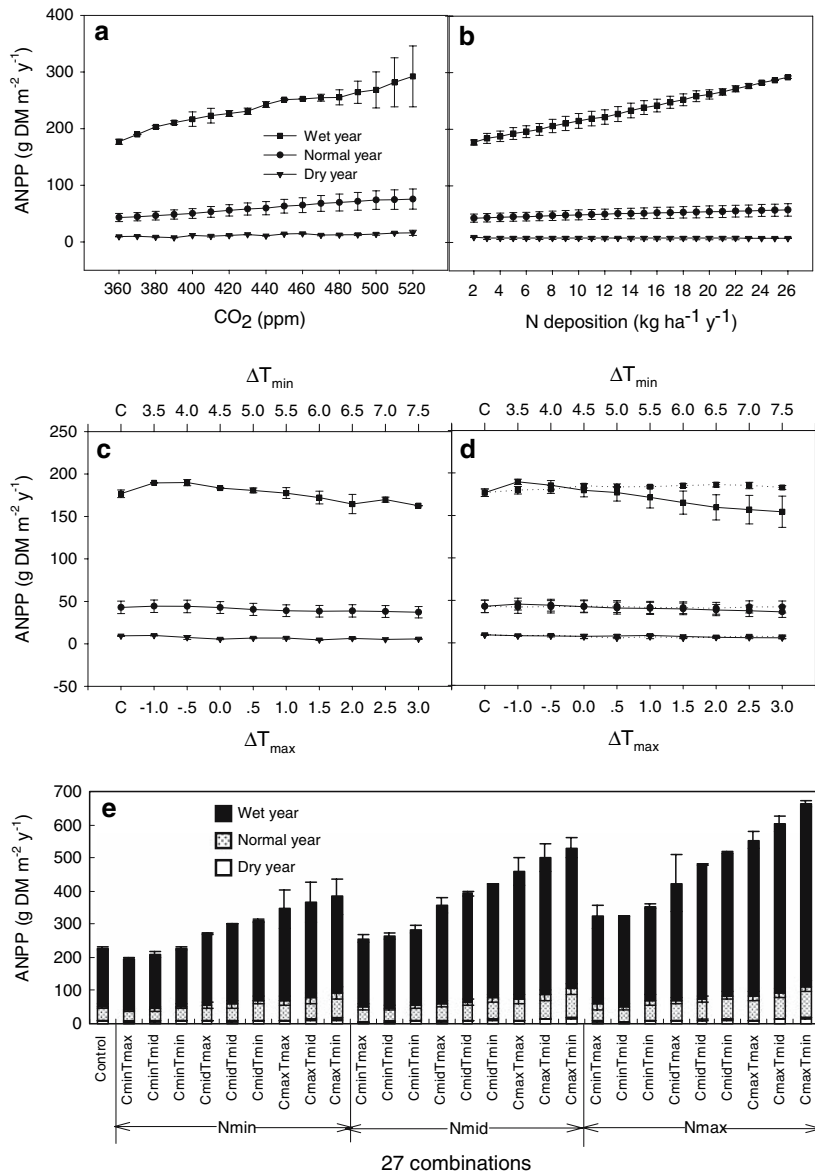
Figure 3. Responses of ecosystem ANPP to changes in **A** atmospheric CO_2 concentration; **B** dry N deposition; **C** maximum and minimum air temperature at the same time; **D** maximum and minimum air temperature separately; and **E** combined effects of the three environmental factors. Note that **A–D** share the same legend as listed in **A**. For **D**, *dotted line* denotes the minimum air temperature and *solid line* denotes the maximum air temperature. *Error bars* are ±1 SE and denote the variations among different years within the same year category defined by precipitation (normal, wet, or dry), and not shown when smaller than symbol used. ANPP for each year category in **E** is the height of portion of the bar corresponding to that category.

came clearer in the combinatorial simulations: higher N deposition rates and CO_2 concentrations led to much larger ANPP increments (Figure 3E). That is also to say that elevated CO_2 and N_{dep} rate magnified each others effects on ecosystem ANPP; whereas increased T_{air} depressed the positive effects of elevated CO_2 and N_{dep} on ANPP. For example, in response to the combination of NmaxCmaxTmax, the mean ANPP increment over 15 years was 108 g DM m^{-2} y^{-1}, which is larger than the sum of the individual-factor effects of the three factors.

SOM Pools. SOM is divided into four pools based on decomposition rates: surface-active organic matter, belowground active SOM, slow SOM, and passive SOM (see Shen and others 2005). In this

paper, we refer to SOM as the sum of the four pools, although most changes in SOM happened in the active SOM pools during the simulation. As with ANPP, SOM responded nonlinearly to changes in CO_2, N_{dep} and T_{air} in wet years, but response was linear in normal and dry years (Figure 4). SOM increased with increasing CO_2 and N_{dep} separately or in combination, and decreased with increasing T_{max}. The response pattern of SOM to various combinations of the three factors was similar to that of ANPP: given the set of parameters for the three environmental factors used in our simulation, CO_2 had the strongest influence on SOM.

As with ANPP, the response of SOM to changes in the three environmental factors was also
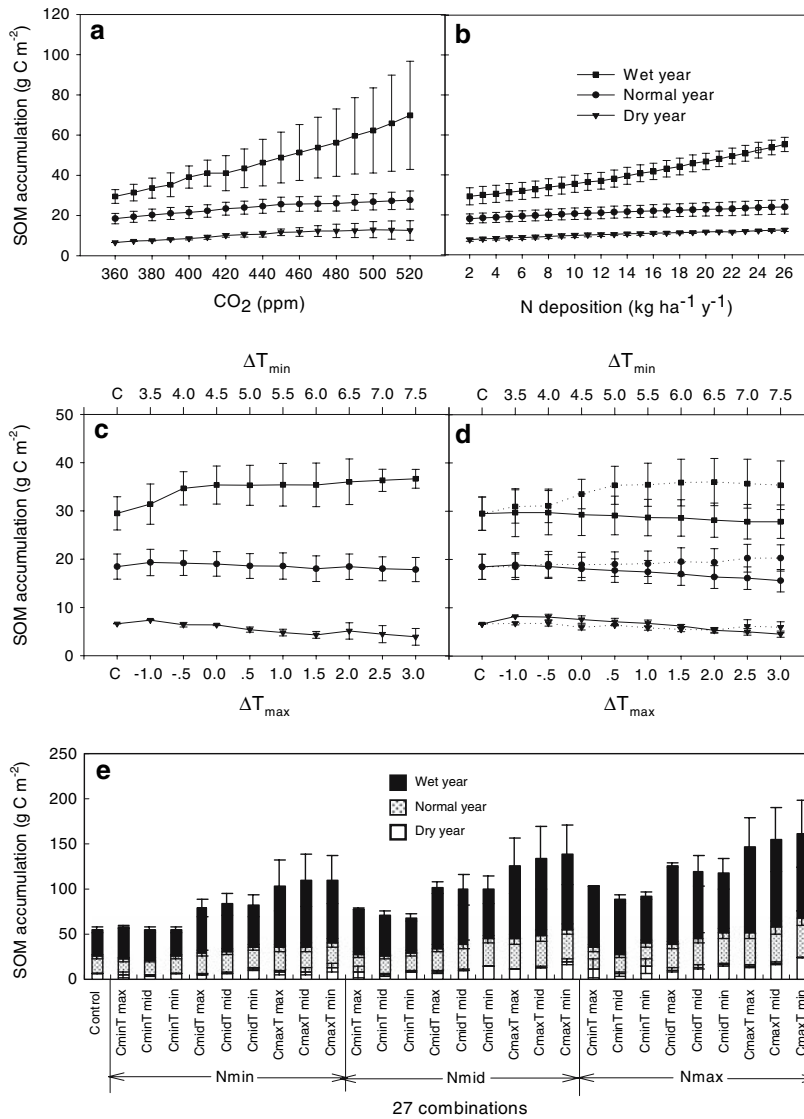
Figure 4. Responses of soil organic matter accumulation to **A** changes in atmospheric CO_2 concentration, **B** dry N deposition, **C** maximum and minimum air temperature at the same time, **D** maximum and minimum air temperature separately, and **E** combined effects of the three environmental factors. **A–D** Share the same legend as listed in **A**. For **D**, *dotted line* denotes the minimum air temperature and *solid line* denotes the maximum air temperature. *Error bars* are ±1 SE and denote the variations among different years within the same year category defined by precipitation (normal, wet, or dry), and not shown when smaller than symbol used.

strongly affected by interannual variation in rainfall; that is, the increment in SOM content was generally larger in wet years than in normal and dry years (Figure 4). For example, in response to the largest increases in CO_2 (160 ppm), N_{dep} (24 kg ha^{-1} y^{-1}), and T_{air} (4.0°C) in the Phoenix urban area (Table 1), annual SOM accumulation rate increased by 40.6, 26, and 7.2 g C m^{-2} y^{-r}, respectively, in wet years; but 9.2, 5.9, and −2.7 g C m^{-2} y^{-1} in normal years and 6.0, 4.9, and −0.62 g C m^{-2} y^{-1} in dry years. Larger variations in SOM in wet years were consistent across all treatment levels of the three environmental factors. But unlike ANPP, the response of SOM to the three factors combined was additive (30.9 g C m^{-2} y^{-1} for the NmaxC-maxTmax combination compared to 18.5 g C m^{-2} y^{-1} for CO_2 + 12.3 g C m^{-2} y^{-1} for N_{dep} + 1.2 g C m^{-2} y^{-1} for T_{air} = 32.0 for individual factor effects).

Soil Nitrogen. Soil N responded nonlinearly to changes in CO_2 and T_{air}, but linearly to changes in N_{dep} (Figure 5). Increases in N_{dep}, T_{air}, and T_{max} had positive effects on N_{soil}, whereas elevated CO_2 and T_{min} had negative impacts on N_{soil}. Soil N was most responsive to changes in atmospheric N deposition, as compared to CO_2 and temperature. In response to the combinational changes in the three environmental factors, soil N showed positive responses when N_{dep} was at medium and high levels, regardless of CO_2 and T levels and rainfall. But when N_{dep} was at the minimum level, CO_2 became the dominant factor in determining whether soil N change was positive or negative (Figure 5E).

Rainfall variations also had substantial impacts on the response of soil N to changes in urban environmental factors. Soil N was always higher in dry years than in normal and wet years (Figure 5).
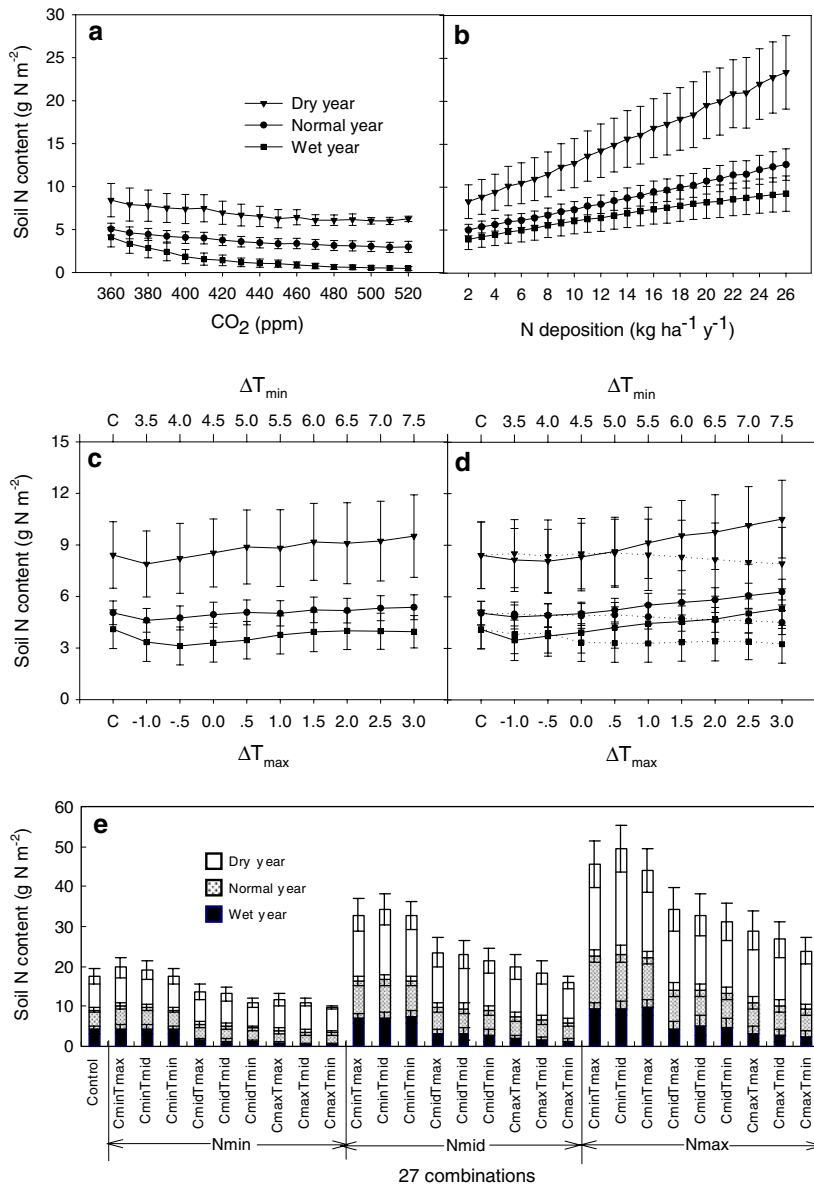
Figure 5. Soil N responses to changes in **A** atmospheric CO_2 concentration, **B** dry N deposition, **C** maximum and minimum air temperature at the same time, **D** maximum and minimum air temperature separately, and **E** combined effects of the three environmental factors. **A–D** Share the same legend as listed in **A**. For **D**, *dotted line* denotes minimum air temperature and *solid line* denotes the maximum air temperature. Error bars are ±1 SE and denote the variations among different years within the same year category defined by precipitation (normal, wet, or dry), and not shown when smaller than symbol used.

However, responses of soil N to changes in CO_2 were larger in wet years than in normal and dry years, and the reverse was true to changes in T_{air} and N_{dep}. For the combinations of NminCmidT, NminCmaxT, and NmidCmaxT, soil N changes were larger in wet years than in normal and dry years; for all other combinations, soil N changes were larger in dry years than in normal and wet years (Figure 5E). The negative effect of increasing CO_2 on soil N was due mainly to increased N uptake for plant growth. This negative effect became more pronounced in wet years.

Responses by Plant Functional Types

In this section, we focus on the responses of ANPP for different plant functional types. Four of the six plant functional types (*Larrea*, subshrub, C_3 annuals, and C_4 annuals) showed strong responses to changes in the three environmental factors and their combinations, whereas perennial grasses and forbs showed little response. The four plant functional types showed nonlinear responses to changes in CO_2, especially in wet years (Figure 6). In contrast, the responses to changes in N_{dep} (Figure 6) and temperature in most cases were linear (Figure 7), particularly in normal and dry years.

In wet years, the ANPP of *Larrea tridentata*, the dominant species of the Sonoran Desert ecosystem, increased with increasing CO_2 over a range (360 to c.a. 450 ppm), and then decreased with further increase in CO_2 concentrations (360 to c.a. 390 ppm) as did the subshrub (Figure 6). In normal and dry years, however, the ANPP of both *Larrea* and
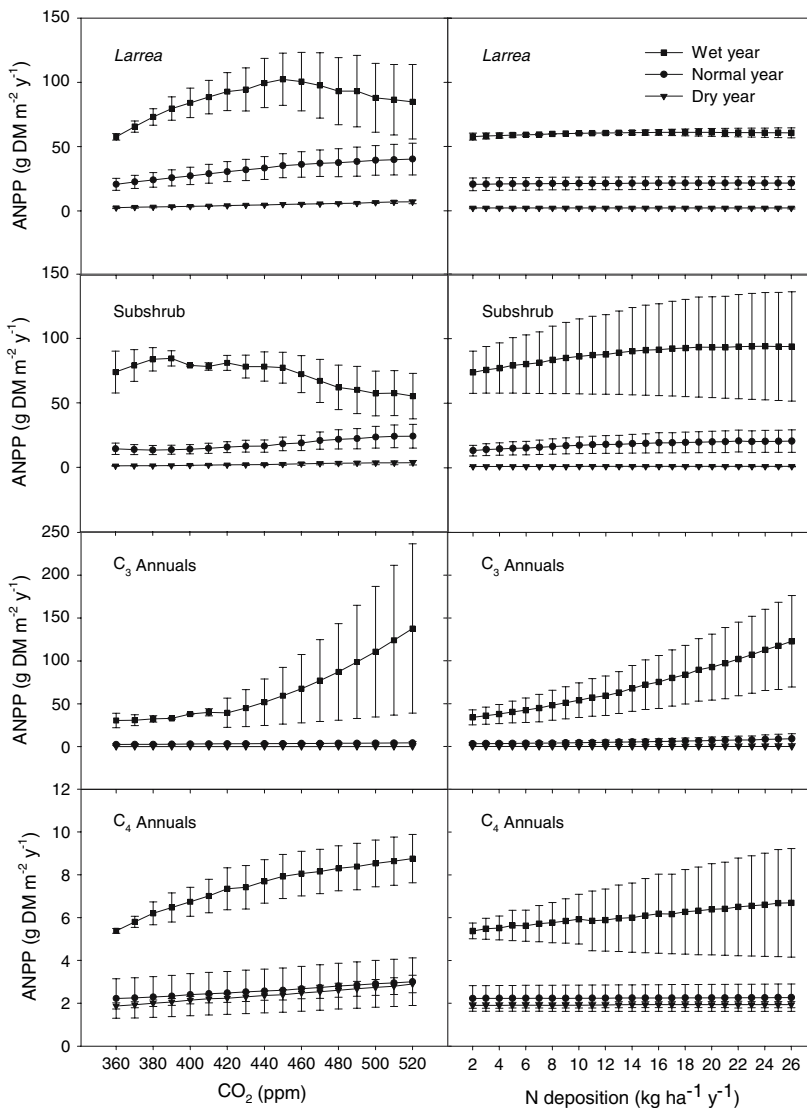
Figure 6. Responses of ANPP by plant functional type to changes in atmospheric CO_2 concentration (*left column*) and dry N deposition (*right column*). *Error bars* are ±1 SE and denote variations among different years within the same year category (normal, wet, or dry) and not shown when smaller than symbol used.

subshrubs increased with increasing CO_2 across the entire range of manipulated CO_2 concentrations. The ANPP of C_3 and C_4 annuals increased across the entire range of CO_2 concentration in all types of years (Figure 6). Among the four functional types, C_3 annuals seemed to respond more strongly at higher CO_2 levels in wet years, whereas the other three functional types seemed to respond more strongly at lower CO_2 levels (c.a., <420 ppm; Figure 6). Interestingly, the variability (error bars) of wet-year responses increased with CO_2 levels as well (Figure 6).

Three of the four plant functional types (except *Larrea*) showed positive responses to increased N deposition (Figure 6). C_3 annuals also were the plant functional type that was most responsive to changes in N_{dep}. With an increase of 24 kg ha^{-1} y^{-1} in N_{dep}, C_3 annuals had the largest relative change

(150%) in ANPP, followed by subshrubs (relative change = 29%) and C_4 annuals (relative change = 10%). Effects of N_{dep} on ANPP of these three plant functional types were magnified in wet years and the variability (error bars) in this year category increased with increasing N_{dep} levels (Figure 6). Overall, ANPP of the four functional types showed very little response to N_{dep} in normal and dry years.

Similar response patterns were found for changing T_{air} (Figure 7). *Larrea* and subshrub showed negative responses to changes in T_{max} and T_{min}. ANPP of the two shrub functional types (*Larrea* and subshrub) decreased 43 and 17% in response to the maximum change of T_{max}, and decreased 3.2 and 10% in response to the maximum change of T_{min}, respectively. C_4 annuals showed positive responses to increased T_{max} and T_{min}, with relative change of ANPP being 7.1 and
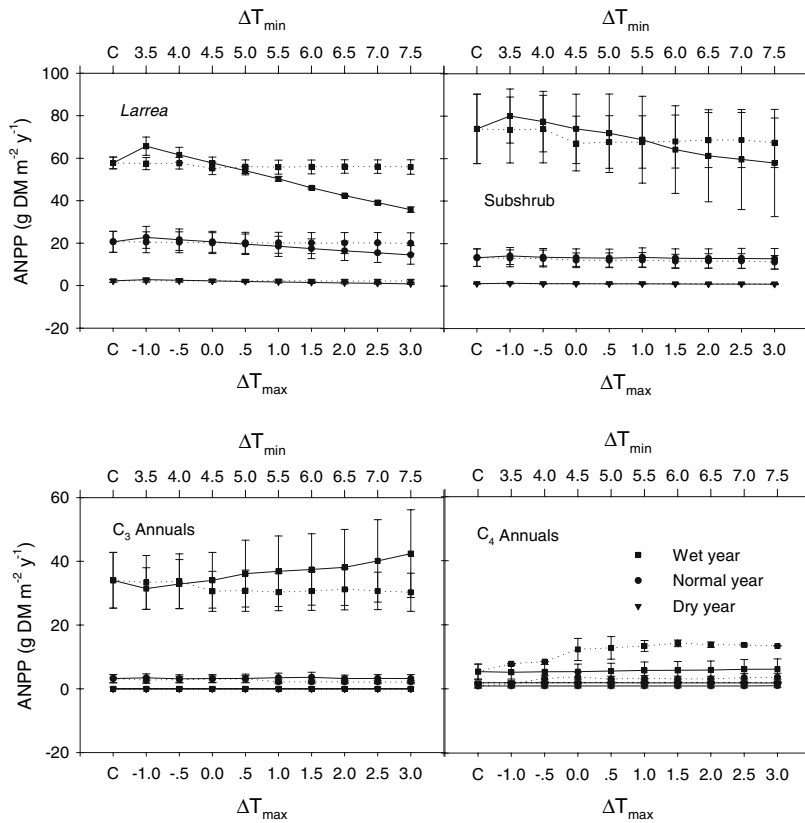
Figure 7. Responses of ANPP by plant functional type to changes in maximum and minimum air temperatures separately. *Error bars* are ±1 SE and reflect variability among different years within the same year category (normal, wet, or dry) and not shown when smaller than symbol used.

150%, respectively. C_3 annuals showed positive response to changes in T_{max} (relative change = 8.5%) but negative response to changes in T_{min} (relative change = −15%). These simulation results indicate that *Larrea*, subshrub, and C_3 annuals were more responsive to changes in T_{max}, whereas C_4 annuals were more responsive to changes in T_{min}. Temperature-induced changes in ANPP were also enhanced by water availability, with ANNP changing little in dry and normal years.

The response pattern to the combined influences of the three environmental factors was determined by relative dominance of the three environmental factors (Figure 8). For the two shrub functional types, CO_2 and N_{dep} had much stronger effects on their ANPP than temperature. CO_2 had the strongest effect on C_3 annuals, whereas temperature had a stronger influence on C_4 annuals than CO_2 and N_{dep}.

Discussion

Water as the Primary Controlling Factor

Our simulation results clearly showed that precipitation exerts an overriding control on ANPP (both at ecosystem and plant-FT level), SOM accumula-tion, and soil N content of the Sonoran Desert ecosystem. Wet years were characterized by much greater ANPP and SOM accumulation, but lower soil N content (Figures 3A, 4A, 5A, 6). The simulated differences in ecosystem functions among different types of years are consistent with the widely accepted positive linear relationship between precipitation and ANPP (Le Houerou and others 1988; Shen and others 2005) and the well established generalization that deserts are water-limited ecosystems (Noy-Meir 1973; Whitford 2002), indicating that the PALS–PHX model is capable of capturing key interactions between desert ecosystem functioning and environmental factors. Unlike the relationship between precipita-tion and ANPP, there is little empirical evidence for the relationships between precipitation and SOM (or N_{soil}), but we think that the simulated positive effects of precipitation on SOM accumulation and the negative effects on N_{soil} are reasonable, because higher ANPP in wet years contributes to SOM via increased litter production but sacrifices soil N due to increased plant N uptake. In contrast, during dry years, soil N accumulates because plant uptake, and possibly denitrification and other microbial N transformations, are water limited (see also Austin and others 2004).
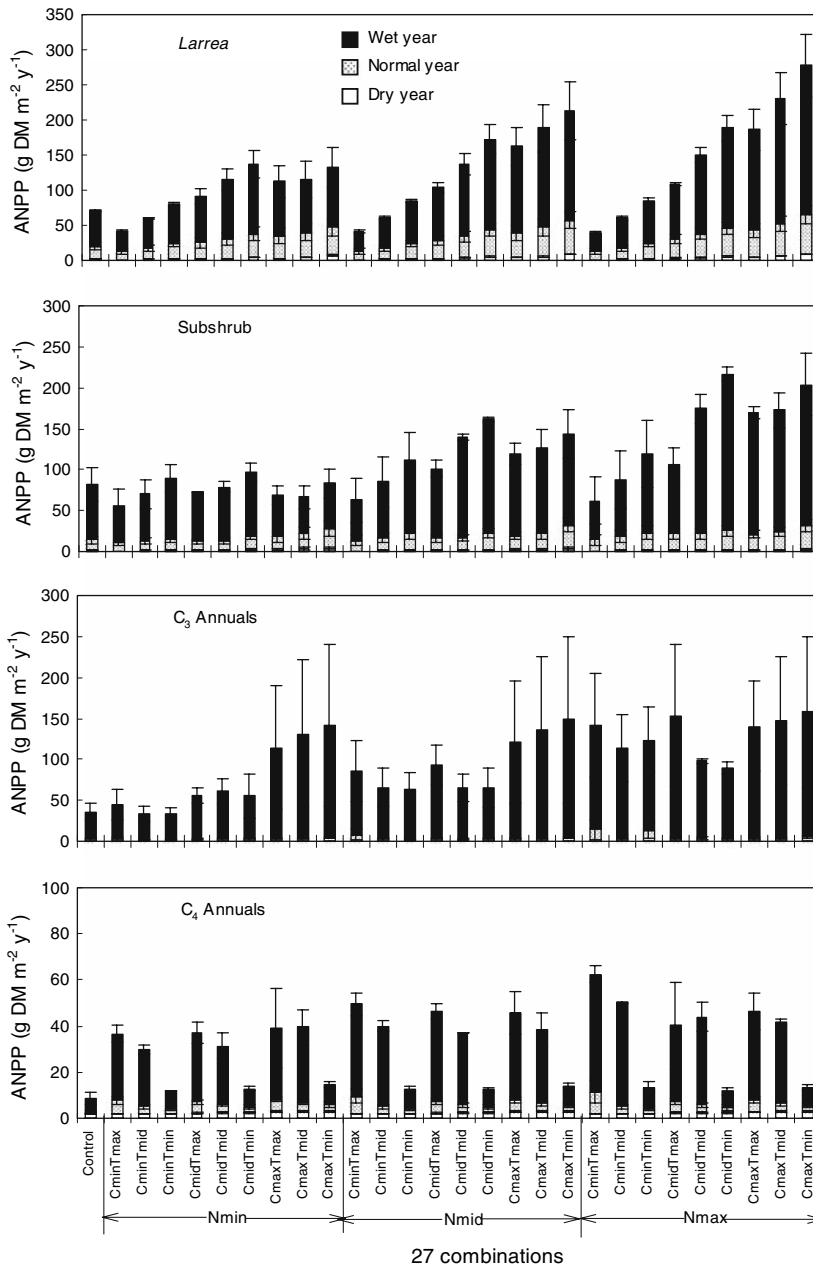
Figure 8. Combined effects of three environmental factors (CO_2, T_{air}, and N_{dep}) on ANPP by plant functional type. *Error bars* are ±1 SE and reflect variability among different years within the same year category (normal, wet, or dry), and not shown when smaller than symbol used. ANPP for each year category in **E** is the height of portion of the bar corresponding to that category.

Water availability also substantially influenced the responses of the *Larrea* ecosystem to the alterations in other environmental factors (that is, CO_2, N_{dep} and T_{air}). For example, the effect of CO_2 on ANPP was much greater in wet years (Figures 3, 6), similar to results from the Mojave Desert FACE studies (Huxman and others 1998; Smith and others 2000; Pataki and others 2000; Naumburg and others 2003; Nowak and others 2001, 2004a; Housman and others 2006). Those authors reported that photosynthetic rate, stomatal/leaf conductance, and ANPP showed responses to elevated CO_2 only in wet years or under well-watered conditions. Their results, along with our simulation results, indicate that increased water availability magnifies CO_2 effects. Several mechanisms may be responsible for such a magnification. In addition to the hypothesis that elevated CO_2 decreases stomatal conductance, thus ameliorating water stress-induced limitations to plant carbon assimilation (Strain and Bazzaz 1983), we suggest at least three additional potential mechanisms. First, improved plant water status in wet years may increase the overall stomatal conductance, offsetting the negative influence of elevated CO_2 on stomatal conductance. Second, improved

soil water conditions enhance N mineralization, soil N availability and plant N uptake (Austin and others 2004; Aranibar and others 2004), which alleviates N limitation of plant growth under elevated CO_2. Third, increased plant growth under improved water and N availability resulted in larger leaf biomass per unit area, which should increase CO_2 uptake.

The above closely interrelated mechanisms may also explain why nonlinear responses to CO_2 enrichment were observed only in wet years, and not in normal and dry years. Nonlinear response patterns have important implications for extrapolating field measured ecosystem responses to environmental changes. In field or laboratory experiments, an environmental factor is often manipulated to only two levels, such as the control (370 ppm) and enriched (550 ppm) CO_2 concentrations in FACE experiments (Nowak and others 2004a). Our simulation results suggest that quantitative predictions of the temporal dynamics of ecosystem responses to rising CO_2 in the twenty-first century would be impossible based upon on such two-level experimental manipulations. The rise in atmospheric $[CO_2]$ is likely to be gradual, covering multiple concentrations over this century (Houghton and others 2001), and prediction is complicated by the non-linear response. Multi-level experiments combined with models such as PALS–PHX may be an effective way to tackle this issue.

Not only the total amount of annual rainfall but also its temporal variability (for example, seasonal distribution) may affect the responses of ecosystem processes to environmental changes. For example, the responses of ecosystem ANPP to the CO_2 level of 520 ppm for two normal years (1988 and 2000), which had very similar annual precipitation (234 and 249 mm; Figure 2), exhibited a twofold difference (114.9 vs. 55.3 g DM y^{-1}). We argue that the relatively even temporal distribution of precipitation in 1988 (18% of the annual precipitation fell in spring, 29% in summer, and 53% in winter) explains the larger ANPP increase in response to elevated CO_2 than in 2000 (only 5% of annual precipitation fell in spring, 14% in summer, and 81% in winter). Thus, our simulation work suggests that there may exist strong interactions between rainfall seasonality and changing environmental factors such as CO_2 in determining desert ecosystem functioning. This has implications for understanding responses to climate change, because precipitation seasonality, as well as total precipitation, is expected to shift over the coming decades (IPCC 2007).

Effects of Interactive Environmental Factors

Our results show that responses of ANPP, SOM, and soil N to combined changes in CO_2, N_{dep} and T_{air} differed quantitatively and qualitatively (even changing the direction of the response; Figure 8C) from those to changes in individual factors. The interactions among altered environmental factors may be both compensatory and suppressive. For example, the combined effect of NmaxCmaxTmax on ecosystem ANPP was less than the sum of the three single-factor effects in normal and dry years, but greater in wet years. For SOM, the combined effect was greater than the sum of single-factor effects in normal and dry years, but less in wet years. For soil N, the combined effect was always less than the sum of individual-factor effects. At the plant functional-type level, the combined effect on shrub ANPP was always greater than the sum of single-factor effects, but the combined effect on ANPP for C_3 annuals was always less than the sum of single-factor effects. These results suggest that effects of multiple factors are not additive. This is important because often only one or two factors are manipulated in field experiments owing to logistic difficulties (Nowak and others 2004a; Ainsworth and others 2005); yet global changes or urbanization-induced environmental changes do involve multiple factors (CO_2, T_{air}, and N_{dep}) that are concurrent. Therefore, field experiments considering multiple-factor interactions are needed to make quantitative and realistic predictions of ecosystem response to environmental changes. Our simulation study demonstrated that processed-based ecosystem models can be very helpful in understanding the nonlinear interactions among various environmental factors.

Among the four environmental factors (CO_2, N_{dep}, T_{air}, and water) examined in this simulation study, increased water availability generally magnified elevated N_{dep} and CO_2 effects on ecosystem C sequestration (as indicated by increases in ANPP and SOM accumulation). As a result, the variability (error bars in Figures 3, 4, 5, 6, 7, 8) of ecosystem C sequestration between two wet years (1992 and 1993) with different annual rainfall increased with increasing CO_2 and N_{dep}. Even though only slightly more rain fell in 1992 than in 1993 (516.5 vs. 463.3 mm in 1993), the 1992 response became larger and the 1993 response became relatively smaller, that is, the responses between the two years diverged as CO_2 and N_{dep} continued to rise. The temperature–CO_2 interaction, in contrast, was suppressive: elevated T_{air} reduced the effects of increased CO_2.

Complex interactions involving competition and compensation among different ecosystem processes might be responsible for these patterns. For example, on the one hand, elevated T_{air} accelerated SOM decomposition and N mineralization and thus ameliorated nutrient limitation to plant C sequestration under elevated CO_2; on the other hand, elevated T_{air} also stimulated water loss from the soil and thus imposed water limitation to C sequestration. In the Sonoran desert ecosystem, the second mechanism appeared to dominate the first one based on our result that elevated T_{air} reduced the magnitude of CO_2 effects.

Responses of Plant Functional Types and their Interactions

Plant functional types are a useful way of aggregating the characteristics of individual species and relating them to the dynamics of ecosystems (Reynolds and others 1997; Nowak and others 2004b; Ellsworth and others 2004). Early research hypothesized that C_3 and non-woody plants would respond more strongly to elevated CO_2 than C_4 and woody plants because C_4 species are CO_2-saturated at current ambient CO_2 concentration (Stain and Bazzaz 1983). However, recent studies have shown mixed results: some support this hypothesis (for example, Reich and others 2001; Ainsworth and Long 2005) whereas others seem at odds with it (for example, Owensby and others 1993; Wand and others 1999; Nowak and others 2004b). Our simulation results support this hypothesis in that the relative change in ANPP for C_3 annuals was much greater than that for C_3 shrubs and C_4 annuals. However, the hypothesis does not hold when C_3 subshrubs, perennial grasses, forbs, and C_4 annuals are compared (Figure 6). Furthermore, as noted above, the responses of desert plant functional types were much more pronounced in wet years. These findings suggest complex relationships as a result of interactions between within-functional type variability and multiplicative environmental conditions.

The down-regulation of ANPP in response to elevated CO_2 for shrub and subshrub functional types in wet years (see Figure 6) further illustrates the complex interactions between plant functional types and environmental factors. In agreement with this simulation result, Huxman and others (1998) and Hamerlynck and others (2000) also found that the dominant shrub species *Larrea tridentata* in the Mojave Desert showed marked down-regulation of photosynthesis, reducing maximum photosynthetic rate (A_{max}) under well-watered conditions or in the wet season but not

under dry conditions. They further suggested that drought could diminish photosynthetic down regulation by *Larrea* under elevated CO_2, similar to our simulation results that the down-regulation of ANPP did not occur in normal and dry years (Figure 6). However, the down regulation found in the two field experimental studies was based on leaf-level measurements of C assimilation rate (A_{net}), whereas our simulation results were for whole-ecosystem aboveground production (ANPP) from six specific plant FTs. The underlying mechanisms for leaf-level photosynthetic down-regulation involve two hypotheses: leaf N dilution, caused by carbohydrate accumulation as a product of photosynthetic enhancement, and N redistribution, whereby specific photosynthetic protein under elevated CO_2 provides N that can be reallocated toward other protein-requiring systems (Drake and others 1997; Ellsworth and others 2004; Nowak and others 2004a). Such leaf-level mechanisms have not been incorporated into the current version of PALS–FT model, so what caused the down-regulation of ANPP of the two shrub FTs that we observed?

Based upon the patterns shown in Figure 6, we believe that inter-FT competition for resources (mainly soil N and water) is responsible for ANPP down-regulation of the two shrub FTs. At lower CO_2 levels (ca. 360–420 ppm), shrub and subshrub FTs were more responsive to rising CO_2, but C_3 winter annuals were relatively unresponsive (Figure 6). With continued increases in CO_2, C_3 winter annuals became more responsive to elevated CO_2 because they were more favored by high winter rainfall, which accounted for 75% of total annual precipitation in wet years (see Figure 2). Thus more soil N was taken up by C_3 annuals, resulting in nutrient limitation to shrub FTs that were relatively less favored by winter rainfall. But why did the large increase in growth of C_3 annuals not suppress the growth of C_4 annuals in responding to elevated CO_2? We argue that this is mainly because C_4 annuals growth occurs mainly in the summer season; thus C_4 annuals were able to avoid resource competition with winter C_3 annuals. Hence, we conclude that inter-FT competition and seasonal differentiation of plant phenology could play important roles in regulating plant responses to rising atmospheric CO_2.

Urban-Wildland Gradients of Ecosystem Functioning

Given that CO_2 concentration and temperature are highest in the urban core and lowest in rural areas

(Idso and others 1998, 2002; Wentz and others 2002), and N deposition is highest in the northeastern fringe of Phoenix and moderate in the urban core (Fenn and others 2003), the combinations NmidCmaxTmax, NmidCmidTmid, and control conditions (Table 1) approximate environmental conditions in urban, suburban, and wildland areas, respectively. Correspondingly, ANPP of the *Larrea* ecosystem was 12–120% higher (Figure 3E) and SOM was 69–180% higher (Figure 4E) in the urban core than in wildland areas over the 15 simulation years, with the smallest enhancement occurring in dry years and the largest in wet years. These simulation results are consistent with some field observations on forest ecosystems. For example, Gregg and others (2003) found that the growth of a cottonwood plantation in the urban area of New York City was twice as much as it is in the rural area; the SOM storage of oak forests was also larger in the urban core of New York City than in suburban and rural areas (Pouyat and others 2002). Conversely, soil N content was higher in the suburban area than in wildland and urban core areas (Figure 5E), with the largest decrease in urban core (−56%) in wet years, and the largest increase in the suburban area in dry years (60%). These model projections provide working hypotheses to be tested in our ongoing field experiments and observations.

Conclusions

Our study showed that urbanization-induced environmental changes in atmospheric CO_2, N deposition, and air temperature in the Phoenix metropolitan area had significant impacts on the ecosystem functioning of the Sonoran Desert. Specifically, four major findings have emerged from this simulation study. First, water availability controls the magnitude and pattern of responses of the desert ecosystem to elevated CO_2, air temperature, N deposition and their combinations. Nonlinear and greater responses occurred in wet years whereas small, linear changes occurred in normal and dry years. Thus, future precipitation patterns in the Phoenix metropolitan region, affected by both urban climatological modifications at the local scale and global climate change, are critically important for predicting how this desert ecosystem will respond to future environmental changes. Second, the four environmental factors (precipitation, CO_2, N_{dep}, T_{air}) may interactively magnify or depress each other's impact on ecosystem functioning in a non-additive manner, depending on ecosystem variables of interest and the particular combination of factors. In terms of the relative importance of the three urbanization-induced environmental forcings, changes in N deposition and CO_2 showed larger impacts on ecosystem properties (ANPP, SOM, and N_{soil}) than air temperature. Third, different plant functional types influenced each other's response to simultaneous changes in environmental factors through resource competition, which could result in down-regulation of ANPP in response to elevated CO_2 for shrubs and subshrub, but up-regulation for C_3 winter annuals. Fourth, the PALS–PHX model predicted that ANPP and SOM accumulation of the *Larrea*-dominated Sonoran Desert ecosystem was maximal at the Phoenix urban core and declined along the urban-wildland environmental gradient, whereas soil N content peaked at the suburban area and was lowest in wildlands. These projections provide specific working hypotheses for our ongoing field experiments.

Our study also demonstrated that ecosystem responses to urbanization-induced environmental changes involve complex interactions within and among plant functional types, multiple environmental factors, and levels of biological organization. Although field manipulative experiments may be viewed as the most credible way of tackling these complex relationships, implementing such experiments with even a few factors is usually formidable on large spatial scales. Our study corroborates the contention that computer simulations with process-based mechanistic models provide a powerful approach complementary (not alternative) to empirical methods. With the objective of providing guiding hypotheses for field-based research activities, our modeling work complements the urban-wildland gradient approach in which the relative importance and interactive effects of multiple factors are difficult to be discriminated (Luck and Wu 2002; Carreiro and Tripler 2005). However, this current modeling work is limited by data availability and our knowledge of how current observations translate into future conditions. Our future work, therefore, will integrate modeling with field manipulative experiments and observations along urban-wildland gradients.

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