

Generalization and evaluation of the process-based forest ecosystem model PnET-CN for other biomes

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Abstract. Terrestrial ecosystems play an important role in carbon, water, and nitrogen cycling. Process-based ecosystem models, including PnET-CN, have been widely used to simulate ecosystem processes during the last two decades. PnET-CN is a forest ecosystem model, originally designed to predict ecosystem carbon, water, and nitrogen dynamics of temperate forests under a variety of circumstances. Among terrestrial ecosystem models, PnET-CN offers unique benefits, including simplicity and transparency of its structure, reliance on data-driven parameterization rather than calibration, and use of generalizable relationships that provide explicit linkages among carbon, water and nitrogen cycles. The objective of our study was to apply PnET-CN to non-forest biomes: grasslands, shrublands, and savannas. We determined parameter values for grasslands and shrublands using the literature and ecophysiological databases. To assess the usefulness of PnET-CN in these ecosystems, we simulated carbon and water fluxes for six AmeriFlux sites: two grassland sites (Konza Prairie and Fermi Prairie), two open shrubland sites (Heritage Land Conservancy Pinyon Juniper Woodland and Sevilleta Desert Shrubland), and two woody savanna sites (Freeman Ranch and Tonzi Ranch). Grasslands and shrublands were simulated using the biome-specific parameters, and savannas were simulated as mixtures of grasslands and forests. For each site, we used flux observations to evaluate modeled carbon and water fluxes: gross primary productivity (GPP), ecosystem respiration (ER), net ecosystem productivity (NEP), evapotranspiration (ET), and water yield. We also evaluated simulated water use efficiency (WUE). PnET-CN generally captured the magnitude, seasonality, and interannual variability of carbon and water fluxes as well as WUE for grasslands, shrublands, and savannas. Overall, our results show that PnET-CN is a promising tool for modeling ecosystem carbon and water fluxes for non-forest biomes (grasslands, shrublands, and savannas), and especially for modeling GPP in mature biomes. Limitations in model performance included an overestimation of seasonal variability in GPP and ET for the two shrubland sites and overestimation of early season ER for the two shrubland sites and Freeman Ranch. Future modifications of PnET-CN for non-forest biomes should focus on belowground processes, including water storage in dry shrubland soils, root growth and respiration in grasslands, and soil carbon fluxes for all biomes.

Key words: ecosystem model; evapotranspiration; grassland; gross primary productivity; savanna; shrubland; water yield.

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INTRODUCTION

Terrestrial ecosystems play an important role in the carbon and water cycles. Quantification of carbon and water fluxes at regional to continental scales requires modeling approaches that are applicable to all major biomes (Xiao et al. 2014), while retaining enough simplicity that they can be parameterized and applied broadly. Process-based terrestrial ecosystem models have been developed to simulate biogeochemical processes and to project ecosystem carbon and water dynamics under changing climate (Ostle et al. 2009). The most widely used ecosystem models include CENTURY (Parton et al. 1987), CASA (Potter et al. 1993), TEM (Raich et al. 1991), Biome-BGC (Running and Hunt 1993), and the PnET family of models (Aber and Federer 1992), all of which were first developed in the late 1980s or early 1990s. All these models have been extensively tested and improved during the last two decades, often with the consequence of increasing model complexity. CASA and TEM were designed to be applicable to most major ecosystem types in the very beginning (Raich et al. 1991, Potter et al. 1993). CENTURY and Biome-BGC were originally designed for grasslands and forests, respectively (Parton et al. 1987, Running and Coughlan 1988), and were later generalized to other biomes (Running and Hunt 1993, Parton 1996). The PnET family of models, originally developed in 1992 to simulate temperate and boreal forests (Aber and Federer 1992), provide a unique simplified approach to modeling carbon and water exchange processes.

Processes in PnET models are modeled based on observed relationships with a small number of drivers, with less emphasis on fine-scale mechanisms such as leaf biochemistry. Despite clear sacrifices in physiological detail, these models have demonstrated a high reliability in a wide range of forest ecosystems (Aber et al. 1995, 1996, 1997, Ollinger et al. 2002a, Wang et al. 2014), raising the question of whether the same simplistic approach is also suitable for non-forest biomes. One of the central attributes of models in the PnET family is the simulation of photosynthesis using the empirical relationship between leaf traits (primarily leaf nitrogen concentrations) and photosynthesis rates per unit leaf mass (e.g., Reich et al. 1990, 1999, Wright et al. 2004), in

contrast with other terrestrial ecosystem models, which commonly either derive landscape-scale photosynthesis from leaf-level physiology as described by the Farquar model (e.g., Biome-BGC, LPJ) or use simplified functions for light use efficiency (e.g., CASA, TOPS-BGC) (reviewed in Wang et al. 2011). While PnET's approach sacrifices many physiological details, including the temperature effects on carboxylation, it offers the advantage of being structurally simpler and more easily parameterized than the Farquar model, while indirectly capturing some of the relevant enzyme kinetics, through the fact that nitrogen is integral to many of the relevant leaf enzymes (Taiz and Zeiger 2002). The focus on leaf nitrogen in this compromise approach provides an inherent and dynamic link between carbon and nitrogen cycling in that leaf nitrogen influences litter decay and nitrogen mineralization in soils, and also respond to changes in soil nitrogen turnover caused by other factors. (Aber et al. 1997). It also permits the incorporation of remotely-sensed data on leaf chemistry into regional photosynthesis estimates (Ollinger et al. 2002b, Smith et al. 2002, Ollinger and Smith 2005), allowing assessment of spatial variability in productivity that is difficult to achieve with models that rely on more detailed parameters for leaf biochemistry. Because leaf nitrogen concentration is tightly correlated with maximum photosynthesis and respiration rates both among and within plant functional types (Wright et al. 2004), this approach may also prove useful beyond temperate forests.

In biomes that are limited by water rather than nitrogen, prediction of transpiration and water use efficiency becomes as important or even more so than accurate estimation of maximum photosynthesis. In all versions of PnET, water use efficiency is determined by the combination of vapor pressure deficit and a single ecosystem-specific parameter, with additional variation occurring under variable atmospheric CO₂ concentrations, which affect both photosynthesis and stomatal conductance (Aber and Federer 1992, Ollinger et al. 2002a). This simple approach has proved sufficient in the moist ecosystems for which PnET has been used in the past (e.g., Aber and Federer 1992). In very dry ecosystems, stomatal conductance is the primary control on transpiration, and photosynthetic potential can

be predicted by water availability (McNaughton and Jarvis 1991). The PnET approach therefore may also work well in these ecosystems, although this becomes dependent on its ability to simulate water availability. In biomes with intermediate moisture levels, more complicated transpiration models become appropriate (McNaughton and Jarvis 1991), and PnET's transpiration model may not be sufficient, especially in ecosystems with seasonal variation in precipitation.

The objective of this study was to assess the ability of PnET-CN to simulate non-forest biomes: grasslands, shrublands, and savannas. Although PnET II has been applied to grasslands at Konza prairie (Wythers et al. 2005), PnET-CN, which includes nitrogen cycling and carbon-nitrogen feedbacks, has not been applied to non-forest biomes. PnET models in general have yet to be systematically applied to diverse biome types for purposes of broad-scale modeling of carbon, water, and nitrogen exchange. We evaluated the suitability of the existing PnET-CN structure for modeling non-forest biomes in North America in order to determine its potential usefulness in continental-scale carbon and water cycle studies. Specifically, to assess the ease of applying PnET-CN functionality to other ecosystems, we slightly modified the phenology routine, determined parameter values for grasslands and shrublands, and compared PnET-CN output to flux tower data for two grassland sites, two shrubland sites, and two savanna sites.

DATA AND METHODS

We reviewed the literature for estimates of model parameters for grasslands and shrublands. As in other terrestrial biogeochemistry models (Raich et al. 1991), we model temperate savannas as two distinct biomes, independently simulating grassland and forest (deciduous broadleaf or evergreen needleleaf depending on the dominant woody vegetation for a site), and combining the outputs such that half of the land area is simulated as grassland, and half as forest.

Model description

The PnET suite of ecosystem models was designed to simulate the coupled cycles of carbon, nitrogen, and water in forests (Aber

and Federer 1992, Aber et al. 1995, 1997, 2002, Aber and Driscoll 1997, Ollinger et al. 2002a). At the core of all PnET models is a daily time-step canopy submodel that simulates physiological processes of a multi-layered canopy using generalized leaf-trait relationships and vertical gradients in physical environmental conditions (PnET-Day) (Aber et al. 1996). PnET-II applies PnET-Day based on monthly meteorological data, and adds a soil water balance and allocates carbon captured through photosynthesis to leaves, wood and root tissues for prediction of total net primary production, respiration, evapotranspiration (ET) and runoff (Aber and Federer 1992, Aber et al. 1995, Ollinger and Smith 2005). PnET-CN builds on PnET-II by incorporating certain components of the nitrogen cycle (Aber et al. 1997). PnET-CN includes allocation and accumulation of carbon and nitrogen in live biomass, litter compartments, and soil organic matter, as well as algorithms for nitrogen mineralization and nitrification, plant nitrogen uptake and leaching losses, producing complete cycles for carbon, water and nitrogen (Aber et al. 1997, Ollinger et al. 2002a).

Carbon and nitrogen cycles interact at several points within PnET-CN. Foliar nitrogen concentrations are not fixed, but change year to year depending on the relative availability of carbon and nitrogen in plants. When plants have high internal nitrogen pools, the efficiency of nitrogen uptake from the soil is reduced and increases in nitrogen concentrations in foliage, wood and roots occur. Increased foliar nitrogen increase net photosynthesis and hence plant demand for nitrogen in the production of new tissues, completing a negative feedback. The carbon:nitrogen ratios in biomass are translated to litter and soil pools, and high carbon:nitrogen ratio pools have a negative effect on net nitrogen mineralization. PnET-CN contains a single woody litter pool and a single soil organic matter pool that is functionally similar to the intermediate pool in CENTURY and related 3-pool soil models. PnET-CN has been applied and tested in closed-canopy forests throughout the U.S. and Europe to simulate effects of climate variability, rising atmospheric CO₂, ozone pollution, and disturbance on ecosystem processes and function (Aber et al. 1997, 2002, Ollinger et al. 1997, 1998, 2002a, Law et al. 2000, Ollinger and Smith 2005,

Pan et al. 2006, Wang et al. 2014). More recently, Tonitto et al. (2014) developed a new soil routine for PnET that simulates C and N turnover in multiple horizons and soil organic matter fractions using ^{14}C -based turnover estimates. However, because ^{14}C data are not widely available across ecosystems, we limited our focus in this study to application of PnET-CN.

We made minor modifications to PnET-CN while maintaining the same model structure (R scripts for the model are available as a Supplement and at <http://globalecology.unh.edu> and the Github repository: <https://github.com/AlexandraThorn/PnETCN-R>). In particular, in order to accommodate winter growing seasons at some sites and plant functional types, we modified the model to calculate carbon and nitrogen allocation at the beginning of each growing season (as determined by GDDFolStart) rather than at the beginning of the calendar year. For simulation of grassland sites, additional modifications are made to reflect the lack of woody biomass at these sites (see next section).

Parameterization for grasslands

To model grasslands using PnET-CN, we expanded the parameter set published for Konza Prairie defined by Wythers et al. (2005). Wythers et al. (2005) defined a complete parameter set for PnET-II, but did not provide values for PnET-CN parameters not included in PnET-II. Most of these parameters deal with modeling nitrogen cycling. Wherever possible we used literature values from Konza Prairie. Parameters not available for Konza Prairie were obtained from literature on other grasslands, or were estimated from other available information (Table 1).

To reflect the fact that grasses do not include woody biomass, we set four parameters dealing with wood biomass balance and N content, MinWoodFolRatio, WoodLitLossRate, WoodLitCLoss, WLPctN, to 0. We modified PnET-CN so that for grasslands, each year all carbon not allocated for foliar growth or kept in reserve would be allocated toward root growth (that is, the quantity PlantC (1 – PlantCReserveFrac) otherwise allocated to WoodC is instead added to the RootC pool each year). Because this method might be expected to produce unrealistically high root biomass in grasslands, we

compared simulated root biomass for Konza Prairie with published values for this site. For the years 2000–2012, our simulation produced annually fluctuating root biomass with annual minimum root biomass ranging between 640 and 720 g/m^2 and an annual maximum root biomass ranging between 810 and 990 g/m^2 . These values are similar to published observations: e.g., Kitchen et al. (2009) measured root densities in the range 1300–2000 g/m^2 , and Zhou et al. (2012) measured root densities in the range 400–900 g/m^2 .

We adapted a value for the parameter SenescStart, which determines when foliage leaf senescence begins, from data on 1995 CO_2 fluxes from Ham and Knapp (1998). According to their measurements, DOY 255 was the last measurement date on which Konza prairie sites operated as net CO_2 sinks. For FolMassMax, the value 650 g/m^2 was selected, a typical late season above-ground biomass for Konza Prairie (Turner et al. 1993, Reed et al. 2005). FolMaxMin was estimated as 0, assuming full foliar senescence, consistent with Turner et al. (1993).

The minimum nitrogen concentrations in leaves (FLPctN) and roots (RLPctN) were assigned as 0.6% and 0.51%, respectively, based on nitrogen concentration data for a tallgrass prairie in central Texas (McCulley and Jackson 2012). Based on published values reviewed by White et al. (2000), we estimated FolNRetrans as 0.5. We estimated the parameter FolNConRange ($=\{\text{maximum nitrogen}/[\text{FLPctN}/(1 - \text{FolNRetrans})]\} - 1$) as 0.6, based on typical maximum nitrogen contents between 1.8% and 2.5% in Konza Prairie grasses (Knapp 1985, Schimel et al. 1991a). The PnET-CN parameter MaxNStore determines the relationship between nitrogen uptake rate and unused nitrogen stored within the plant. Because this parameter is difficult to measure directly, we assume that MaxNStore is 20 g/m^2 , the same value estimated for other biomes.

We initially used the estimate for WUEConst (the parameter that relates WUE to VPD) from Wythers et al. (2005), but this value resulted in substantial underestimation of ET for Konza Prairie, so for the simulations presented here, we used 10.9, the same value as for other biomes. This value is consistent with the available eddy covariance estimates for Konza Prairie in July.

Table 1. Biome-specific PnET-CN parameter values.

Parameter	Description	Spruce- fir	Red pine	Source	Northern hardwoods	Source	Grass	Source	Shrub	Source
Canopy variables										
k	Canopy light attenuation constant	0.5	0.5	1	0.58	1	0.68	2	0.58	3
FolReten	Foliage retention time years	4	2.25	1	1	1	1	2	2.25	4
SLWmax	Top canopy specific leaf weight g/m^2	170	200	1	100	1	100	2	185.2	after 3
SLWdel	Change in SLW with increasing foliar mass above g m^{-2}	0	0	1	0.2	1	0.2	2	0.2	5
FolRelGrowMax	Maximum relative growth rate for foliage year^{-1}	0.3	0.3	1	0.95	6	1	7	0.65	8
Photosynthesis variables										
AmaxA	Intercept of relationship between foliar N and photosynthesis $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$	5.3	5.3	1	-46	1	-75	2	-19.8	9
AmaxB	Slope of relationship between foliar N and photosynthesis $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} [\%N]^{-1}$	21.5	21.5	1	71.9	1	190	2	66.5	9
BaseFolRespFrac	Respiration as a fraction of maximum photosynthesis	0.1	0.1	1	0.1	1	0.1	2	0.1	5, after 9
HalfSat	Half saturation light level $\mu\text{mol m}^{-2} \text{ s}^{-1}$	200	200	1	200	1	300	2	200	10
AmaxFrac	Daily Amax as a fraction of early morning instantaneous rate	0.75	0.75	6	0.75	6	0.8	2	0.75	11
PsnTOpt	Optimum temperature for photosynthesis $^{\circ}\text{C}$	20	24	1	24	1	28	2	24	11
PsnTMin	Minimum temperature for photosynthesis $^{\circ}\text{C}$	0	4	1	4	1	4	2	4	11
RespQ10	Q10 value for foliar respiration	2	2	1	2	1	2	2	2	13
Water balance variables										
DVPD1	Coefficients for power function converting VPD to fractional loss in photosynthesis	0.21	0.05	1	0.05	1	0.05	2	0.2	14
DVPD2		1	2	1	2	1	2	2	1	14
PrecIntFrac	Fraction of precipitation intercepted and evaporated	0.15	0.15	1	0.11	1	0.06	2	0.04	15
WUEConst	Constant in equation for water use efficiency WUE as a function of VPD	10.9	10.9	1	10.9	1	10.9	5, 12	6	16
FastFlowFrac	Fraction of water inputs lost directly to drainage	0.1	0.1	1	0.1	1	0.1	2	0.1	5
f	Soil water release parameter	0.04	0.04	1	0.04	1	0.04	2	0.04	5

Table 1. Continued.

Parameter	Description	Spruce- fir	Red pine	Source	Northern hardwoods	Source	Grass	Source	Shrub	Source
Carbon allocation variables										
CfracBiomass	Carbon fraction of biomass	0.45	0.45	1	0.45	1	0.45	2	0.45	5
RootAllocA	Intercept of relationship between foliar and root allocation	0	0	1	0	1	0	2	0	5
RootAllocB	Slope of relationship between foliar and root allocation	2	2	1	2	1	2	2	1.5	3
GrespFrac	Growth respiration, as a fraction of allocation	0.25	0.25	1	0.25	1	0.25	2	0.25	11
RootMRespFrac	Ratio of fine root maintenance respiration to biomass production	1	1	1	1	1	2	2	1	11
WoodMRespA	Wood maintenance respiration as a fraction of photosynthesis	0.07	0.07	1	0.07	1	0.07	2	0.07	11
PlantCReserveFrac	Fraction of plant C held in reserve after allocation to bud carbon	0.75	0.75	1	0.75	1	0.75	2	0.75	5
MinWoodFolRatio	Minimum ratio of carbon allocation to wood and foliage	1.25	1.25	1	1.5	1	0	17	0.15	18, after 3
Biomass turnover and N concentration variables										
WoodTurnover	Fractional mortality of live wood per year	0.03	0.03	19	0.03	19	0	17	0.03	5
WoodLitLossRate	Fractional transfer from dead wood to SOM per year	0.1	0.1	19	0.1	19	0	17	0.1	5
WoodLitCLoss	Fractional loss of mass in wood decomposition	0.8	0.8	6	0.8	6	0	17	0.8	5
RootTurnoverA	Coefficients for fine root turnover fraction year ⁻¹ as a function of annual N mineralization quadratic equation	0.79	0.79	19	0.79	19	0.5	20	0.79	5
RootTurnoverB	(see RootTurnoverA)	0.19	0.19	19	0.19	19	0	21	0.19	5
RootTurnoverC	(see RootTurnoverA)	0.02	0.02	19	0.02	19	0	21	0.02	5
MaxNStore	Maximum N content in mobile plant pool g/m ²	20	20	19	20	19	20	22	7	23
Kho	Decomposition constant for soil organic matter pool year ⁻¹	0.07	0.08	19	0.07	19	0.08	5	0.08	5
NImmoba	Coefficients for fraction of mineralized N reimmobilized as a function of SOM C:N ratio	151	151	19	151	19	151	5	151	5
NImmobb		-35	-35	19	-35	19	-35	5	-35	5

Table 1. Continued.

Parameter	Description	Spruce- fir	Red pine	Source	Northern hardwoods	Source	Grass	Source	Shrub	Source
RLPctN	Minimum N concentration in root litter %	0.01	0.01	19	0.01	19	0.01	24	0.03	25
FLPctN	Minimum N concentration in foliar litter %	0	0	19	0.01	6	0.01	24	0.01	25
WLPctN	Minimum N concentration in wood litter %	0	0	19	0	19	0	17	0	11
FolNConRange	Maximum fractional increase in N concentration	0.6	0.7	19	0.6	19	0.6	26, 27	0.5	28
FolNRetrans	Fraction of foliar N retranslocated out of senescing foliage	0.5	0.5	19	0.5	19	0.5	3	0.5	3

Notes: Sources (or parameter justifications) are: 1, Aber et al. (1995); 2, Wythers et al. (2005); 3, White et al. (2000); 4, Same as pine; 5, Same as other biomes; 6, Ollinger et al. (2002a); 7, Similar to northern hardwoods; 8, Huenneke et al. (2001); 9, GLOPNET; 10, Valladares et al. (1997); 11, Same as trees; 12, Consistent with flux tower data; 13, VEMAP Members (1995); 14, Brenner and Incoll (1997); 15, Calculated from LAI in Griffith et al. (2010); 16, Letts et al. (2010); 17, No wood; 18, 10% of allocation for pine; 19, Aber et al. (1997); 20, Zhou et al. (2012); 21, Woodland-specific parameter; 22, Reed et al. (2005) combined with Kitchen et al. (2009); 23, From Gao and Reynolds (2003) foliar biomass; 24, McCulley and Jackson (2012); 25, TRY database; 26, Knapp (1985); 27, Schimel et al. (1991a); 28, Estimated from Serrano et al. (2002).

PnET-CN's root turnover parameters—RootTurnoverA, RootTurnoverB, and RootTurnoverC—are the coefficients of a quadratic model for the influence of nitrogen mineralization rates on root turnover (Aber et al. 1997). To our knowledge, this relationship has only been quantified for temperate woodlands (Aber et al. 1985), and may not be relevant for grasslands. Based on published turnover rates for a tallgrass prairie in Oklahoma (Zhou et al. 2012), we set the intercept (RootTurnoverA) to 0.5. In absence of data on a relationship between mineralization and root turnover, we set the other two parameters to 0.

FolRelGrowMax characterizes the rate at which the maximum foliage biomass for the following year is permitted to asymptotically approaches the amount of biomass that would maximize canopy photosynthesis (based on net photosynthesis at the bottom of the canopy in the previous year; Aber et al. 1995). We used a value of 1.0 yr^{-1} , similar to published estimates for temperate hardwood biomes (Ollinger et al. 2002a). Similarly, the PnET-CN parameter values for soil organic matter decomposition (Kho) and nitrogen immobilization (NimmobA and NimmobB) were assumed to be the same as published values for other biomes.

Parameterization for shrublands

Shrubs are in many respects functionally similar to trees, although shorter in stature and therefore containing relatively less biomass as wood. Ecologically, shrubs often occupy water-limited biomes, so the vegetation class as a whole has more tendency toward adaptations for water-limited conditions. To deal with these functionally distinct attributes, wherever possible, we obtained shrubland parameter values from publications on shrublands or from shrub traits in plant trait datasets (Table 1). Where shrub-specific parameter values could not be obtained, published PnET-CN parameter values for deciduous broadleaf or evergreen needleleaf forests were used. This choice is consistent with the assumptions of other terrestrial ecosystem models (e.g., White et al. 2000).

The photosynthesis parameters AmaxA and AmaxB for shrublands were obtained by linear regression of photosynthesis per leaf biomass versus nitrogen per leaf biomass for shrubs in the GLOPNET database (Wright et al. 2004). We set parameter HalfSat to $200 \mu\text{mol m}^{-2} \text{ s}^{-1}$, a typical value across plant functional types (Marino et al. 2010, Lachapelle and Shipley 2012), including shrubs (Valladares et al. 1997). The ratio of respiration to photosynthesis (BaseFolRespFrac) was also assumed to be 0.1, the same as

published values for trees. The Q10 value for respiration (RespQ10) is set to 2.0, the same as for other biomes, and a standard value used in most terrestrial ecosystem models (VEMAP Members 1995).

Following the example of Biome-BGC parameterization by White et al. (2000)—who use evergreen needleleaf forest parameters for shrubs when insufficient data are available—we assume that minimum (P_{snTMin}) and optimal (P_{snTOpt}) temperatures for shrubland photosynthesis as well as the ratio of daily maximum photosynthesis to morning photosynthesis ($A_{maxFrac}$) are the same as published PnET parameters for red pine. We also assume that the leaf longevity parameter $FolReten$ is the same as for pine.

The specific leaf weight at the top of the canopy (SLW_{max}) for shrublands is estimated as 185 g/m^2 , based on specific leaf weight per gram carbon from White et al. (2000), and the tissue carbon concentration ($C_{fracBiomass}$), which is assumed to be the same as for other biomes in PnET. The change in specific leaf weight with canopy depth (SLW_{del}) is assumed to be the same as for other biomes ($0.2 \text{ g m}^{-2} \text{ g}^{-1}$) based on the observation that the ratio of specific leaf weights between sun and shade leaves is similar among plant species and functional types, including trees, shrubs, and herbs (Poorter and Evans 1998).

For the light extinction coefficient (k), we used the same value that has previously been used for deciduous broadleaf trees (0.58), based on the similarity of shrubs and broadleaf tree light coefficients in literature reviewed by White et al. (2000). It is worth noting, however, that the estimates by White et al. (2000) for these functional groups are slightly lower than values that have been used for PnET (0.54 or 0.55 for Biome-BGC versus 0.58 for PnET).

We estimated the overall yearly foliage growth potential ($FolRelGrowMax$) as 0.65, based on fall productivity divided by spring biomass in 1991 for a mesquite shrubland site at the Jornada Basin LTER (Huenneke et al. 2001). We assumed that the minimum ratio of wood to leaf carbon allocation ($MinWoodFolRatio$) in shrubs is 0.15, following the example of parameter estimates for Biome-BGC (White et al. 2000) where wood allocation for shrubs is assumed to be 10% that of trees. Similarly, we estimated the slope of the

relationship between foliar and root allocation ($RootAllocB$) to be 1.5, calculated from Biome-BGC carbon allocation parameters as estimated by White et al. (2000). As for other PnET-CN biomes, we assume that the intercept of the relationship between root and leaf allocation ($RootAllocA$) is zero.

The respiration parameters $GrespFrac$, $WoodMRespA$, and $RootMRespFrac$ are all assumed to be the same for shrubs as for trees, as is the parameter determining what fraction of plant carbon is kept in reserve at the end of the year ($PlantCReserveFrac$).

For the vapor pressure deficit parameters $DVPD1$ and $DVPD2$, we used the standard values from the shrubland ET model by Brenner and Incoll (1997), $0.2 \text{ mol m}^{-2} \text{ s}^{-1} \text{ kPa}^{-1}$ and 1.5 kPa , respectively. We estimated the relationship between water use efficiency and the inverse of the vapor pressure deficit ($WUEConst$) to be 6, based on shrub data from Letts et al. (2010). We estimate the precipitation interception fraction ($PrecIntFrac$) as 0.04, based on a precipitation interception per one-sided LAI between the values used by Bond-Lamberty et al. (2005) and for the default parameter values for Biome-BGC (Golinkoff 2010) and an LAI of 1.0 based on data for the Great Basin Desert (Griffith et al. 2010). The hydraulic parameters determining the fraction of precipitation that is directly lost as surface water or drainage ($FastFlowFrac$) and the soil water release parameter (f) are assumed to be the same as estimates for other biomes (0.1 and 0.04, respectively).

Estimates for the nitrogen concentration in senesced foliar ($FLPctN$) and root ($RLPctN$) tissue in shrubs were obtained from the TRY database (Kattge et al. 2011). We estimated $FLPctN$ as 0.98%, the mean nitrogen content for senesced shrub leaves (Kattge et al. 2011), and $RLPctN$ as 1.67%, half of the mean nitrogen content for roots (Kattge et al. 2011, no data available for senesced shrub roots). The nitrogen concentration of shrub wood ($WLPctN$) was assumed to be the same as published estimates for trees. The maximum fractional change in leaf nitrogen ($FolNConRange$) for shrublands was estimated as 0.5, based on the maximum range in nitrogen concentration for a single shrub species for chaparral vegetation in Southern California (Serrano et al. 2002), and the fraction of leaf

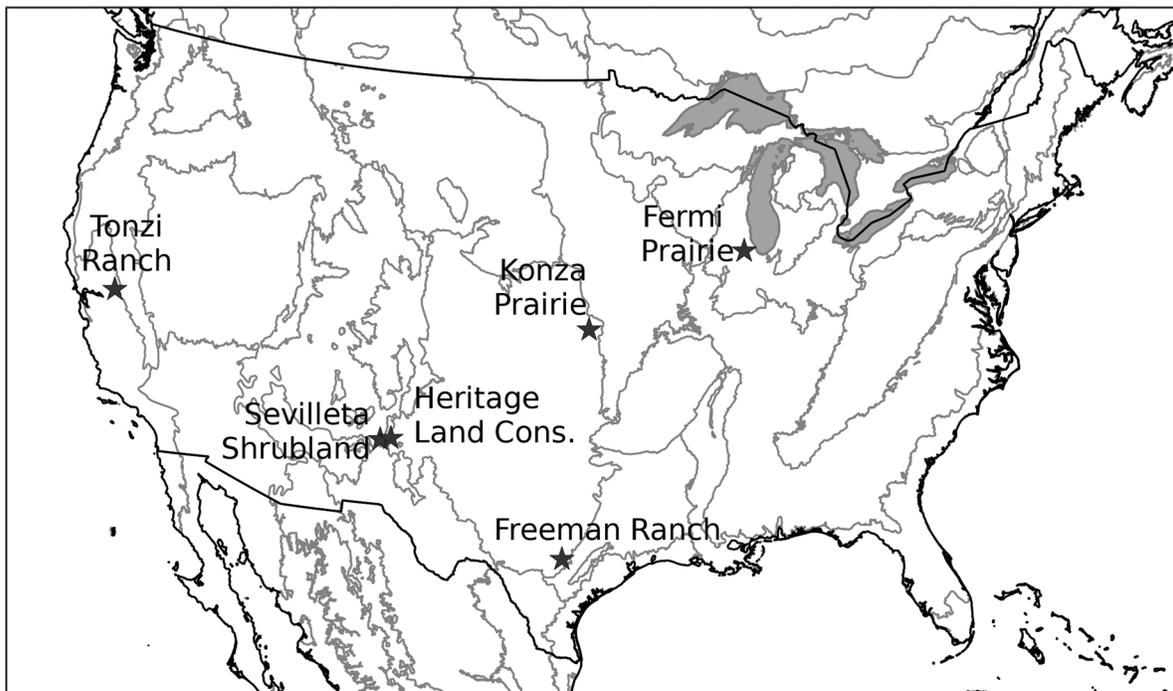


Fig. 1. Locations of the AmeriFlux sites used for model evaluation. Each site is marked with a star. The gray lines show the boundaries of North American ecoregions.

nitrogen retranslocated at senescence (FolNRe-trans) was estimated as 0.5 based on data reviewed by White et al. (2000). The maximum nitrogen content of the mobile plant pool (MaxNStore) was estimated to be roughly one-third of the estimated value for trees (20 g/m^2), giving 7 g/m^2 for shrublands. This estimate is based on the assumption that this pool size scales with leaf biomass and data from Chihuahuan Desert shrublands indicating that the maximum foliar biomass is around 100 g/m^2 (Gao and Reynolds 2003), compared to deciduous forest estimates of 300 g/m^2 (Aber et al. 1995).

We assumed that the fractional rate of live wood mortality per year (WoodTurnover) was 0.02, the same value as for other biomes, and that the parameters for root turnover fraction per year as a function of nitrogen mineralization (RootTurnoverA, RootTurnoverB, and RootTurnoverC) were the same as published values for Red Pine (0.789, 0.191, and 0.0211, respectively).

The parameters for wood litter decomposition (WoodLitLossRate and WoodLitCLoss), soil organic matter decomposition (Kho), and nitrogen immobilization as a function of soil organic

matter carbon:nitrogen ratio (NImmoba and NImmobB) were all assumed to equal published values used for other woodland biomes.

Site-specific parameters

We assessed the model performance using six representative AmeriFlux sites: Konza Prairie and Fermi Prairie (grasslands); Heritage Land Conservancy Pinyon Juniper Woodland and Sevilleta Desert Shrubland (shrublands); and Freeman Ranch Mesquite Juniper and Tonzi Ranch (woody savannas) (Fig. 1). The site properties, including physical parameters, are summarized in Table 2.

In addition, we also determined site-specific estimates for the phenological parameters GDDFolStart, GDDFolEnd, GDDWoodStart, GDDWoodEnd, and SenescStart (Table 3). The Konza Prairie phenology parameters were obtained from Wythers et al. (2005). For other sites, we visually estimated foliage phenology parameters (GDDFolStart, GDDFolEnd, and SenescStart) from published data on seasonal changes in LAI. For Tonzi Ranch, these estimates were obtained from Ryu et al. (2012). Values for other

Table 2. Site properties for biomes used for validation.

Site name	Latitude (decimal degrees)	Longitude (decimal degrees)	Elevation (m)	WHC (cm)	MAP (cm/yr)	MAT (°C)	AI
Grasslands							
Fermi Prairie, Illinois USA	41.84	-88.24	226	23.6	99	9.3	0.92
Konza Prairie, Kansas USA	39.08	-96.56	443	12.0	81	14.3	0.77
Woody savannas							
Freeman Ranch Mesquite Juniper, Texas USA	29.95	-98.00	272	15.0	93	20.6	0.58
Tonzi Ranch, California USA	38.43	-120.97	169	14.4	68	16.0	0.43
Shrublands							
Heritage Land Conservancy Pinyon Juniper Woodland, New Mexico USA	34.43	-106.24	2138	12.0	42	10.3	0.34
Sevilleta Desert Shrubland, New Mexico USA	34.33	-106.74	1593	12.0	24	14.2	0.17

Notes: Biome types (Grasslands, Woody savannas, Shrublands), latitude, longitude, and elevation were obtained from the AmeriFlux site descriptions. Soil water holding capacity (WHC) for 0-50 cm was obtained from the gridded database generated by Kittel et al. (1996). Mean annual precipitation (MAP) data were calculated from 32 years of gridded data from the DayMet database (Thornton et al. 2012). Precipitation estimates were taken directly from DayMet. Temperature estimates were first transformed based on site-specific meteorological data. The unitless aridity index (AI) was obtained from the CGIAR-CSI Global-Aridity and Global-PET Database (Zomer et al. 2006, Zomer et al. 2008).

sites were estimated from the MODIS land subset LAI data product. For non-grass plant functional types, we assumed that wood growth phenology (determined by GDDWoodStart and GDDWoodEnd) tracked leaf growth phenology (determined by GDDFolStart and GDDFolEnd). For grasslands we assumed no wood production, and so, like Wythers et al. (2005), we assigned the wood growth parameters as GDDWoodStart = GDDWoodEnd = 0.

Input data

For each of the selected representative sites, we obtained necessary input data for the models, as well as flux data to compare with model output. For the period of flux tower coverage, we used half hourly meteorological data from the Ameri-

Flux Level 2 data product. We aggregated AmeriFlux half hourly data to monthly values. In order to capture longer term climate patterns, we supplemented AmeriFlux meteorological data with data extracted from the Daymet database (Thornton et al. 2012). We obtained Daymet daily interpolated meteorological data for the latitude and longitude of each site, which we aggregated to monthly values. Because interpolated data only approximate site-specific conditions, we then transformed temperature parameters using linear regression of monthly aggregated AmeriFlux data against Daymet monthly values. We also used interpolation of AmeriFlux photosynthetically active radiation (PAR) against Daymet interpolated solar radiation data to estimate PAR for dates without flux

Table 3. Site-specific PnET-CN phenology parameters by plant functional type.

Parameter	Fermi Prairie	Konza Prairie	Freeman Ranch		Tonzi Ranch		Heritage Conservancy Pinyon Juniper Woodland	Sevilleta Desert Shrubland
	Grasses	Grasses	Grasses	Evergreen needleleaf trees	Grasses	Deciduous broadleaf trees	Shrubs	Shrubs
GDDFolStart	80	550	700	600	4750	800	100	100
GDDFolEnd	1000	1800	2000	2000	850	1200	800	1000
GDDWoodStart	0	0	0	600	0	800	100	100
GDDWoodEnd	0	0	0	2000	0	1200	800	1000
SenescStart	217	255	265	270	160	290	290	257
Phenology parameter source	MODIS	Wythers et al. (2005)	MODIS	MODIS	Ryu et al. (2012)	Ryu et al. (2012)	MODIS	MODIS

Note: Parameter abbreviations are: GDDFolStart, growing degree days of foliage production onset; GDDFolEnd, growing degree days at which foliage production ends; GDDWoodStart, growing degree days of wood production onset (assumed same as for foliage); GDDWoodEnd, growing degree days at which wood production ends (assumed same as for foliage); SenescStart, day of year at which foliage begins to senesce.

tower data. We did not transform Daymet precipitation data.

In addition to meteorological data, PnET-CN also requires atmospheric CO₂ concentrations and nitrogen deposition (NH₄ and NO₃) data. For the years with AmeriFlux data coverage, we used mean monthly CO₂ concentrations based on direct flux tower measurements for model input. For other years, CO₂ concentrations were estimated using the same algorithm as Ollinger et al. (2002a): concentrations were assumed to be 280 ppm prior to 1800 and afterward to increase according to the function: $\text{CO}_2 = 280 + [0.0188 \times (\text{year} - 1800)]^{3.35}$. Additional model inputs include latitude and water holding capacity. Water holding capacity for each site was estimated from soils data developed by Kittel et al. (1996).

Model simulations and evaluation

We used PnET-CN to simulate carbon and water fluxes for each site using monthly temperature, precipitation, PAR, and atmospheric CO₂ concentrations. For each biome, we used the parameter values (Table 1) that we determined using the literature and ecophysiological databases. For each site, after model spinup of 1200 years, model simulations were conducted using transient climate data for the period 1980 to 2011. For each site, we analyzed the magnitude and patterns of monthly carbon fluxes (GPP, ER, and NEP), ET, WUE, and water yield; we also aggregated monthly outputs to the annual scale and examined the magnitude and interannual variability of annual fluxes.

We compared simulated carbon and water fluxes (GPP, ER, NEP, and ET) with data from the AmeriFlux sites. We used the AmeriFlux Level 2 data product for all sites except for Fermi Prairie, for which we used the AmeriFlux Level 4 product. For each site, we compared simulated fluxes with tower fluxes at the monthly and annual scales. In addition, we calculated water use efficiency ($\text{WUE} = \text{GPP}/\text{ET}$) and water yield ($= \text{precipitation} - \text{ET}$) from each simulation to be compared with those values calculated from tower data. It should be noted that tower-based estimates of carbon and water fluxes are, themselves, prone to numerous sources of uncertainty. These have been discussed elsewhere in the literature and include random

measurement uncertainty (Richardson et al. 2006), lack of nocturnal mixing (Baldocchi 2003), and gap-filling errors (Dragoni et al. 2007) among others. Efforts to partition net CO₂ exchange into its component fluxes add additional uncertainties to estimates of GPP and ER, largely related to difficulties estimating variation in ER (e.g., Law et al. 2002). Although the uncertainties of the carbon and water fluxes at these sites have not been quantified, the potential biases should be considered when evaluating differences between measured and modeled flux estimates.

Model performance was evaluated for each of these variables by computing the root mean square error (rmse) and normalized root mean square error (nrmse) for the difference between PnET-CN and monthly flux tower-based estimates for NEP, ER, GPP, ET, WUE, and water yield. In addition, we used Taylor diagrams (Taylor 2001) to summarize overall model performance and compare performance across sites. These plots simultaneously display correlation coefficients, model standard deviation (normalized by reference standard deviation), and root mean squared differences (normalized by reference standard deviation, permitting rapid comparison of model performance).

RESULTS

Monthly carbon and water fluxes

The PnET-CN simulations captured most patterns of magnitude, seasonality, and interannual variation in monthly carbon fluxes (GPP, ER, and NEP) for the AmeriFlux sites (Figs. 2–7). Predictions of GPP tended to have a higher accuracy than ER and NEP. For GPP, the grassland and woody savanna sites exhibited higher accuracy than the two shrubland sites. For predictions of ER and NEP, the model exhibited higher accuracy at Konza Prairie and Tonzi Ranch than at the other four other sites.

Only minor discrepancies between simulated and tower values existed for GPP. The model slightly underestimated maximum annual GPP in Konza Prairie for years 2007, 2008, 2010, and 2011, and for 2012 PnET-CN predicted almost no GPP throughout the year, despite similar tower estimates for that year as for 2011 (Fig. 3). Modeled GPP showed slightly different season-

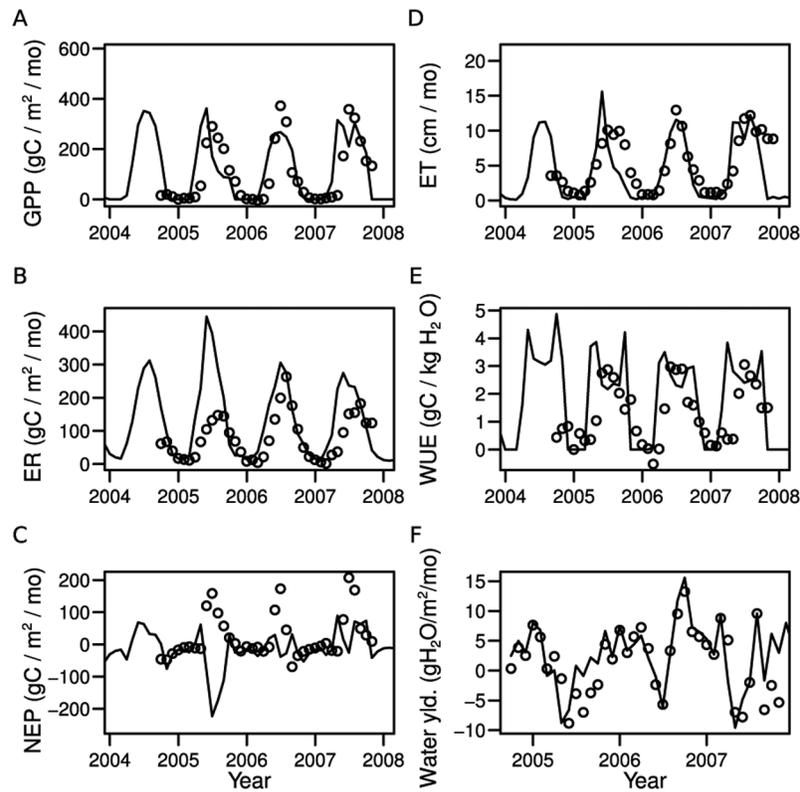


Fig. 2. PnET-CN simulation and tower estimates of gross primary productivity (GPP; A), ecosystem respiration (ER; B), net ecosystem productivity (NEP; C), of evapotranspiration (ET; D), water use efficiency (WUE; E), and water yield (F) for the grassland Fermi Prairie. In each graph, values from AmeriFlux L4 tower data products are shown as circles, and PnET-CN output for the corresponding years are shown as lines.

ality from tower data for Freeman Ranch and Tonzi Ranch, with PnET-CN predicting maximum GPP somewhat earlier in the season than was apparent from flux tower measurements (Figs. 4 and 5). For the Heritage Land Conservancy Pinyon-Juniper Woodland, PnET-CN predicted higher maximum GPP and lower minimum GPP, and slightly different timing of maximal GPP, although the direction of the temporal shift varied between years (Fig. 6). For Sevilleta Desert Shrubland, PnET-CN correctly predicted late season GPP for most years, but generally overestimated early season GPP and predicted an early season maximum that was not present in the tower data (Fig. 7). A Taylor Diagram (Taylor 2001) for GPP shows that overall model performance was best for the two grasslands, especially for Konza Prairie, which had the highest correlation coefficient and the lowest normalized RMS difference (Fig. 8). In

addition, the RMS difference was particularly high for the Heritage Land Conservancy Pinyon-Juniper Woodland, and the correlation coefficient was particularly low for Tonzi Ranch because of the slight shift in phenology between the model and tower observations (Fig. 8).

In the case of ER, model performance was more variable among sites. PnET-CN correctly predicted most of the within-year variation of ER for Fermi Prairie, Konza Prairie, and Tonzi Ranch, except for overestimation of ER for Fermi Prairie in 2005, for Konza Prairie in 2011, and for Tonzi Ranch in 2008, and underestimation of ER for Tonzi Ranch in 2005 (Figs. 2, 3, and 5). For Freeman Ranch and the two shrublands, PnET-CN tended to overestimate ER, including an earlier maximum ER for simulated than for tower data, especially for the two shrublands (Figs. 4, 6, and 7). The Taylor Diagram for ER illustrates high model performance for Konza Prairie and

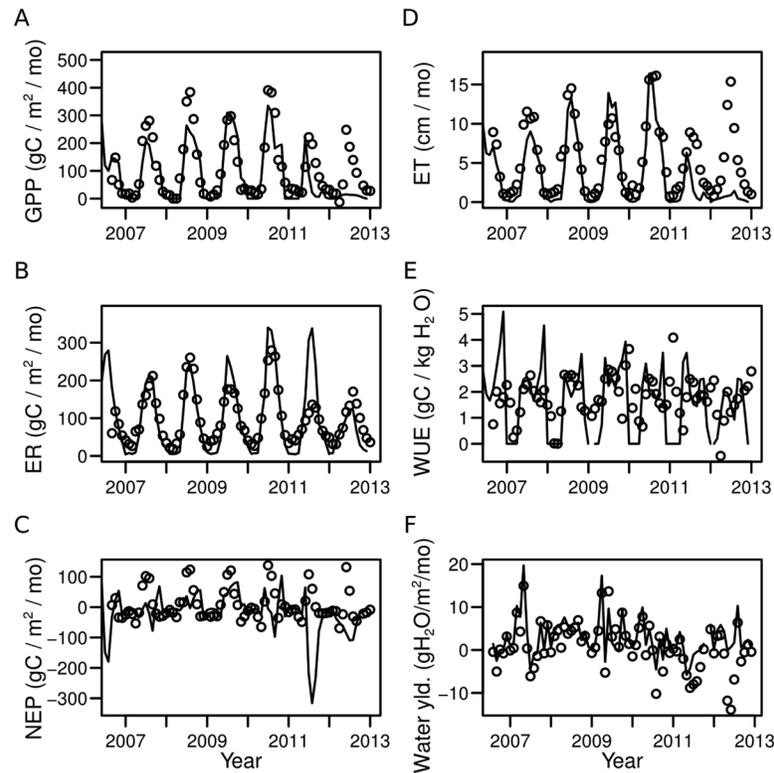


Fig. 3. PnET-CN simulation and tower estimates of gross primary productivity (GPP; A), ecosystem respiration (ER; B), net ecosystem productivity (NEP; C), of evapotranspiration (ET; D), water use efficiency (WUE; E), and water yield (F) for the grassland Konza Prairie. In each graph, values from AmeriFlux L2 tower data products are shown as circles, and PnET-CN output for the corresponding years are shown as lines.

moderate performance for the other sites (Fig. 8).

The accuracy of modeled monthly NEP generally depended on the accuracy of modeled ER. For example, the mid-season NEP for Fermi Prairie in 2005 was negative for PnET-CN, but positive for the tower data, reflecting PnET-CN's large overestimation of ER for that year (Fig. 2). Overall, modeled ER and NEP generally agreed well with tower estimates for Fermi Prairie, Konza Prairie, and Tonzi Ranch, but less well for the other sites, largely due to discrepancies in ER (Figs. 2–7). Due to the sensitivity of NEP to estimates of ER, overall model performance was poor for all sites, with correlation coefficients close to zero (Fig. 8).

PnET-CN predictions of ET tended to closely track tower measurements for all sites (Figs. 2–7). The main discrepancies were underestimation of ET for Konza Prairie in 2011 and 2012 (Fig. 3), overestimation of winter ET for Freeman Ranch

in 2007 (Fig. 4), slight underestimation of ET for Tonzi Ranch 2010 (Fig. 5), and underestimation of the winter ET for all years in the two shrubland sites (Figs. 6 and 7). The overall model performance for ET was moderate for all sites, with the best performance for Konza Prairie and Sevilleta Desert Shrubland, and the worst performance for the Heritage Land Conservancy Pinyon-Juniper Woodland (Fig. 9).

PnET-CN generally captured the magnitude, seasonality, and interannual variability of WUE across sites, especially for the two grassland sites and Freeman Ranch (Figs. 2–4). PnET-CN simulation of WUE did not capture tower data as well for Tonzi Ranch as for the other sites, including mismatches in seasonal variation and underestimation of tower WUE for 2008, 2009, and 2010 (Fig. 5). The Taylor Diagram for WUE shows low but positive correlation coefficients for the two grasslands and Freeman Ranch, and zero or

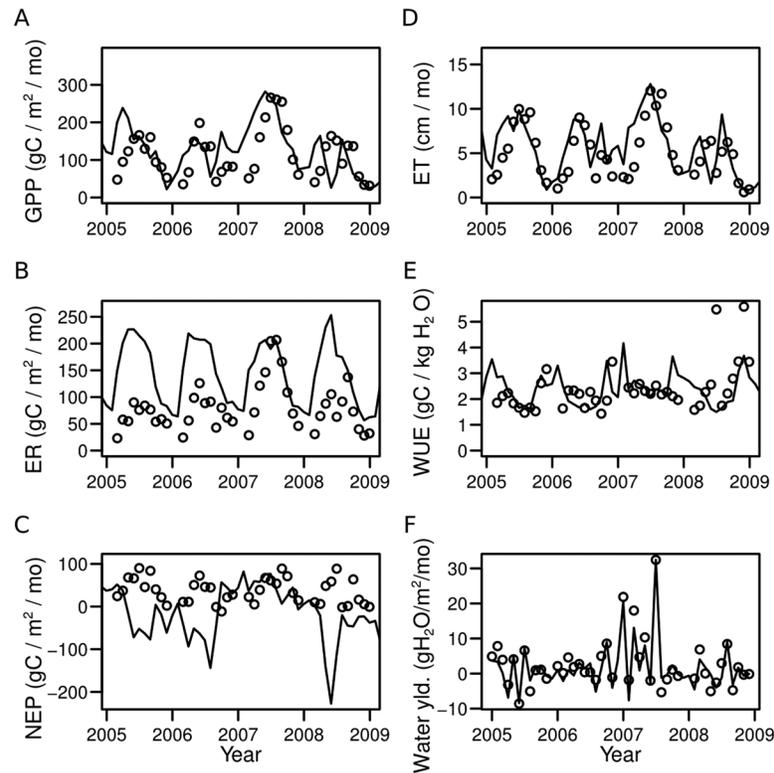


Fig. 4. PnET-CN simulation and tower estimates of gross primary productivity (GPP; A), ecosystem respiration (ER; B), net ecosystem productivity (NEP; C), of evapotranspiration (ET; D), water use efficiency (WUE; E), and water yield (F) for the woody savanna Freeman Ranch. Symbols are as in Fig. 3.

negative correlation coefficients for the other sites. Tonzi Ranch showed the lowest normalized RMS difference, and Fermi Prairie showed the highest correlation coefficient (Fig. 9).

PnET-CN predictions of water yield also generally agreed with tower estimates well, particularly for Fermi Prairie and Tonzi Ranch (Figs. 2 and 5). For the two shrublands, PnET-CN tended to slightly underestimate water yield in months with negative water yield, and to overestimate water yield in months with positive water yield (Figs. 6 and 7). The Taylor Diagram for water yield shows excellent model performance for all sites, with the highest correlation coefficient and lowest normalized RMS difference for the two woody savannas, and the highest normalized RMS difference for the two shrublands (Fig. 9).

Detailed analysis of model performance (including R^2 , RMSE, and statistical comparisons of intercepts and slopes to 0 and 1 respectively for

the linear model of PnET-CN simulations versus observations to flux tower estimates) are shown in Table 4. Although R^2 was generally moderate to high for GPP, ER, ET, and water yield, in most of these cases the model differed significantly from the expectation of 1:1 correspondence between simulation and tower data. Response variables that did not differ significantly from the expectation included ER and ET for Fermi Prairie, water yield for Freeman Ranch, GPP and ET for the Heritage Land Conservancy Pinyon-Juniper Woodland, and ET for Sevilleta Desert Shrubland (Table 4).

Annual carbon and water fluxes

Despite some limitations of PnET-CN's monthly predictions, PnET-CN performed well in predicting interannual and between-site variation in annual GPP, ER, and NEP (Fig. 10). Modeled annual GPP captured most inter-annual variation for Konza Prairie, Freeman Ranch, and

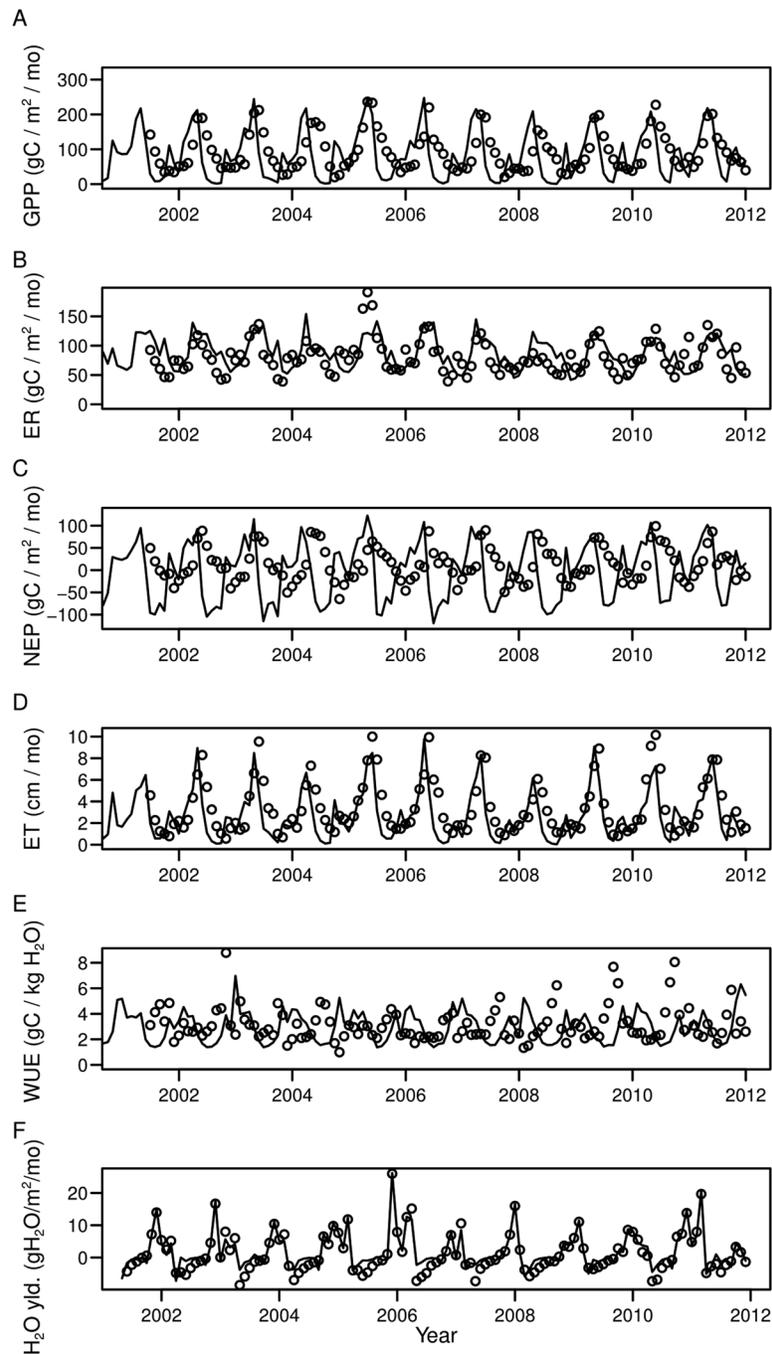


Fig. 5. PnET-CN simulation and tower estimates of gross primary productivity (GPP; A), ecosystem respiration (ER; B), net ecosystem productivity (NEP; C), of evapotranspiration (ET; D), water use efficiency (WUE; E), and water yield (F) for the woody savanna Tonzi Ranch. Symbols are as in Fig. 3.

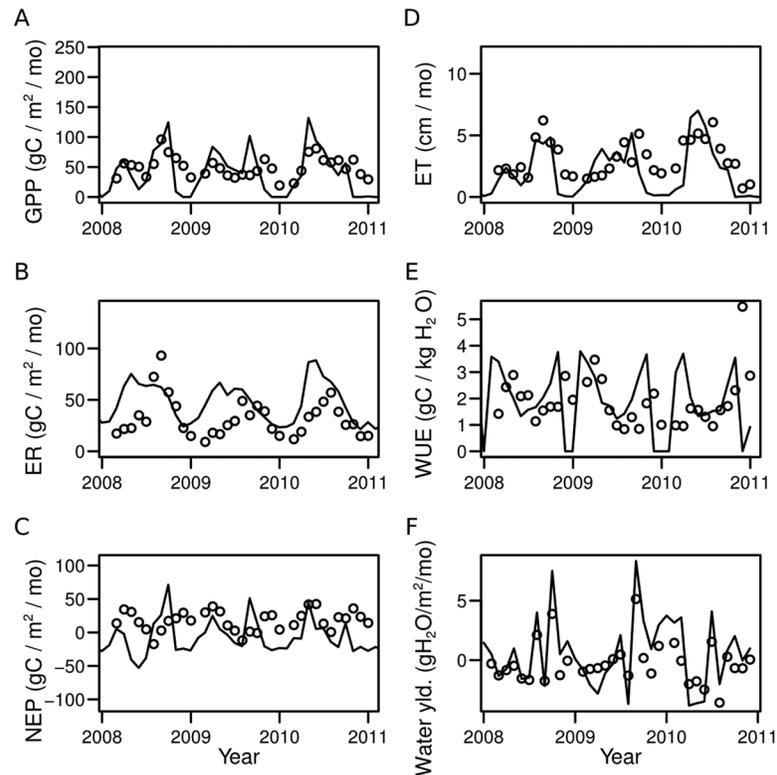


Fig. 6. PnET-CN simulation and tower estimates of gross primary productivity (GPP; A), ecosystem respiration (ER; B), net ecosystem productivity (NEP; C), of evapotranspiration (ET; D), water use efficiency (WUE; E), and water yield (F) for the shrubland Heritage Land Conservancy Pinyon Juniper Woodland. Symbols are as in Fig. 3.

Tonzi Ranch, and correctly predicted the general site-level GPP for other sites. Annual GPP tended to be slightly overestimated by PnET-CN for Fermi Prairie, Freeman Ranch, and Sevilleta Desert Shrubland, and to be slightly underestimated for Konza Prairie and Tonzi Ranch. The only major discrepancies for annual GPP were for Konza Prairie 2011 and 2012.

Simulated ER for Tonzi Ranch closely matched tower data, but for other sites the PnET-CN predictions did not match tower estimates as well as for GPP. PnET-CN almost consistently led to higher annual ER values than were estimated from tower data, across sites and years, and did not correctly predict inter-annual variability for the two grasslands (Fig. 10).

Across sites and years, modeled NEP was generally more negative than observed values (Fig. 10). It should be noted that NEP represents the small difference of two larger carbon fluxes: GPP and ER. While differing in sign for most

sites and years PnET-CN and tower estimates were fairly similar, and within site temporal trends in annual NEP were generally similar between PnET-CN and tower measurements. Notable exceptions were Konza Prairie in 2011 and 2012, for which PnET-CN underestimated GPP, and Fermi Prairie in 2005 and Freeman Ranch 2005, 2006, and 2008 for which PnET-CN substantially overestimated ER.

Similar to annual GPP predictions, PnET-CN's annual ET predictions closely matched tower measurements (Fig. 6). The model captured the interannual variability of ET for all three biomes and all the six sites, except for Konza Prairie 2011 and 2012. The model also captured the magnitude and interannual variability of annual WUE fairly well across all sites, and the model correctly predicted nearly all interannual and between site variation in water yield (Fig. 11).

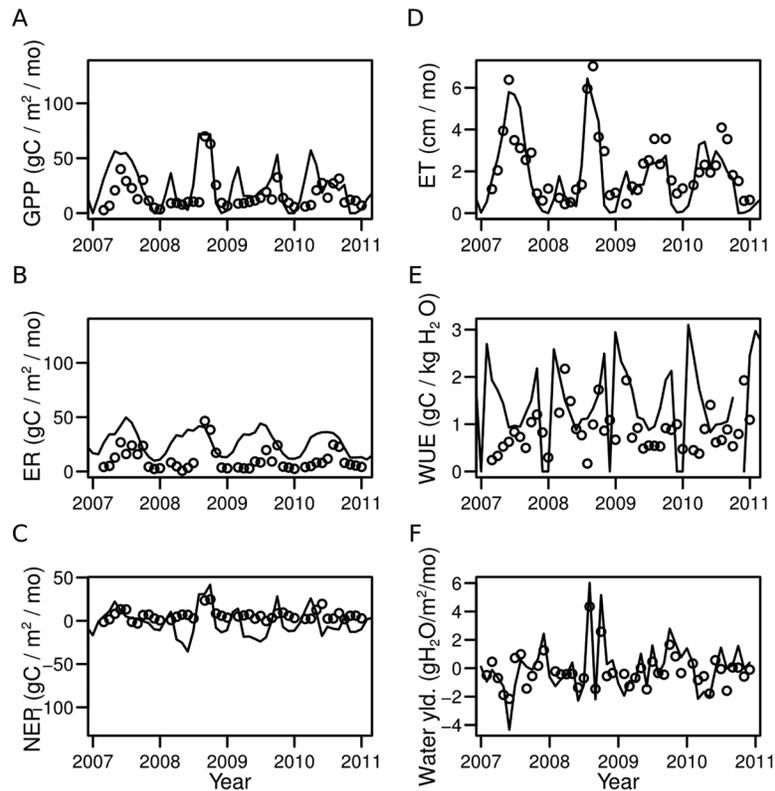


Fig. 7. PnET-CN simulation and tower estimates of gross primary productivity (GPP; A), ecosystem respiration (ER; B), net ecosystem productivity (NEP; C), of evapotranspiration (ET; D), water use efficiency (WUE; E), and water yield (F) for the shrubland Sevilleta Desert Shrubland. Symbols are as in Fig. 3.

DISCUSSION

Modeled carbon fluxes, ET, WUE, and water yield generally matched eddy covariance estimates from the AmeriFlux sites, especially in the case of metrics based on GPP and ET estimates. Importantly, close correspondence between simulated and observed fluxes was achieved using uncalibrated parameter values from the literature, similar to, e.g., the literature-based parameterization of Biome-BGC described by White et al. (2000). These results indicate high generalizability of the simple empirical relationships underlying PnET-CN as a process-based model: aboveground processes were successfully modeled for a variety of biomes by changing the parameters for a relatively small number of known relationships, such as the relationship between photosynthesis and leaf nitrogen and the dependence of water use efficiency on vapor pressure deficit. However, it is also important to

note that PnET-CN simulations were most accurate for the grassland sites and Tonzi Ranch. Like temperate forests, these sites combined high rainfall with moderate temperatures and moderate to high aridity indices (Table 2), resulting in high-productivity systems with closed canopies. Model performance on most metrics was also better for Freeman Ranch, a southern and relatively moist site, compared to the two arid shrubland sites. The success of PnET-CN here may particularly reflect the general usefulness of the PnET canopy routine, which defines maximum foliar biomass such that there is a positive carbon assimilation even at the bottom of the canopy, and is therefore particularly appropriate for closed-canopy systems (Aber and Federer 1992).

Although PnET-CN performed best for the moist sites, the model also captured most variation in GPP and ET (and therefore WUE) for water-limited systems. This success points to

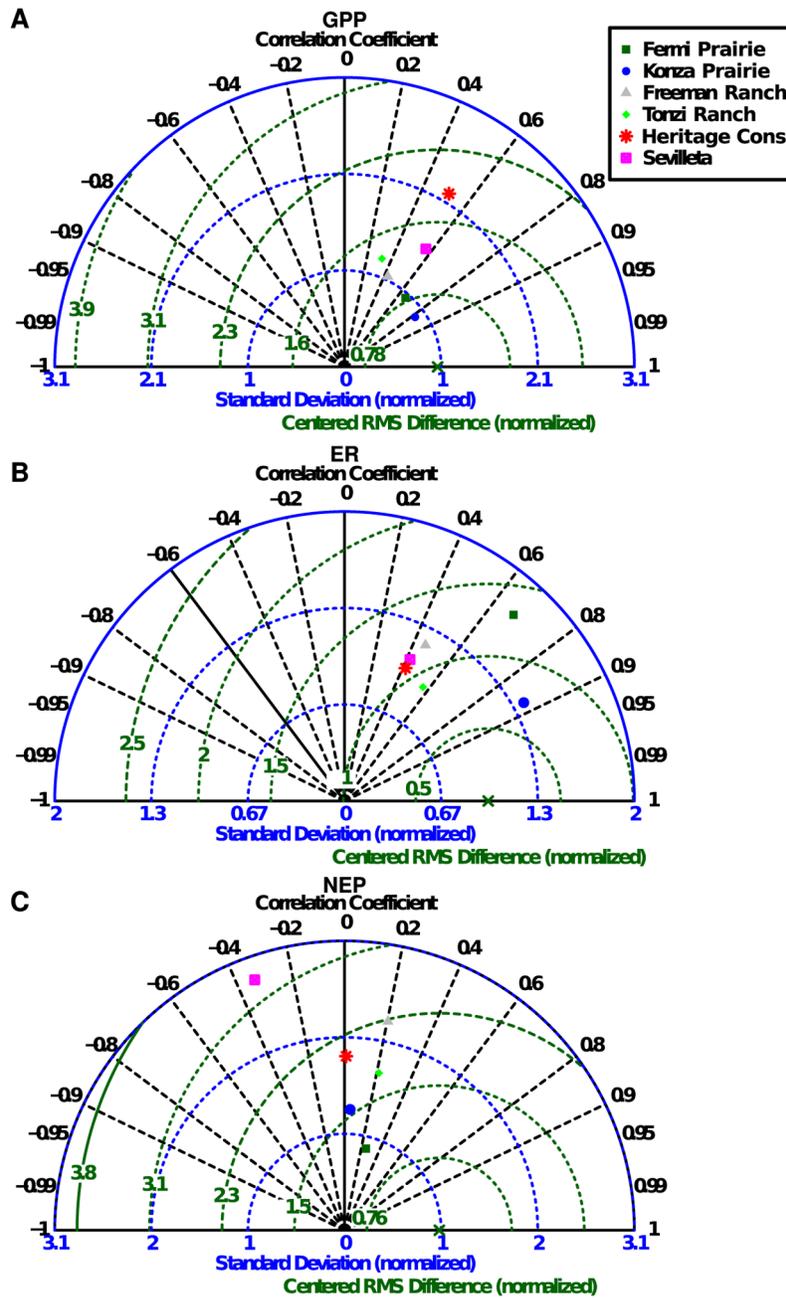


Fig. 8. Taylor diagrams for model performance of monthly PnET-CN values compared to tower estimates of gross primary productivity (GPP; A), ecosystem respiration (ER; B), and net ecosystem productivity (NEP; C). The diagrams show the correlation coefficient (black), the normalized standard deviation (blue), and the normalized root mean squared differences (green). Standard deviation and root mean squared differences are normalized by the standard deviation in tower values.

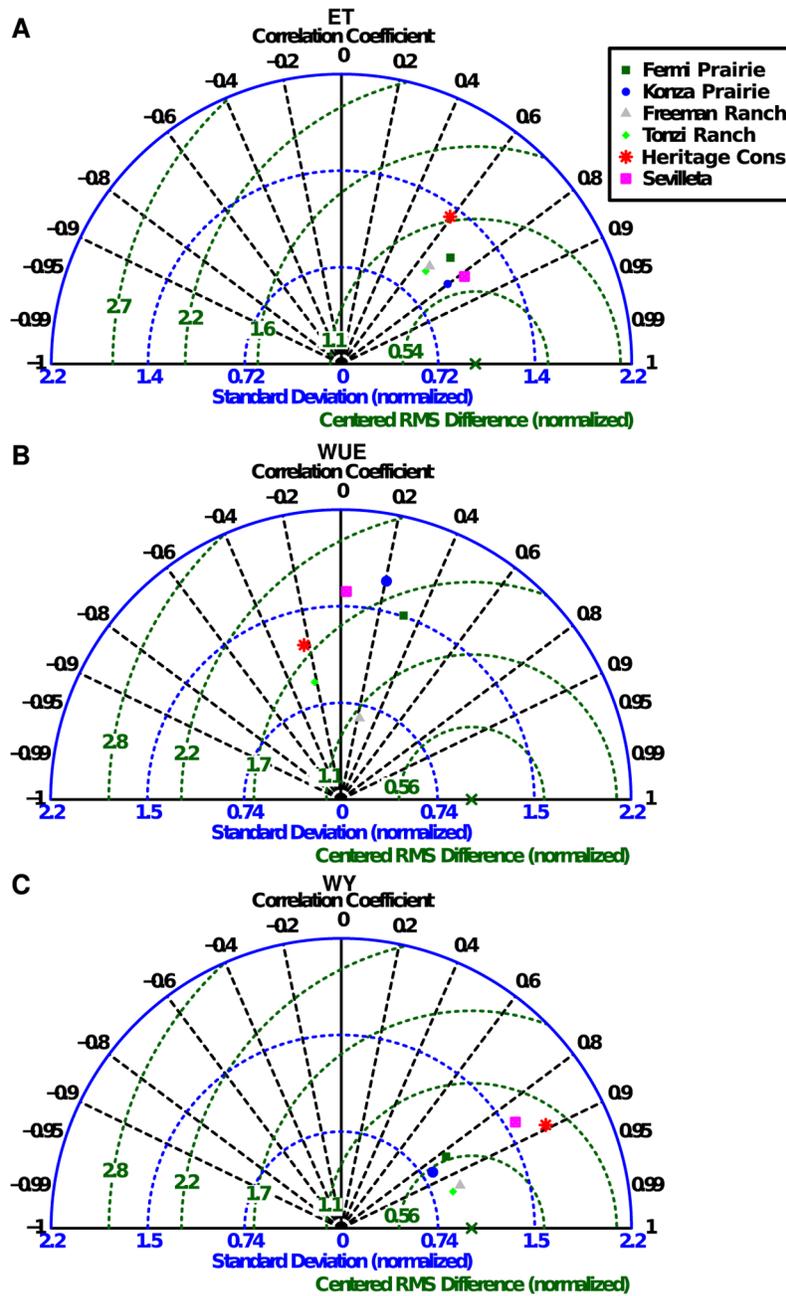


Fig. 9. Taylor diagrams for model performance of monthly PnET-CN values compared to tower estimates of evapotranspiration (ET; A), water use efficiency (WUE; B), and water yield (WY; B). The diagrams show the correlation coefficient (black), the normalized standard deviation (blue), and the normalized root mean squared differences (green). Standard deviation and root mean squared differences are normalized by the standard deviation in tower values.

Table 4. Summary of PnET-CN model performance for the grasslands Fermi Prairie and Konza Prairie, the woody savannas Freeman Ranch and Tonzi Ranch, and the shrublands Heritage Land Conservancy Pinyon Juniper Woodland and Sevilleta Desert Shrubland.

Variable	Adjusted R ²	RMSE	Intercept	Slope	Units
Fermi Prairie					
GPP	0.4216	97.96	48.77*	0.655**	gC/m ² /mo
ER	0.4356	102.24	41.71	1.176	gC/m ² /mo
NEP	0.0376	78.11	14.00	0.225***	gC/m ² /mo
ET	0.4639	3.44	0.23	0.793	cm/mo
WUE	0.0792	1.64	1.27**	0.480*	gC/kg H ₂ O
Water yield	0.6722	3.41	1.34*	0.804*	cm/mo
Konza Prairie					
GPP	0.6615	68.82	-0.59	0.758***	gC/m ² /mo
ER	0.765	48.50	-29.21**	1.247**	gC/m ² /mo
NEP	-0.0115	80.96	14.96	0.059***	gC/m ² /mo
ET	0.6344	3.44	-0.89	0.793**	cm/mo
WUE	0.0283	1.42	0.97*	0.349**	gC/kg H ₂ O
Water yield	0.7229	3.46	2.28***	0.702***	cm/mo
Freeman Ranch					
GPP	0.1644	72.68	82.00***	0.464**	gC/m ² /mo
ER	0.1913	94.27	113.93***	0.563*	gC/m ² /mo
NEP	0.0168	67.09	5.96	0.458	gC/m ² /mo
ET	0.4357	2.59	2.56***	0.658**	cm/mo
WUE	0.0255	0.93	1.97***	0.143***	gC/kg H ₂ O
Water yield	0.8823	2.59	-0.57	0.911	cm/mo
Tonzi Ranch					
GPP	0.0994	73.81	44.73	0.402***	gC/m ² /mo
ER	0.3143	26.12	42.80***	0.546***	gC/m ² /mo
NEP	0.0379	68.35	0.034	0.363***	gC/m ² /mo
ET	0.4456	2.06	0.543*	0.629***	cm/mo
WUE	0.0397	1.98	3.569***	-0.200***	gC/kg H ₂ O
Water yield	0.9020	2.06	0.907***	0.858***	cm/mo
Heritage Land Conservancy Pinyon Juniper Woodland					
GPP	0.2427	32.10	-10.518	1.123	gC/m ² /mo
ER	0.1469	27.00	36.667***	0.424**	gC/m ² /mo
NEP	-0.0322	32.92	4.845	0.017**	gC/m ² /mo
ET	0.3309	1.82	-0.191	0.811	cm/mo
WUE	0.0231	1.63	2.455***	-0.282***	gC/kg H ₂ O
Water yield	0.7901	1.82	0.936***	1.569***	cm/mo
Sevilleta Desert Shrubland					
GPP	0.3051	20.20	11.536*	0.873	gC/m ² /mo
ER	0.1559	20.54	23.010***	0.456**	gC/m ² /mo
NEP	0.0923	19.45	8.563*	-0.948***	gC/m ² /mo
ET	0.6556	1.05	-0.030	0.918	cm/mo
WUE	-0.0237	0.95	1.263***	0.042***	gC/kg H ₂ O
Water yield	0.7222	1.05	0.279	1.336*	cm/mo

Notes: Adjusted R², root mean square error (RMSE), model intercept, and model slope are shown for the regression of monthly simulated PnET-CN values against monthly AmeriFlux estimates for gross primary productivity (GPP), ecosystem respiration (ER), net ecosystem productivity (NEP), evapotranspiration (ET), water use efficiency (WUE), and water yield. Asterisks are used to indicate intercept values significantly different from 0 and slope values significantly different from 1 (*P ≤ 0.05; ** P ≤ 0.01 level, *** P ≤ 0.001 level).

the usefulness of PnET's relatively simple ET routine, which does not include all the physical details of the Penman-Monteith evaporation model used by many other models (reviewed by VEMAP Members 1995). Instead, PnET-CN calculates WUE from vapor pressure deficit, and uses WUE to determine ET from GPP (Aber and Federer 1992). When combined with simple rules for water limitation (i.e., photosynthesis cannot occur when soil water is unavailable for transpiration), this simplified approach seems to be

sufficient to capture most within- and between-site variability in photosynthesis and transpiration. This result is generally consistent with the analysis of McNaughton and Jarvis (1991), who conclude that relatively simple "big leaf" models for transpiration are appropriate for both moist and arid systems, although the authors also concluded that specific estimates of the relative contribution of stomatal and canopy resistance become important in systems with intermediate moisture levels.

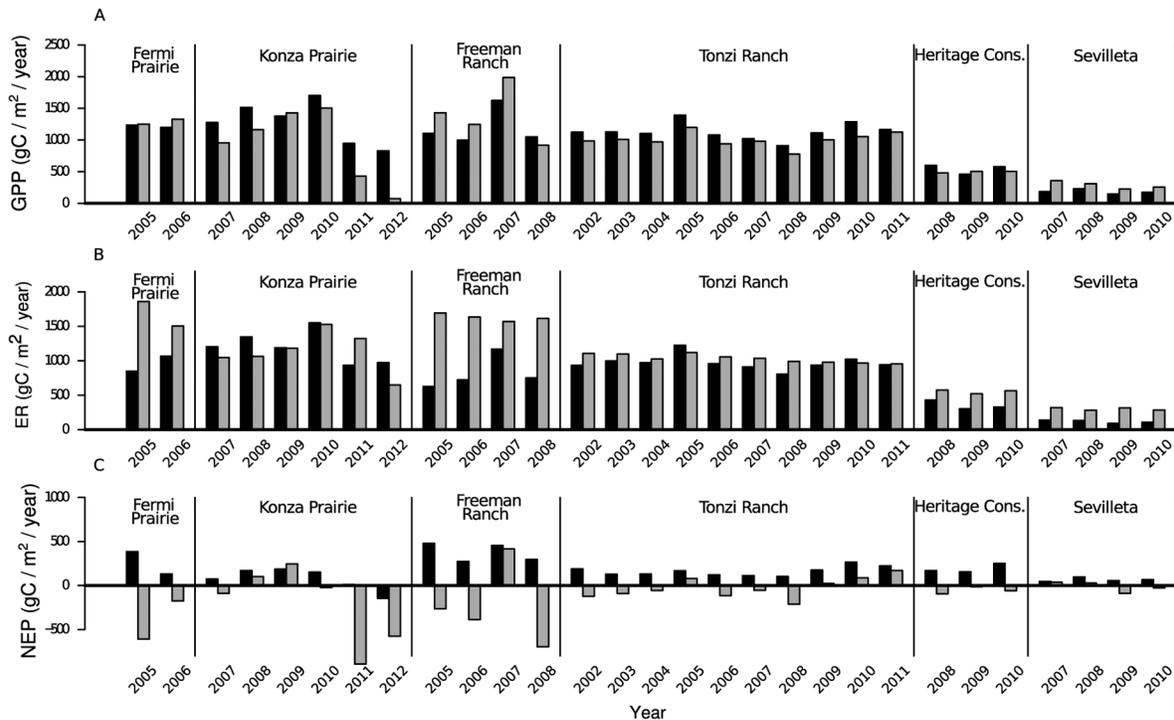


Fig. 10. AmeriFlux tower estimates and PnET-CN simulations of annual gross primary productivity (GPP; A), ecosystem respiration (ER; B), and net ecosystem productivity (NEP; C) for Fermi Prairie, Konza Prairie, Freeman Ranch, Tonzi Ranch, Heritage Conservancy Pinyon Juniper Woodland, and Sevilleta Shrubland. In the each pair, the black bar represents the AmeriFlux estimate and the gray bar represents PnET-CN output. For all sites except for Fermi Prairie and Tonzi Ranch, some or all years had coverage gaps preventing inclusion of one or two months in the AmeriFlux datasets. In particular, data were missing for 2008 and 2012 in Konza Prairie, and for all years for Freeman Ranch, Heritage Conservancy Pinyon Juniper Woodland, and, Sevilleta Desert Shrubland. Freeman Ranch was missing two winter months for each year except 2008, for which only one month was missing. Incomplete years for other sites were only missing a single month. Missing months were always in the winter or fall, and therefore are expected to have little effect on total annual photosynthesis. In these cases, missing months were also omitted from the PnET-CN simulation output before computing annual totals.

The discrepancies between our simulations and observed carbon and water fluxes indicate possible areas for future refinements of the model. For example, the exaggerated intra-annual variability in GPP and ET in PnET-CN simulations for the two desert shrublands implies that PnET-CN did not capture an apparent time-lag in the physiological availability of water relative to precipitation events. Such a time lag most likely results from some combination of spatial heterogeneity in water capture by plants (Breshears 2006, Newman et al. 2010), movement of water between patches with different types of vegetation cover (Breshears 2006), water storage in surface litter (Pierson et al. 2010), and the

ability of some species to redistribute soil water through hydraulic redistribution in soils mediated by roots (Meinzer et al. 2004).

Spatial heterogeneity in vegetation and soil hydrology are a particularly important consideration. In shrublands with large intercanopy land area, precipitation falling onto vegetation patches may be stored in surface litter (Pierson et al. 2010) and once it percolates into the soil is rapidly taken up by roots (Breshears 2006, Newman et al. 2010), whereas precipitation falling on bare soil is not absorbed by the soil as readily (Pierson et al. 2010). Based on the distribution of chlorine ions in a New Mexico semiarid woodland, it has been hypothesized

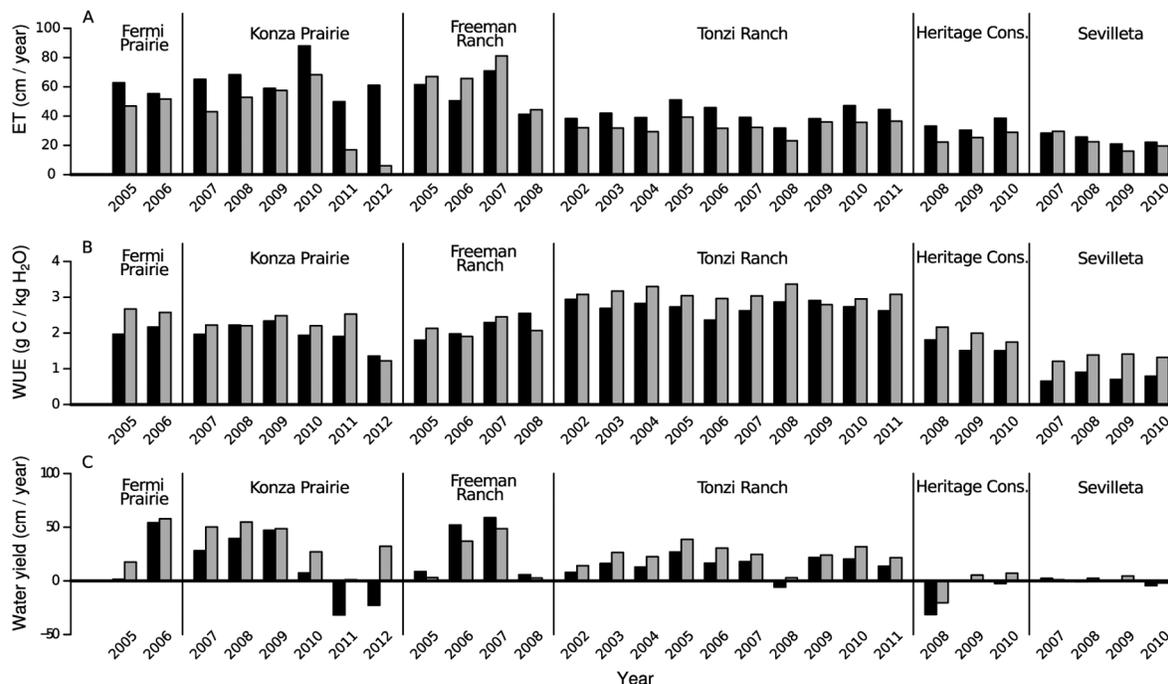


Fig. 11. AmeriFlux tower estimates and PnET-CN simulations of evapotranspiration (ET; A), water use efficiency (WUE; B), and water yield (C) for Konza Prairie, Fermi Prairie, Heritage Conservancy Pinyon Juniper Woodland, Sevilleta Shrubland, Freeman Ranch, and Tonzi Ranch. Symbols are as in Fig. 10. For all sites except for Fermi Prairie and Tonzi Ranch, some or all years had coverage gaps preventing inclusion of one or two months in the AmeriFlux datasets. In particular, data were missing for for 2008 and 2012 in Konza Prairie, and for all years for Freeman Ranch, Heritage Conservancy Pinyon Juniper Woodland, and, Sevilleta Desert Shrubland. Freeman Ranch was missing two winter months for each year except 2008, for which only one month was missing. Incomplete years for other sites were only missing a single month. Missing months were always in the winter or fall, and therefore are expected to have little effect on total annual photosynthesis. In these cases, missing months was also omitted from the PnET-CN simulation output before computing annual totals.

that water infiltrating the soil of intercanopy patches tends to slowly move from the intercanopy to the rooting zone, presumably driven by transpiration-induced water potential gradients (Newman et al. 2010). These factors are all expected to result in delayed availability of water relative to more uniform ecosystems. In addition, the slight underestimation of ET and resulting overestimation of WUE for the two shrublands could be explained by the fact that PnET-CN does not account for evaporation from bare soil, a particularly important water loss in dry shrublands (Newman et al. 2010).

Limitations to the simulation of water storage and movement in PnET-CN likely also contribute to the dramatic underestimation of GPP and ET for Konza Prairie in 2011 and 2012. These years

were characterized by strongly negative water yield according to meteorological and tower data, but not for PnET-CN. This pattern suggests that Konza vegetation was able to make use of deep soil water not included in the simulation model.

Temporal offsets of peak ER predicted by PnET-CN for the two shrublands may also result from soil moisture heterogeneity and water storage. In PnET-CN simulations of the shrublands, soil respiration and wood growth respiration are the two largest contributors to ER. Soil respiration depends on soil moisture and temperature. Therefore, because soil organic matter tends to be the highest beneath canopy patches (Breshears 2006), delays in the arrival of soil moisture in the rooting zone would also delay

soil respiration. Because wood growth respiration was another major contributor to ER for the shrublands, the temporal offset may have been intensified if wood phenology parameters were not correct. The wood phenology parameters concentrate wood growth in the early season, with the consequence of high wood growth respiration during that interval. Unfortunately, wood phenology parameters are some of the most difficult PnET-CN parameters to estimate from field data.

Another area for future refinement of PnET-CN is improved prediction of inter-annual variability in ER, particularly for the two grasslands. Simulated root respiration was a major driver of ER for both of these biomes, and may have contributed to incorrect simulation of variability between years. For Fermi Prairie, the simulated soil respiration matched AmeriFlux estimates of ecosystem respiration, and the mismatch in interannual variability likely results from dramatically higher simulated root respiration in 2005 than in 2006. For Konza Prairie, PnET-CN predicted little inter-annual variation in soil respiration while predicting low root respiration for 2008 and 2009 and high root respiration for 2010 and 2011. Therefore the overall lack of correspondence to flux tower estimates is likely to be driven by both of these components of ER. One possible explanation is that the model may have overestimated the contribution of root respiration to ER, perhaps due to metabolic variation among root classes not included in the model. For instance, coarse roots greater than 1 mm in diameter can comprise as much as 30% of the root biomass in prairie biomes (Reinhardt and Miller 1990), and coarser roots tend to have lower respiration rates (Bahn et al. 2006).

Overall, our simulations captured most variation among sites as well as intra- and inter-annual variation in important fluxes. The discrepancies between simulations and observed values suggest that the most important areas for future model refinement deal with belowground processes. Most importantly, for arid biomes, the model should be modified to incorporate an appropriate time lag in soil water availability. Because soil heterogeneity is likely to play a key role in these systems, an important starting point will be to subdivide soil water into two or more

distinct pools, corresponding to different land cover types and/or different soil water depths. Movement of water between pools would serve as a realistic buffer decoupling ET from precipitation events. Similar subdivision of soil organic matter could permit more accurate simulation of the effects of moisture levels on soil respiration. Such an approach may work well in conjunction with more structurally complex soil models, which include multiple soil organic matter pools, similar to the approach of the CENTURY model (Schimel et al. 1991b). A particularly fruitful approach may be to incorporate several soil moisture pools into the newly developed PnET model PnET-SOM (Tonitto et al. 2014), which uses separate soil organic matter pools to characterize the spatial movement of organic matter between soil layers. Simulation of evaporation from bare soil will also be important, especially for shrublands, where bare soil is a significant proportion of land cover. Additional refinements may come from closer analysis of ER and the relative contributions of plant growth, plant maintenance, and soil respiration to ER, including phenology of carbon allocation to root and wood growth.

Conclusions

We applied the process-based forest ecosystem model PnET-CN for other biomes—grasslands, shrublands, and savannas—and evaluated the model's performance for simulating carbon and water fluxes. Simulated fluxes were generally similar to tower observations for all sites, although the model performance varied by site and biome type. Simulated GPP and ET more closely matched observations than did simulated ER, and in general PnET-CN performed best at moist sites with similar climate to the temperate forests for which the PnET models were originally developed. Despite these limitations, the model captured nearly all variation in annual fluxes among years and among sites, suggesting that with minimal modifications PnET-CN will be well suited for modeling long-term trends in carbon and water exchange at regional to continental scales. The model performed particularly well for predicting ET and water yield across all sites, and also performed well for predicting GPP, especially for the two grassland sites. Overall, our results suggest that PnET-CN

is a promising tool for modeling carbon exchange in a variety of biome types, especially with regard to aboveground processes and for moist temperate biomes.

Important areas for future refinement should include more detailed modeling of soil water storage and water availability in heterogeneous dry sites and an improved belowground carbon model. In particular, subdivision of soil water into several pools for dry sites with heterogeneous land cover is a promising avenue for more accurate simulation of carbon and water fluxes for those sites. Another area for model improvement will be improvement of belowground carbon dynamics for grassland systems. Future research should assess the predictive power of PnET-CN generalization across a broader range of grasslands, shrublands, and savannas.

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LITERATURE CITED

- Aber, J. D., and C. T. Driscoll. 1997. Effects of land use, climate variation, and N deposition on N cycling and C storage in northern hardwood forests. *Global Biogeochemical Cycles* 11:639–648.
- Aber, J. D., and C. A. Federer. 1992. A generalized, lumped-parameter model of photosynthesis, evapotranspiration and net primary production in temperate and boreal forest ecosystems. *Oecologia* 92:463–474.
- Aber, J. D., J. M. Melillo, K. J. Nadelhoffer, C. A. McLaugherty, and J. Pastor. 1985. Fine root turnover in forest ecosystems in relation to quantity and form of nitrogen availability: a comparison of two methods. *Oecologia* 66:317–321.
- Aber, J. D., S. V. Ollinger, and C. T. Driscoll. 1997. Modeling nitrogen saturation in forest ecosystems in response to land use and atmospheric deposition. *Ecological Modelling* 101:61–78.
- Aber, J. D., S. V. Ollinger, C. A. Féderer, P. B. Reich, M. L. Goulden, D. W. Kicklighter, J. M. Melillo, and R. G. Lathrop, Jr. 1995. Predicting the effects of climate change on water yield and forest production in the northeastern United States. *Climate Research* 5:207–222.
- Aber, J. D., P. B. Reich, and M. L. Goulden. 1996. Extrapolating leaf CO₂ exchange to the canopy: a generalized model of forest photosynthesis compared with measurements by eddy correlation. *Oecologia* 106:257–265.
- Bahn, M., M. Knapp, Z. Garajova, N. Pfahringer, and A. Cernusca. 2006. Root respiration in temperate mountain grasslands differing in land use. *Global Change Biology* 12:995–1006.
- Baldocchi, D. D. 2003. Assessing the eddy covariance technique for evaluating carbon dioxide exchange rates of ecosystems: past, present and future. *Global Change Biology* 9:479–492.
- Bond-Lamberty, B., S. T. Gower, D. E. Ahl, and P. E. Thornton. 2005. Reimplementation of the Biome-BGC model to simulate successional change. *Tree Physiology* 25:413–424.
- Brenner, A. J., and L. D. Incoll. 1997. The effect of clumping and stomatal response on evaporation from sparsely vegetated shrublands. *Agricultural and Forest Meteorology* 84:187–205.
- Breshears, D. D. 2006. The grassland–forest continuum: trends in ecosystem properties for woody plant mosaics? *Frontiers in Ecology and the Environment* 4:96–104.
- Dragoni, D., H. P. Schmid, C. S. B. Grimmond, and H. W. Loescher. 2007. Uncertainty of annual net ecosystem productivity estimated using eddy covariance flux measurements. *Journal of Geophysical Research* 112. doi: 10.1029/2006JD008149
- Gao, Q., and J. F. Reynolds. 2003. Historical shrub–grass transitions in the northern Chihuahuan Desert: modeling the effects of shifting rainfall seasonality and event size over a landscape gradient. *Global Change Biology* 9:1475–1493.
- Golinkoff, J. 2010. Biome BGC version 4.2: the theoretical framework. Numerical Terra-dynamic

- Simulation Group, College of Forestry and Conservation, University of Montana, Missoula, Montana, USA.
- Griffith, A. B., H. Alpert, and M. E. Loik. 2010. Predicting shrub ecophysiology in the Great Basin Desert using spectral indices. *Journal of Arid Environments* 74:315–326.
- Ham, J. M., and A. K. Knapp. 1998. Fluxes of CO₂, water vapor, and energy from a prairie ecosystem during the seasonal transition from carbon sink to carbon source. *Agricultural and Forest Meteorology* 89:1–14.
- Huenneke, L. F., D. Clason, and E. Muldavin. 2001. Spatial heterogeneity in Chihuahuan Desert vegetation: implications for sampling methods in semi-arid ecosystems. *Journal of Arid Environments* 47:257–270.
- Kattge, J., et al. 2011. TRY: a global database of plant traits. *Global Change Biology* 17:2905–2935.
- Kitchen, D. J., J. M. Blair, and M. A. Callahan. 2009. Annual fire and mowing alter biomass, depth distribution, and C and N content of roots and soil in tallgrass prairie. *Plant and Soil* 323:235–247.
- Kittel, T. G. F., N. A. Rosenbloom, T. H. Painter, D. S. Schimel, H. H. Fisher, A. Grimsdell, VEMAP Participants, C. Daly, and E. R. Hunt. 1996. The VEMAP Phase I Database: an integrated input dataset for ecosystem and vegetation modeling for the conterminous United States. <http://www.cgd.ucar.edu/vemap/>
- Knapp, A. K. 1985. Effect of fire and drought on the ecophysiology of *Andropogon gerardii* and *Panicum virgatum* in a tallgrass prairie. *Ecology* 66:1309–1320.
- Lachapelle, P.-P., and B. Shipley. 2012. Interspecific prediction of photosynthetic light response curves using specific leaf mass and leaf nitrogen content: effects of differences in soil fertility and growth irradiance. *Annals of Botany* 109:1149–1157.
- Law, B. E., P. M. Anthoni, and J. D. Aber. 2000. Measurements of gross and net ecosystem productivity and water vapour exchange of a *Pinus ponderosa* ecosystem, and an evaluation of two generalized models. *Global Change Biology* 6:155–168.
- Law, B. E., et al. 2002. Environmental controls over carbon dioxide and water vapor exchange of terrestrial vegetation. *Agricultural and Forest Meteorology* 113:97–120.
- Letts, M. G., D. R. E. Johnson, and C. A. Coburn. 2010. Drought stress ecophysiology of shrub and grass functional groups on opposing slope aspects of a temperate grassland valley. *Botany* 88:850–866.
- Marino, G., M. Aqil, and B. Shipley. 2010. The leaf economics spectrum and the prediction of photosynthetic light-response curves. *Functional Ecology* 24:263–272.
- McCulley, R. L., and R. B. Jackson. 2012. Conversion of tallgrass prairie to woodland: consequences for carbon and nitrogen cycling. *American Midland Naturalist* 167:307–321.
- McNaughton, K. G., and P. G. Jarvis. 1991. Effects of spatial scale on stomatal control of transpiration. *Agricultural and Forest Meteorology* 54:279–302.
- Meinzer, F. C., J. R. Brooks, S. Bucci, G. Goldstein, F. G. Scholz, and J. M. Warren. 2004. Converging patterns of uptake and hydraulic redistribution of soil water in contrasting woody vegetation types. *Tree Physiology* 24:919–928.
- Newman, B. D., D. D. Breshears, and M. O. Gard. 2010. Evapotranspiration partitioning in a semiarid woodland: ecohydrologic heterogeneity and connectivity of vegetation patches. *Vadose Zone Journal* 9:561.
- Ollinger, S. V., J. D. Aber, and A. Federer. 1998. Estimating regional forest productivity and water yield using an ecosystem model linked to a GIS. *Landscape Ecology* 13:323–334.
- Ollinger, S. V., J. D. Aber, P. B. Reich, and R. J. Freuder. 2002a. Interactive effects of nitrogen deposition, tropospheric ozone, elevated CO₂ and land use history on the carbon dynamics of northern hardwood forests. *Global Change Biology* 8:545–562.
- Ollinger, S. V., and M.-L. Smith. 2005. Net primary production and canopy nitrogen in a temperate forest landscape: an analysis using imaging spectroscopy, modeling and field data. *Ecosystems* 8:760–778.
- Ollinger, S. V., M. L. Smith, M. E. Martin, R. A. Hallett, C. L. Goodale, and J. D. Aber. 2002b. Regional variation in foliar chemistry and N cycling among forests of diverse history and composition. *Ecology* 83:339–355.
- Ostle, N. J., et al. 2009. Integrating plant-soil interactions into global carbon cycle models. *Journal of Ecology* 97:851–863.
- Pan, Y., R. Birdsey, J. Hom, K. McCullough, and K. Clark. 2006. Improved estimates of net primary productivity from MODIS satellite data at regional and local scales. *Ecological Applications* 16:125–132.
- Parton, W. J. 1996. The CENTURY model. Pages 283–293 in D. S. Powlson, P. S. Smith, and J. U. Smith, editors. *Evaluation of soil organic matter models using existing long-term datasets*. Springer-Verlag, Berlin, Germany.
- Parton, W. J., D. S. Schimel, C. V. Cole, and D. S. Ojima. 1987. Analysis of factors controlling soil organic matter levels in Great Plains grasslands. *Soil Science Society of America Journal* 51:1173–1179.
- Pierson, F. B., C. J. Williams, P. R. Kormos, S. P. Hardegree, P. E. Clark, and B. M. Rau. 2010. Hydrologic vulnerability of sagebrush steppe

- following pinyon and juniper encroachment. *Rangeland Ecology & Management* 63:614–629.
- Poorter, H., and J. R. Evans. 1998. Photosynthetic nitrogen-use efficiency of species that differ inherently in specific leaf area. *Oecologia* 116:26–37.
- Potter, C. S., J. T. Randerson, C. B. Field, P. A. Matson, P. M. Vitousek, H. A. Mooney, and S. A. Klooster. 1993. Terrestrial ecosystem production: A process model based on global satellite and surface data. *Global Biogeochemical Cycles* 7:811–841.
- Raich, J. W., E. B. Rastetter, J. M. Melillo, D. W. Kicklighter, P. A. Steudler, B. J. Peterson, A. L. Grace, B. Moore Iii, and C. J. Vorosmarty. 1991. Potential net primary productivity in South America: application of a global model. *Ecological Applications* 1:399–429.
- Reed, H. E., T. R. Seastedt, and J. M. Blair. 2005. Ecological consequences of C4 grass invasion of a C4 grassland: a dilemma for management. *Ecological Applications* 15:1560–1569.
- Reich, P. B., M. D. Abrams, D. S. Ellsworth, E. L. Kruger, and T. J. Tabone. 1990. Fire affects ecophysiology and community dynamics of central Wisconsin oak forest regeneration. *Ecology* 71:2179–2190.
- Reich, P. B., D. S. Ellsworth, M. B. Walters, J. M. Vose, C. Gresham, J. C. Volin, and W. D. Bowman. 1999. Generality of leaf trait relationships: a test across six biomes. *Ecology* 80:1955–1969.
- Reinhardt, D. R., and R. M. Miller. 1990. Size classes of root diameter and mycorrhizal fungal colonization in two temperate grassland communities. *New Phytologist* 116:129–136.
- Richardson, A. D., et al. 2006. A multi-site analysis of random error in tower-based measurements of carbon and energy fluxes. *Agricultural and Forest Meteorology* 136:1–18.
- Running, S. W., and J. C. Coughlan. 1988. A general model of forest ecosystem processes for regional applications i. hydrologic balance, canopy gas exchange and primary production processes. *Ecological Modelling* 42:125–154.
- Running, S. W., and E. R. Hunt, Jr. 1993. Generalization of a forest ecosystem process model for other biomes, BIOME-BGC, and an application for global-scale models. Pages 141–158 in J. R. Ehleringer and C. Field, editors. *Scaling processes between leaf and landscape levels*. Academic Press, San Diego, California, USA.
- Ryu, Y., J. Verfaillie, C. Macfarlane, H. Kobayashi, O. Sonnentag, R. Vargas, S. Ma, and D. D. Baldocchi. 2012. Continuous observation of tree leaf area index at ecosystem scale using upward-pointing digital cameras. *Remote Sensing of Environment* 126:116–125.
- Schimel, D. S., T. G. F. Kittel, A. K. Knapp, T. R. Seastedt, W. J. Parton, and V. B. Brown. 1991a. Physiological interactions along resource gradients in a tallgrass prairie. *Ecology* 72:672–684.
- Schimel, D. S., T. G. F. Kittel, and W. J. Parton. 1991b. Terrestrial biogeochemical cycles: Global interactions with the atmosphere and hydrology. *Tellus* 43AB:188–203.
- Serrano, L., J. Penuelas, and S. L. Ustin. 2002. Remote sensing of nitrogen and lignin in Mediterranean vegetation from AVIRIS data: Decomposing biochemical from structural signals. *Remote Sensing of Environment* 81:355–364.
- Smith, M. L., S. V. Ollinger, M. E. Martin, J. D. Aber, R. A. Hallett, and C. L. Goodale. 2002. Direct estimation of aboveground forest productivity through hyperspectral remote sensing of canopy nitrogen. *Ecological Applications* 12:1286–1302.
- Taiz, L., and E. Zeiger. 2002. *Plant physiology*. Third edition. Sinauer, Sunderland, Massachusetts, USA.
- Taylor, K. E. 2001. Summarizing multiple aspects of model performance in a single diagram. *Journal of Geophysical Research* 106:7183–7192.
- Thornton, P. E., M. M. Thornton, B. W. Mayer, N. Wilhelm, Y. Wei, and R. B. Cook. 2012. *Daymet: Daily surface weather on a 1 km grid for North America, 1980–2011*. Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, USA. <http://daymet.ornl.gov/>
- Tonitto, C., C. L. Goodale, M. S. Weiss, S. D. Frey, and S. V. Ollinger. 2014. The effect of nitrogen addition on soil organic matter dynamics: a model analysis of the Harvard Forest Chronic Nitrogen Amendment Study and soil carbon response to anthropogenic N deposition. *Biogeochemistry* 117:431–454.
- Turner, C. L., T. R. Seastedt, and M. I. Dyer. 1993. Maximization of aboveground grassland production: the role of defoliation frequency, intensity, and history. *Ecological Applications* 3:175–186.
- Valladares, F., M. T. Allen, and R. W. Pearcy. 1997. Photosynthetic responses to dynamic light under field conditions in six tropical rainforest shrubs occurring along a light gradient. *Oecologia* 111:505–514.
- VEMAP Members. 1995. *Vegetation / ecosystem modeling and analysis project: Comparing biogeography and biogeochemistry models in a continental-scale study of terrestrial ecosystem responses to climate change and CO₂ doubling*. *Global Biogeochemical Cycles* 9:407–437.
- Wang, W., J. Dungan, H. Hashimoto, A. R. Michaelis, C. Milesi, K. Ichii, and R. R. Nemani. 2011. Diagnosing and assessing uncertainties of terrestrial ecosystem models in a multimodel ensemble experiment: 1. Primary production. *Global Change Biology* 17:1350–1366.
- Wang, W., J. Xiao, S. V. Ollinger, A. R. Desai, J. Chen, and A. Noormets. 2014. Quantifying the effects of harvesting on carbon fluxes and stocks in northern

- temperate forests. *Biogeosciences* 11:6667–6682.
- White, M. A., P. E. Thornton, S. W. Running, and R. R. Nemani. 2000. Parameterization and sensitivity analysis of the BIOME-BGC terrestrial ecosystem model: net primary production controls. *Earth Interactions* 4:1–85.
- Wright, I. J., et al. 2004. The worldwide leaf economics spectrum. *Nature* 428:821–827.
- Wythers, K. R., P. B. Reich, M. G. Tjoelker, and P. B. Bolstad. 2005. Foliar respiration acclimation to temperature and temperature variable Q₁₀ alter ecosystem carbon balance. *Global Change Biology* 11:435–449.
- Xiao, J., et al. 2014. Data-driven diagnostics of terrestrial carbon dynamics over North America. *Agricultural and Forest Meteorology* 197:142–157.
- Zhou, X., S. Fei, R. Sherry, and Y. Luo. 2012. Root biomass dynamics under experimental warming and doubled precipitation in a tallgrass prairie. *Ecosystems* 15:542–554.
- Zomer, R. J., A. Trabucco, D. A. Bossio, and L. V. Verchot. 2008. Climate change mitigation: A spatial analysis of global land suitability for clean development mechanism afforestation and reforestation. *Agriculture, Ecosystems and Environment* 126:67–80.
- Zomer, R. J., A. Trabucco, O. van Straaten, and D. A. Bossio. 2006. Carbon, land and water: A global analysis of the hydrologic dimensions of climate change mitigation through afforestation/reforestation. International Water Management Institute, Colombo, Sri Lanka. http://www.iwmi.cgiar.org/Publications/IWMI_Research_Reports/PDF/pub101/RR101.pdf

SUPPLEMENTAL MATERIAL

SUPPLEMENT

R code for running PnET-CN simulations for AmeriFlux sites, as in text (*Ecological Archives*, <http://dx.doi.org/10.1890/ES14-00542.1.sm>).