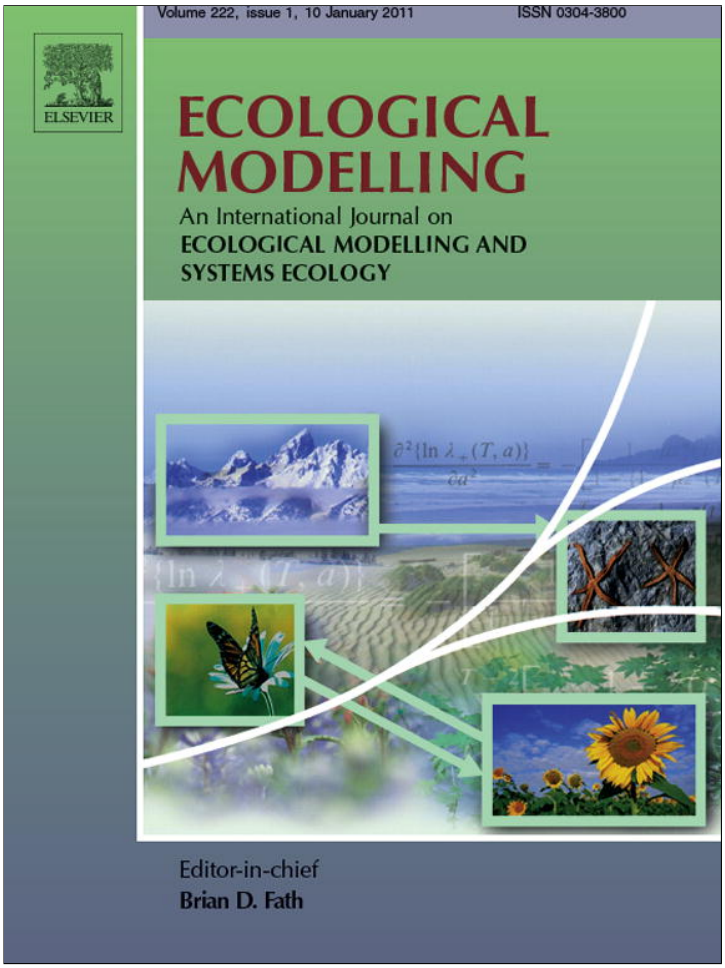
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Modeling regional variation in net primary production of pinyon–juniper ecosystems

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ABSTRACT

Spatial dynamics of carbon fluxes in dryland montane ecosystems are complicated and may be influenced by topographic conditions and land tenure. Here we employ a modified version of the Carnegie Ames Stanford Approach (CASA) ecosystem model to estimate annual net primary production (NPP) at a fine spatial resolution (30 m) in pinyon–juniper (P–J) woodlands of the Colorado Plateau. NPP estimated by CASA was generally comparable to validation data from a statistical NPP model and field observations. We then compared modeled NPP results with spatial layers of topography and managed grazing to assess the influences of these factors on NPP. At the regional scale, there was a positive correlation between elevation and NPP ($r^2 = 0.20$, $p < 0.0001$), mainly due to an orographic effect, but slope and slope facing-derived dryness indices failed to explain modeled variation in NPP. Topographic analyses based on six terrain aspect classes showed that cooler and wetter north-facing slopes yielded higher NPP than did south-facing slopes. A multiple regression consisting of three numerical topographical attributes (elevation, slope and a dryness index) yielded the highest predictability for CASA NPP (adjusted $r^2 = 0.24$, $p < 0.0001$). Modeled NPP of a grazed site was significantly higher than that of an ungrazed site. Combining the results from this study and previous research efforts suggests that grazing may be correlated with higher woody vegetation cover, which elevates NPP in P–J woodlands of the Colorado Plateau. The findings reveal that the spatial pattern of NPP is complex, and can be strongly affected by topographic and/or anthropogenic factors even in relatively remote areas of this dryland region.

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1. Introduction

Dryland ecosystems are spatially extensive, occupying up to 45% of the global terrestrial biosphere (Bailey, 1998). Patterns of net primary production (NPP) in drylands are spatially and temporally heterogeneous, especially across topographic gradients (Whittaker and Niering, 1975). In topographically diverse terrain, micro-climate (e.g., precipitation, temperature and solar radiation) is mainly controlled by altitude, slope and aspect (Gosz and Sharpe, 1989), with feedbacks to soil moisture availability (McAuliffe, 1994). These topo-bioclimatic attributes may dictate the spatial arrangement of carbon (C) storage (Greenwood and Weisberg, 2009; Weisberg et al., 2007), and are known regulators of NPP (Cramer et al., 1999). But to date, we know little of how these factors affect NPP at local to regional scales.

Land use is another major factor affecting NPP in arid and semi-arid environments. The most extensive form of land use in global drylands is managed grazing (Asner et al., 2004), and woody vegetation encroachment is one of the most significant impacts of grazing-related disturbances (e.g., Archer, 1995a,b; Barger et al., 2011; Hibbard et al., 2001, and many others). Grazing may facilitate the growth of woody plants by reducing herbaceous cover, favoring the establishment of woody seedlings due to less competition of resources from herbaceous plants (Hughes et al., 2006; Sankaran et al., 2008). Grazing may also reduce fine fuel loads resulting in alterations of fire regimes (Archer, 1995b; Fuhlendorf and Smeins, 1997). This can feed back to lower woody plant mortality by decreasing fire frequency and intensity (see reviews by Asner et al., 2004; Van Auken, 2000). However, other research suggests that woody plant proliferation may lower NPP in some dryland systems (Huenneke et al., 2002; Jackson et al., 2002; Schlesinger et al., 2000). Indeed, several studies reveal contrasting findings of changing

Abbreviations: CASA, Carnegie Ames Stanford Approach; CLAS, Carnegie Landsat Analysis System; CLIM-MET, Southwest Climate Impact Meteorological Stations; CNP, Canyonlands National Park; GLOVIS, Global Visualization Viewer; GSENM, Grand Staircase-Escalante National Monument; K–S, Knapp and Smith model; NPV, Non-photosynthetic vegetation; P–J, Pinyon–juniper; PRISM, Parameter-elevation Regressions on Independent Slopes Model; PV, Photosynthetic vegetation; ReGAP, Regional Gap Analysis Program.

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C fluxes (Geesing et al., 2000; Hughes et al., 2006; McCulley et al., 2004; Scott et al., 2006).

Understanding the factors governing the net C uptake in dryland ecosystems is central to quantifying the C budget of a region. NPP can be rapidly estimated over large geographic areas using remote sensing-based production efficiency models (C. Huang et al., 2010; N. Huang et al., 2010; Ruimy et al., 1999). The foundation of these models is:

$$\mathrm{NPP} = \mathrm{APAR} \times \varepsilon \quad (1)$$

where APAR is absorbed photosynthetically active radiation ($\mathrm{MJ\,yr^{-1}\,m^{-2}}$) and ε is light use efficiency of *NPP* ($\mathrm{g\,C\,yr^{-1}\,m^{-2}}$). Time-integrated APAR can be estimated from satellite time-series of the Normalized Difference Vegetation Index (NDVI), which is a metric correlated with photosynthetic activity and associated greenness (Tucker and Sellers, 1986). In most cases, the spatial resolution of this approach is coarse due to satellite sensor limitations (e.g., 250–1000 m for the Terra MODIS sensor) (Cramer et al., 1999), which is insufficient to resolve the complexity of land surfaces in arid and semi-arid mountain terrain (Hudak and Wessman, 1998). The NDVI is also very sensitive to bright soil and rock background, often leading to an underestimation of vegetation cover and greenness (van Leeuwen and Huete, 1996), which can render a model of NPP very difficult to apply in these regions.

We implemented a production efficiency model, the Carnegie Ames Stanford Approach (CASA) ecosystem model (Potter et al., 1993), to estimate NPP in pinyon–juniper (P–J) woodlands of the Colorado Plateau, the dominant dryland vegetation type in the western US (Lowry et al., 2007). Based on the limitations described above, we modified CASA to ingest fine spatial resolution (30 m) photosynthetic vegetation (PV) cover estimates from Landsat images to drive model simulations of NPP (Huang et al., 2008). This approach afforded a means to bypass the dependence on coarse spatial resolution NDVI time-series that has been employed in most previous versions of CASA (e.g., Randerson et al., 1997). In addition, the model incorporated high spatial resolution grids of long-term mean climate records and soil texture data, which are new features to CASA. The overall objective of this study was to quantify the effects of topography and historical livestock grazing on regional NPP estimates in P–J ecosystems. The specific questions we sought to answer were: (1) Which topographic factors account for spatial patterns in NPP; and (2) does long-term grazing enhance or degrade the productivity of P–J systems?

2. Methods

2.1. Site description

The study focused on P–J woodlands throughout 849,870 ha of Grand Staircase-Escalante National Monument (GSENM) (Fig. 1). The Monument is located in a remote area in southern Utah, ranging in elevation from 1168 to 2619 m (Fig. 2a). The climate of the region is temperate, semi-arid; the mean annual precipitation (MAP) and temperature of the region are 305 mm and 12.3 °C, respectively, with hot (22 °C) summers and cold (3 °C) winters (PRISM Group, Corvallis, OR). The spatial extent of P–J woodlands was determined from the southwest Regional Gap Analysis Program (ReGAP) vegetation coverage (Lowry et al., 2007). Dominant overstory plants in P–J ecosystems in GSENM are Colorado pinyon (*Pinus edulis*) and Utah juniper (*Juniperus osteosperma*) with a diverse understory community across the nine ecological site types that occur within the monument (Miller, 2009).

A relict 142 ha mesa, No Man's Mesa, located in the southwestern GSENM served as an ungrazed control landscape for our study (Fig. 1c). Due to the steep cliffs that surround this mesa, no domestic livestock grazing has taken place here since the late 1920s (Mason et al., 1967). An adjacent 261 ha non-mesa area (Deer Springs Point) was selected as the historically grazed area for comparison to No Man's Mesa. This site has been subjected to long-term managed grazing for more than a century (Harris and Asner, 2003; Wrabley, 2009). Because of the contrasting disturbance regimes, large sizes, similar topo-edaphic settings and close proximity with similar climatic conditions, these two areas afforded a unique opportunity to study the effects of managed grazing on NPP at a large scale.

2.2. Model description

We used a new formulation of the CASA model for this study (Huang et al., 2008; Huang and Asner, 2010); the framework of model is shown in Fig. 3. CASA is a production efficiency model, whose two key variables, absorbed photosynthetically active radiation and light use efficiency (Eq. (1)) can be further partitioned into five factors (Field et al., 1995) (Eq. (2)):

$$NPP = \underbrace{fPAR \times S}_{APAR} \times \underbrace{\varepsilon_{\max} \times W \times T}_{\varepsilon} \quad (2)$$

where fPAR is the fraction of incident PAR absorbed by green vegetation, *S* is the downwelling solar radiation or irradiance. Light-use efficiency in each grid cell is based upon the maximum ε ($\varepsilon_{\max}$), which is down-regulated by water (*W*) and temperature (*T*) stress. The water scalar (*W*) is a function of the ratio of estimated evapotranspiration to potential evapotranspiration, which is influenced by mean air temperature (MAT) and latitude, and precipitation and soil texture, respectively. Estimation of *T* requires the knowledge of MAT of the month that optimizes plant growth of a site by referring to vegetation greenness (the Normalized Difference Vegetation Index [NDVI], Sellers et al., 1994) time series profile. Detailed description of the functions of *W* and *T* can be found in Field et al. (1995). In the following two sections, we provide descriptions of input data for CASA, which is summarized in Table 1.

2.3. Model parameter acquisition-fPAR

Conventionally, CASA estimates fPAR using time-series NDVI derived from a high temporal but coarse spatial resolution sensors, such as Terra/Aqua MODIS. Asner et al. (2005, 2006) demonstrated that PV fractions (Fig. 1a) derived from Landsat pixels were highly correlated to gap fraction (GAP) (Campbell and Norman, 1998) (Eq. (3)), which can be used to estimate fPAR through time in evergreen vegetation (Huang et al., 2009; C. Huang et al., 2010; N. Huang et al., 2010).

$$\mathrm{fPAR} = 1 - \mathrm{GAP} \quad (3)$$

A model for estimating GAP from remotely sensed PV of forests was provided by Asner et al. (2005). Here, we adjusted the original model for P–J woodlands on the Colorado Plateau by referring to Grier et al. (1992):

$$\mathrm{GAP} = 0.93 - 0.53 \ \ \mathrm{PV} \quad (4)$$

To our knowledge, Grier et al. (1992) was the only published study providing detailed information on the cover fractions of different life-forms (woody and herbaceous plants), non-photosynthetic vegetation (NPV), and productivity at different successional stages in P–J woodlands. To obtain contemporary PV cover for GSENM, two Landsat Enhanced Thematic Mapper Plus (ETM+) images were acquired on 18 May and 12 June of 2002 (Worldwide Reference System: P38R34 and P37R34, respectively) to cover the entire study site. The images were acquired during the dry period of the region and PV cover would be relatively stable

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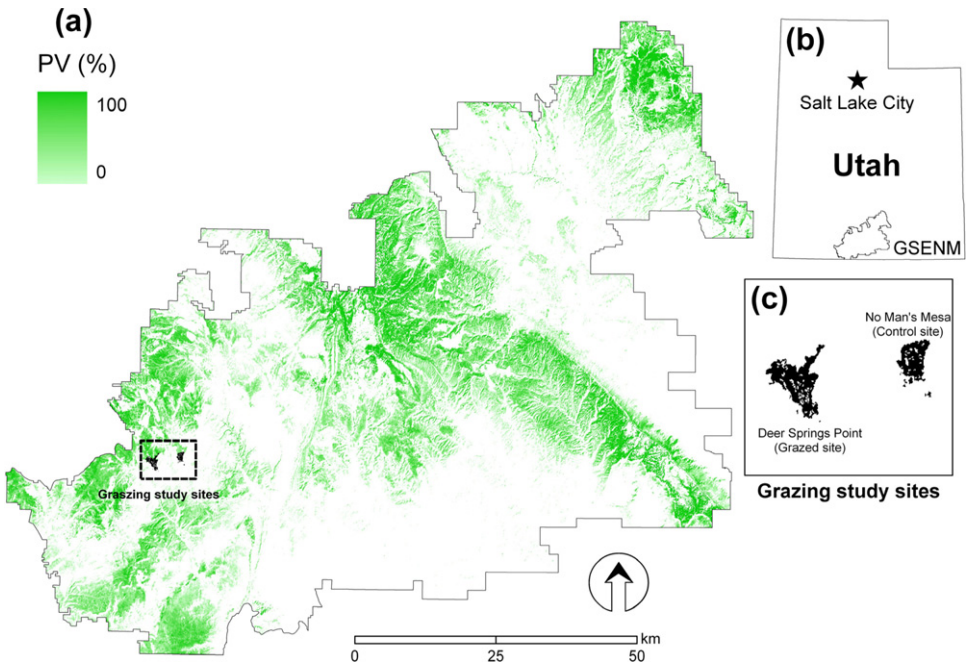


Fig. 1. (a) The study site, Grand Staircase-Escalante National Monument (GSENM), (b) its location and (c) a close-up look of grazing study sites. The background is photosynthetic vegetation (PV) fraction of the pinyon–juniper vegetation derived from two Landsat Enhanced Thematic Mapper plus images (the Worldwide Reference Systems: P38R34 and P37R34) acquired in 2002 (May 18 for P38R34 and June 12 for P37R34).

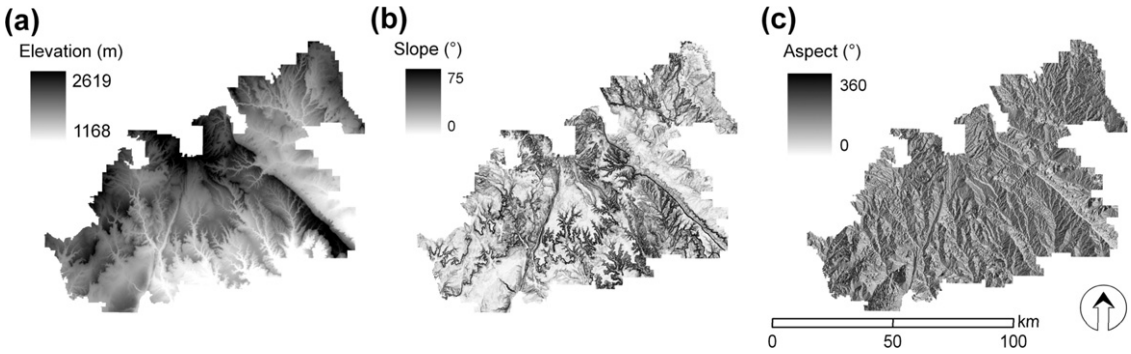


Fig. 2. Topographical characteristics of the Grand Staircase-Escalante National Monument: (a) Elevation, (b) slope and (c) aspect.

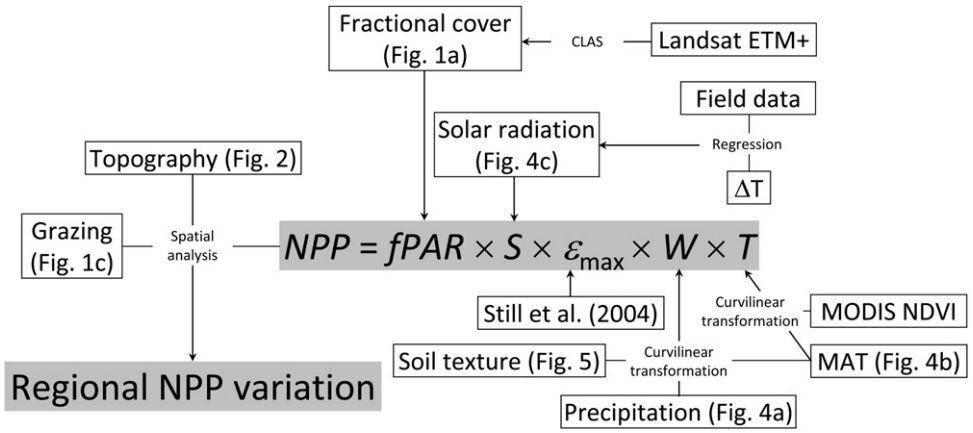


Fig. 3. Framework (with indexes of illustrations) of the new spatially explicit CASA (Carnegie-Ames-Stanford Approach) model and analyses of the study. *Abbreviations*: CLAS, Carnegie Landsat Analysis System; ETM+, Enhanced Thematic Mapper plus; fPAR, fraction of incident photosynthetically active radiation absorbed by green vegetation; MAT: mean air temperature; MODIS, The Moderate Resolution Imaging Spectroradiometer; NDVI, The Normalized Difference Vegetation Index; NPP, annual net primary production; S, solar radiation; *T*, temperature scalar; W, water availability; ΔT: difference between monthly mean maximum and minimum temperature; ε_{max}: maximum light use efficiency.

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Table 1
Information of parameters used to estimate net primary production of pinyon–juniper woodlands in the Grand Staircase-Escalante National Monument (GSENM).

Parameters (units)	Spatial		Temporal		References
	Resolution	Extent	Resolution	Extent	
Climate attributes					
Precipitation (mm)	4 km	US	Monthly	1895–2006	PRISM
Air temperature (°C)	4 km	US	Monthly	1895–2006	PRISM
Solar radiation ($W m^{-2}$)	4 km	US	Monthly	1895–2006	PRISM/CLIM-MET
Diurnal cycle	Hourly	CNP	Monthly	1998–2006	CLIM-MET
Substrate attributes					
Soil texture (%)	30 m	GSENM			SSURGO
Vegetation attributes					
Photosynthetic vegetation fraction (%)	30 m	GSENM		2002	GLOVIS
Maximum light use efficiency ($g C MJ^{-1}$)	One value	24–40°N			Still et al. (2004)

CLIM-MET, Southwest Climate Impact Meteorological Stations; CNP, Canyonlands National Park; GLOVIS, Global Visualization Viewer; PRISM, Parameter-elevation Regressions on Independent Slopes Model; SSURGO, Soil Survey Geographic Database.

through years and not be influenced by inter-annual climate variation. The Carnegie Landsat Analysis System (CLAS) (Asner et al., 2005) was used to calculate the PV images. CLAS is an automated Landsat image processing system consisting of three major components: (1) atmospheric correction to estimate surface reflectance from raw digital number using the 6S model (Vermote et al., 1997); (2) deconvolution of spectral profiles to extract sub-pixel fractional cover of PV using an automated Monte Carlo unmixing approach (Asner and Heidebrecht, 2002); and (3) cloud and water removal by referring to the Landsat thermal band. Detailed summary of the remote sensing procedures can be found in Asner et al. (2009).

2.4. Climate and substrate data

Long-term (1895–2006) MAP data were acquired from PRISM (Parameter-elevation Regressions on Independent Slopes Model) (PRISM Group, Corvallis, OR) (Fig. 4a). These 4 km resolution precipitation surfaces were generated by interpolating National Climatic Data Center (NCDC) monthly precipitation point measurements to regularly spaced grid cells. A digital elevation model (DEM) (a 5 arc minute grid) was integrated in PRISM to account for orographic effects (Daly et al., 1994). Long-term monthly MAT (°C) was acquired by averaging the mean of the minimum and maximum temperature of PRISM products. The averaging approach was validated by referring to the mean, minimum and maximum temperature records from 28 NCDC meteorological stations in the vicinity of GSENM. MAT for the maximum growing month per cell was selected by referring to the MODIS (the Moderate Resolution Imaging Spectroradiometer) NDVI time-series data (Huang et al., 2009). Monthly mean downwelling solar radiation data ($W m^{-2}$) collected by the field stations closest to the study site located in Canyonlands National Park (~90 km northeast to GSENM) were obtained from the Southwest Climate Impact Meteorological Stations (CLIM-MET, US Geological Survey). These data were spatially extrapolated to GSENM based on a relationship between solar radiation and the difference between monthly mean maximum and minimum temperature (ΔT) (Bristow and Campbell, 1984; Potter, 2004; Thornton and Running, 1999). In addition, solar diurnal cycle was also computed using the CLIM-MET field data. Maximum light use efficiency (ε_{max}) of the region was set to 0.61 by referring to Still et al. (2004). Soil texture (% sand, silt and clay), which has a direct effect on soil water availability, was obtained from SSURGO (Soil Survey Geographic Database, US Department of Agriculture) (Fig. 5). The texture data were originally in vector format, so we converted them to 30 m grids to match the Landsat image data.

2.5. Model validation

It is extremely difficult to validate modeled NPP using field data especially over a large area with rugged terrain (Clark et al., 2001; Gower et al., 1999, 2001). Therefore, a model comparison approach was taken for this study which compared CASA NPP with estimates derived from a statistical model published by Knapp and Smith (2001) (hereafter, the K–S model). This model used MAP (mm) as an independent variable to estimate annual aboveground NPP (ANPP) ($Mg C ha^{-1}$) using a linear equation. The fitness of the model (r^2) was 0.55, and can be significantly improved ($r^2 = 0.83$) after excluding data collected in temperature- and nutrient-limited arctic and alpine-tundra sites (see Knapp and Smith, 2001 for details) (Eq. (5)).

$$\text{ANPP} = 0.21 + 0.0023 \quad \text{MAP} \tag{5}$$

About 1% of pixels ($n = 18{,}000$) was randomly selected for the CASA and K–S model comparison. The sample size is sufficient for a statistically sound test (sampling error <1%) (Yamane, 1967), and the random selection procedure helps minimize spatial autocorrelation (Brus and DeGruijter, 1993; Gruijter and Braak, 1990).

We also conducted a literature review to identify field data on NPP collected in environmental settings and vegetation structures similar to those found in GSENM (Barrett et al., 2002; Esser et al., 1997; Gholz, 1982; Grier et al., 1992; Lauenroth and Sala, 1992; Turner et al., 2005). These field data were used as the third reference to assess the quality of CASA NPP estimates. The production data estimated from the K–S model and some field observations only included ANPP (Barrett et al., 2002; Gholz, 1982; Grier et al., 1992; Hui and Jackson, 2006; Lauenroth and Sala, 1992). Therefore, we converted ANPP data generated from the K–S model and field observations to NPP using a NPP:ANPP ratio of 1.75. This number was the average of NPP:ANPP ratios based on field data from 52 sites in the similar climate to our study site from a worldwide NPP database (Esser et al., 1997).

2.6. Influences of topography and long-term grazing on NPP

Relationships between the CASA NPP values and topography (elevation, slope and aspect) were investigated to understand its role in influencing the spatial arrangement of NPP in P–J ecosystems of the Colorado Plateau. Only 1% of randomly selected pixels were used to minimize spatial autocorrelation. Elevation data were acquired from a 30 m DEM that was originally used to ortho-rectify the Landsat ETM+ images for this study. Thus, the geo-registrations for the CASA NPP and DEM were seamlessly matched. Slope and aspect (both in θ°) were computed from the DEM. Two additional transformed slope metrics – normalized slope (slope/maximum slope) and percent-rise slope ($\tan\theta^\circ \times 100$) – were also evaluated. Aspect was not directly used because this is not an incremental metric (e.g., 0° was more similar to 350° [both north-facing] than 90° [east-facing]). Hence, *aspect* was transformed trigonometrically to south-facing indices: "*Southwestness*", "*southeastness*" and "*southness*" (Eqs. (6), (7) and (8), respectively) according to Franklin et al. (2000). These indices can indicate the dryness of an

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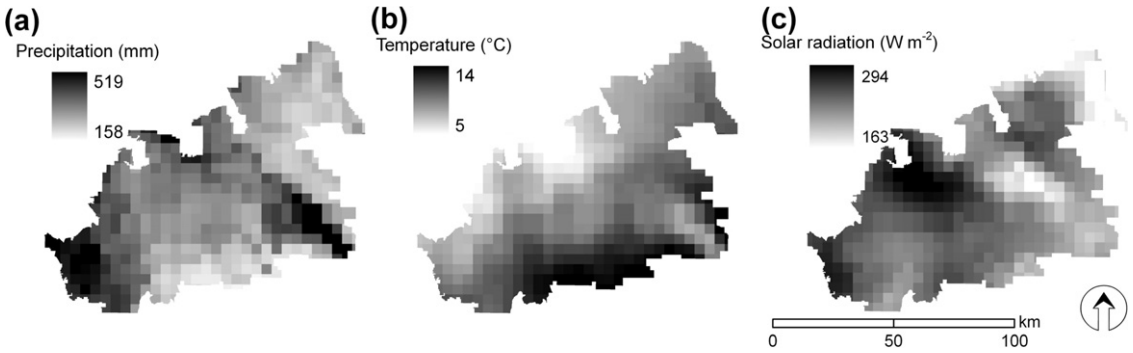


Fig. 4. Long-term average (1895–2006) of (a) annual precipitation, and monthly (b) temperature and (c) solar radiation in the Grand Staircase-Escalante National Monument.

environment because south-facing aspect is often dryer in the Western US, and more arid settings would yield higher values.

$$southwestness = \cos(aspect - 225^\circ) \quad (6)$$

$$southeastness = \cos(aspect - 135^\circ) \quad (7)$$

$$southness = \cos(aspect - 180^\circ) \quad (8)$$

Aspect was also re-grouped into sextiles for NPP multi-group comparison (north-facing: 0–30° and 330–360°; northeast-facing: 30–90°; southeast-facing: 90–150°; south-facing: 150–210°; southwest-facing: 210–270°; northwest-facing: 270–330°, where north is 0°/360°, east is 90°, south is 180° and west is 270°). Note that flat terrains (slope < 5°) without apparent facing were excluded from the aspect analyses. We conducted the Tukey–Kramer multiple comparison procedure to test modeled NPP difference among the aspect classes. A strict significance level of difference (α) between classes was set to 0.01 due to a large number of samples produced by remotely sensed data. The Tukey–Kramer multiple comparison utilizes the unique structure of the multiple comparisons by selecting a specific multiplier from the studentized range distributions rather than from the *t*-distributions (Ramsey and Schafer, 1997). This is a statistical method to test difference among several uneven sized groups, and the overall (family-wise) confidence interval is not as strict as the *F*-test and not as conservative as other comparison methods (e.g. Scheffé's procedure [Ramsey and Schafer, 1997]). Finally, we utilized a multiple regression model (Ramsey and Schafer, 1997) with numerical topographical variables (elevation, slope and dryness [Eqs. (6), (7) or Eq. (8)]) as independent variables to estimate NPP (the dependent variable) and to understand the overall predictability of topography to P–J woodland productivity.

The boundaries of the grazed (Deer Springs Point) and control (No Man's Mesa) sites were delineated by setting a threshold of ≥2150 m due to the high elevation of both sites (Figs. 1 and 2a). The corresponding CASA NPP data for both sites were extracted. An arbitrary set of 300 pixels controlling sampling errors to about 5% (Yamane, 1967) were randomly selected for each site and they were compared using a one-way Analysis of Variance (ANOVA). The random selection procedure applied here was developed to minimize spatial autocorrelation.

3. Results

3.1. Spatial input layers for CASA

Long-term (1895–2006) MAP in GSENM derived from PRISM was 272.3 mm, and the standard deviation was more than 20% of the mean (s.d. = 61.5 mm). Long-term monthly MAT was 10.1 (±1.6) °C (Fig. 4). The correlation between field observations of mean monthly solar radiation and ΔT was significant (positive linear relationship; $r^2 = 0.56$, $p < 0.0001$), which allowed us to estimate monthly mean (±s.d.) solar radiation for GSENM ($235.5 \pm 24.7\ W\ m^{-2}$) (Fig. 4c). Other core spatial inputs to CASA are the Landsat estimates of PV for the P–J woodlands as well as soil texture. The spatial arrangement of PV derived from Landsat was heterogeneous, with the mean PV (±s.d.) of 16.0 (±11.2)% (Fig. 1a). Fig. 5 illustrates the spatial patterns of soil texture as the percentages of sand (63.6 ± 19.8%), silt (22.2 ± 12.0%) and clay (14.2 ± 9.1%).

3.2. Regional NPP

Our modeled NPP values were weakly correlated ($r = 0.35$, $p < 0.0001$) with estimates derived from the K–S model, with an absolute deviation of $-0.3\ Mg\ C\ ha^{-1}\ yr^{-1}$ (Fig. 6). Nonetheless, the CASA data cloud encompassed the variation indicated by field-based NPP estimates, especially those collected in P–J vegetation of different successional stages (young growth = $1.9\ Mg\ C\ ha^{-1}\ yr^{-1}$; mature = $2.5\ Mg\ C\ ha^{-1}\ yr^{-1}$) (Grier et al., 1992). We calculated a regionally averaged NPP (±s.d.) for the 3577 km^2 P–J woodlands

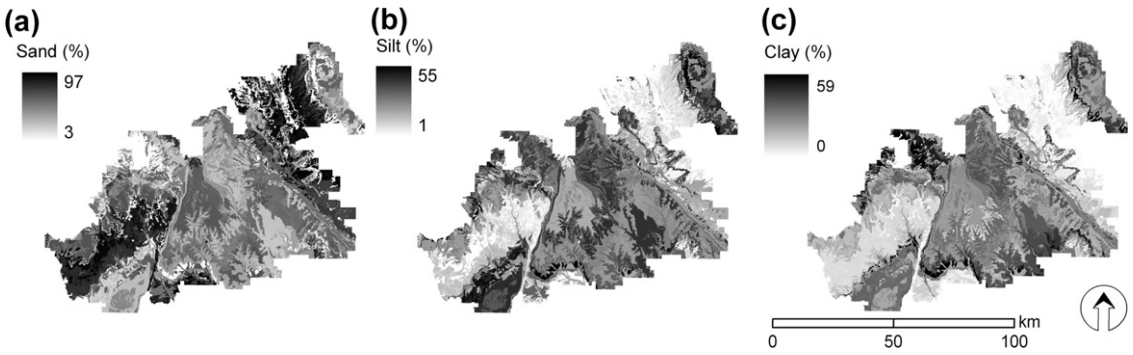


Fig. 5. Soil texture indicated as the percentages of (a) sand, (b) silt and (c) clay in Grand Staircase-Escalante National Monument from Soil Survey Geographic Database.

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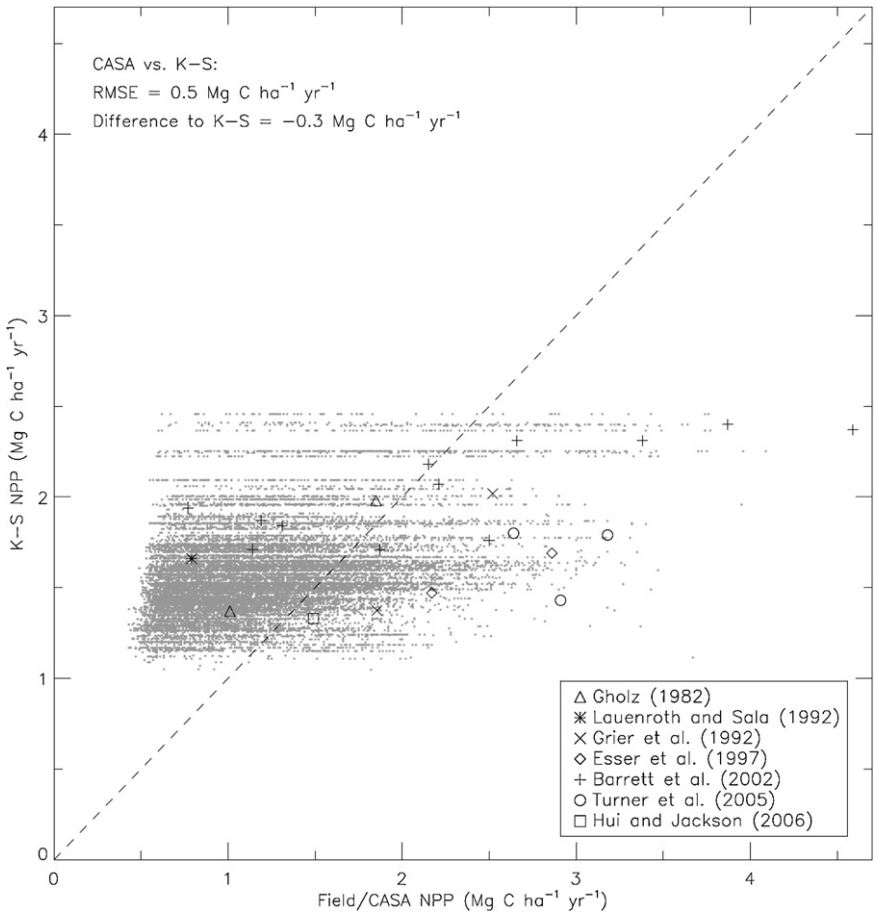


Fig. 6. Validation of the Carnegie Ames Stanford Approach (CASA) model estimated annual net primary production (NPP) by comparing to it from the Knapp and Smith (K–S) model using approximately 1% (n = 18,000) of randomly selected pixels (light colored dots). Previously published NPP field data (x-axis) from sites in similar climatic conditions to our study region (n = 23) are also shown here. The dashed line represents a 1:1 relationship.

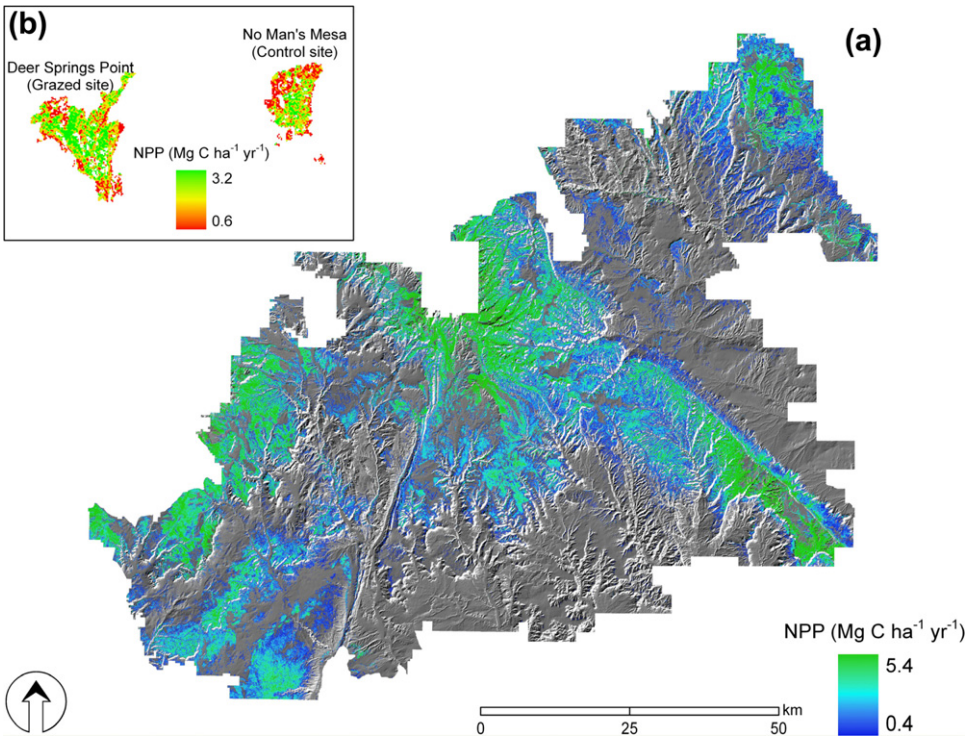


Fig. 7. (a) Annual net primary production (NPP) of the pinyon–juniper vegetation in the study site at the spatial resolution of 30 m estimated using the Landsat-based Carnegie Ames Stanford Approach (CASA) model and (b) the NPP of control and grazed sites.

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Table 2
Environmental characteristics (±standard deviation) of control (No Man's Mesa) and grazed (Deer Springs Point) sites in the Grand Staircase-Escalante National Monument (1). The soil texture data were acquired from the Soil Survey Geographic Database.

	Control site No man's mesa	Grazed site Deer springs point
Elevation (m)	2171.7 (±15.0)	2173.8 (±16.7)
Slope (°)	3.1 (±3.8)	3.9 (±3.9)
Sand (%)	73.0 (±0.1)	72.3 (±5.4)
Silt (%)	17.9 (±1.2)	17.8 (±4.3)
Clay (%)	9.1 (±1.3)	9.9 (±1.9)
Area (ha)	141.5	260.8

in GSENM of 1.2 (±0.5) Mg C ha^{-1} yr^{-1} (Fig. 7a). The spatial pattern of modeled NPP was highly variable, ranging from 0.4 to 5.4 Mg C ha^{-1} yr^{-1}. Integrating these results to the regional level, we estimated that the P–J woodlands of GSENM fix about 0.4 Tg C (1 Tg = 1 million metric tonnes) in NPP per year.

3.3. NPP and topography

Compared to other topographic attributes, elevation was the most important factor for plant growth (e.g., fPAR, $r = 0.35$, $p < 0.0001$) by explaining 20% of the variability ($p < 0.0001$) in modeled NPP, and NPP increased by approximately 0.1 g C m^{-2} per meter in elevation (Fig. 8a). However, the data pattern was erratic in upland sites (i.e., >2100 m; $r^2 = 0.05$, $p < 0.0001$) with a higher rate of increase (0.2 g C m^{-2}) per meter a.s.l. No relationships between NPP and slope and dryness indices were observed (e.g., Figs. 8b and 9a, $r^2 \leq 0.02$). As expected, differences were significant among aspect classes (one-way ANOVA F-test, $p < 0.0001$) (Fig. 9b). North-facing (15.9% of the total samples) and northwest-facing (23.8%) classes yielded the highest NPP levels, whereas southeast-facing (13.6%) and south-facing (11.4%) classes were least productive. The northeast-facing (15.8%) and southwest-facing (19.6%) classes also produced low NPP but no statistical difference to the south-facing class according to the Tukey–Kramer multiple comparison. Correlations among elevation, slope (in degrees) and an aspect-related dryness index (southeastness; yielding the highest model fitness) were not observed ($r^2 < 0.01$), which permitted the use of a multiple regression model including these three independent variables to test against modeled NPP. Predictability of the model was highest (adjusted $r^2 = 0.24$, $p < 0.0001$) relative to these three topographical models; the significance of the coefficients for elevation and slope was apparent ($p < 0.0001$) but not for the dryness ($p = 0.28$).

3.4. Grazing analysis

Referring to topography and SSURGO spatial data (Figs. 2 and 5), it is clear that topography and soil texture were very similar between No Man's Mesa (the control site) and Deer Springs Point (the grazed site) (Table 2). The random selection of 300 pixels was about 20% and 11% of the control and grazed sites, respectively. NPP estimated by CASA (mean ± s.d.) at the site with long-term grazing was 1.6 ± 0.4 Mg C ha^{-1} yr^{-1}, which was significantly higher than the control site (1.4 ± 0.4 Mg C ha^{-1} yr^{-1}) (one-way ANOVA F-test, $p < 0.0001$). Note that the spatial pattern of modeled NPP in the grazed site was relatively more homogenous than in the ungrazed site based upon the visual investigation (Fig. 7b). NPP values were either high (>2 Mg C ha^{-1} yr^{-1}) in the core area or low (<1 Mg C ha^{-1} yr^{-1}) around the edge. The center of No Man's Mesa also yielded high NPP values. However, the proportion of mixture area containing both high and low NPP pixels was slightly greater in this grazing control site.

4. Discussion

4.1. Regional NPP

This is the first regional-scale, spatially explicit assessment of NPP using CASA integrated with high resolution Landsat fractional PV cover and spatial layers of topography, climate and edaphic characteristics. Our modeled NPP generally agreed but was moderately lower than that derived from the K–S model (Fig. 6). These differences could result from several factors. First, the deviation between estimates from CASA and K–S models could be exaggerated due to the difference of spatial resolutions (30 m for CASA vs. 4000 m for K–S). Second, the K–S NPP estimate is directly linked to a constant NPP:ANPP ratio based upon previously reported field data (Esser et al., 1997). However, the partitioning of NPP could vary across landscapes (s.d. of NPP:ANPP ratios = 0.4; Esser et al., 1997) and would be strongly influenced by topo-edaphic characteristics and disturbance (Pucheta et al., 2004; Tateno et al., 2004). Unfortunately, the information for belowground NPP variation is very difficult to obtain. Finally, the relationships between ANPP and MAP would be altered due to the dominance of different life forms (a linear relationship in woodlands and a curvilinear relationship in grasslands) (Knapp et al., 2008); uncertainties that cannot be resolved using the K–S model. Nevertheless, the data cloud produced by the model comparison (Fig. 6) generally covered the range of field measurements. Undoubtedly, the model validation scheme would be more robust if there were spatially resolved field data readily available since that the comparisons may not demonstrate that the additional MAP unrelated factors (see K–S NPP vs. field NPP in Fig. 6) can be explained by CASA. However, it is very difficult to collect adequate NPP data to validate modeled outcomes at the regional scale (Clark et al., 2001; Gower et al., 1999, 2001) especially in topographically diverse terrains (Belcher et al., 2008).

The P–J woodlands of GSENM represent about 3.2% of total P–J vegetation found on the Colorado Plateau (Lowry et al., 2007). Extrapolating our NPP estimates to this larger scale, we estimate that NPP of P–J woodlands on the Colorado Plateau is roughly 13.9 Tg C yr^{-1}. This value would represent approximately 37% of all P–J systems in the US (West, 1999), and about 5% of the total estimated NPP of the 11 western states of the contiguous US estimated using the K–S model.

4.2. NPP and topography: elevation

Topography is a key element influencing NPP, not necessarily in a direct manner, but via co-varying climate factors. Topography can significantly affect spatial variations of climate regionally and soil water movement and substrate properties locally (Briggs and Knapp, 1995; Chen et al., 2007; Conant et al., 1998), which are key regulators to NPP (Chapin et al., 2002). In addition, topography can influence disturbance regimes such as fire frequency and severity (Turner and Romme, 1994) and wind exposure (Burke et al., 1989), which may also create heterogeneous NPP patterns across landscape (Briggs and Knapp, 1995). Topographic effects were validated by this large-scale modeling study, which indicates that 24% of NPP variation can be explained by the topographical factors, especially elevation (Fig. 8a).

NPP generally increases with elevation in arid and semi-arid regions of the West in lower to mid elevation ranges (1000–2400 m), which is mainly governed by water-limitation to NPP (Fritts, 1974; Jobbágy et al., 2002; Whittaker and Niering, 1975). A linear positive trend was best to depict the relationship between elevation and NPP (Fig. 8a). An orographic effect plays a role in this topographically diverse region as a consequence of more precipitation at higher elevations (Daly et al., 1994). A similar trend was also found in a mountain range in Sonoran Desert

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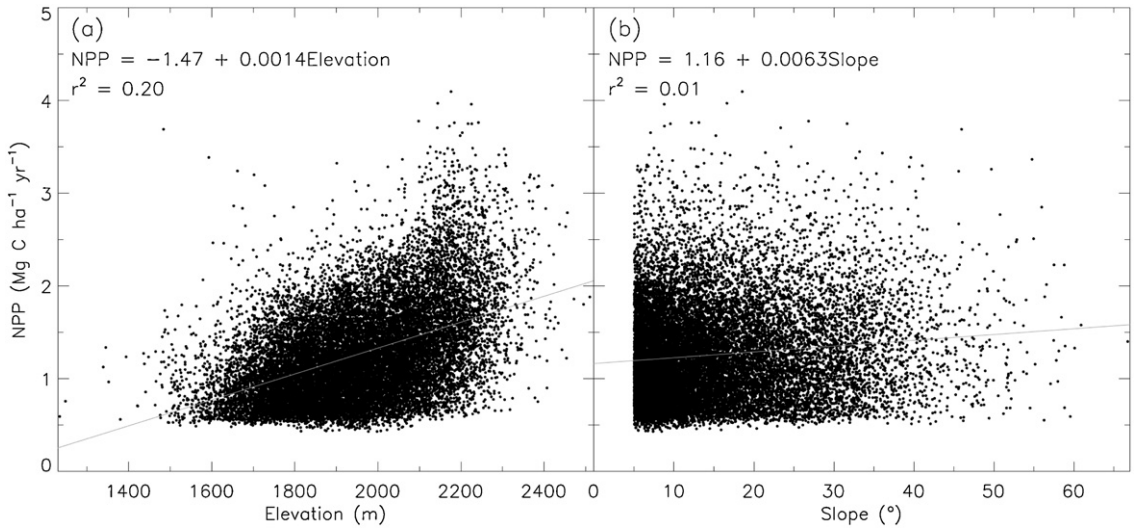


Fig. 8. The relationship between modeled annual net primary production (NPP) and (a) elevation and (b) slope using approximately 1% (n = 18,000) of randomly selected pixels in the Grand Staircase-Escalante National Monument.

(Whittaker and Niering, 1975), but it is in contrast to other ecosystems such as temperate montane (Hansen et al., 2000) and tropical forest (Schuur, 2003) ecosystems, where temperature is the predominant factor affecting NPP. This demonstrates that bioclimatic factors to ecosystem productivity can be regulated by topography and the influences may be different from region to region. This is pivotal when studying NPP spatial variation at the continental or global scales.

4.3. NPP and topography: slope

The relationships between CASA NPP and slope were poor regardless of slope at different scales after data transformations. The complex interactions between slope and NPP may be due to two factors. First, in some cases, a setting with steeper slope may imply higher elevation receiving more MAP (and vice versa). On the other hand, steeper slopes may generate higher water runoff in soils that tend to be shallower resulting in lower plant available water (Le Houérou, 1984). Additionally, the mortality of trees may be higher on hillslopes due to stressed physical conditions (e.g., shallow soils, high soil moisture variation and pronounced soil erosivity) (Greenwood and Weisberg, 2008; McAuliffe, 1994). Hence, these contrasting factors would obscure the relationships between NPP and slope variables. In addition, these might also explain the erroneous pattern of NPP-elevation relation at higher elevation (Fig. 8a).

Another terrain-related issue is the relationship between slope and NPP: slope may introduce uncertainty to the Landsat-based PV cover estimation, which is closely related to fPAR (Eqs. (3) and (4)). On steep slopes, Landsat ETM+ may view not only the projected cover but a small portion of the canopy profile. Therefore, the PV value in hilly terrain is likely to be slightly higher than the same amount of vegetation on a flat surface. Unfortunately, this is inevitable for two-dimensional (2-D) optical remote sensing applications. One possible solution would be to integrate Landsat spectral information with air- or spaceborne light detecting and ranging (LiDAR) that quantifies vegetation height (Asner et al., 2010). This data fusion approach would provide a 3-D perspective of vegetation and terrain and might tease out the slope-induced PV variation.

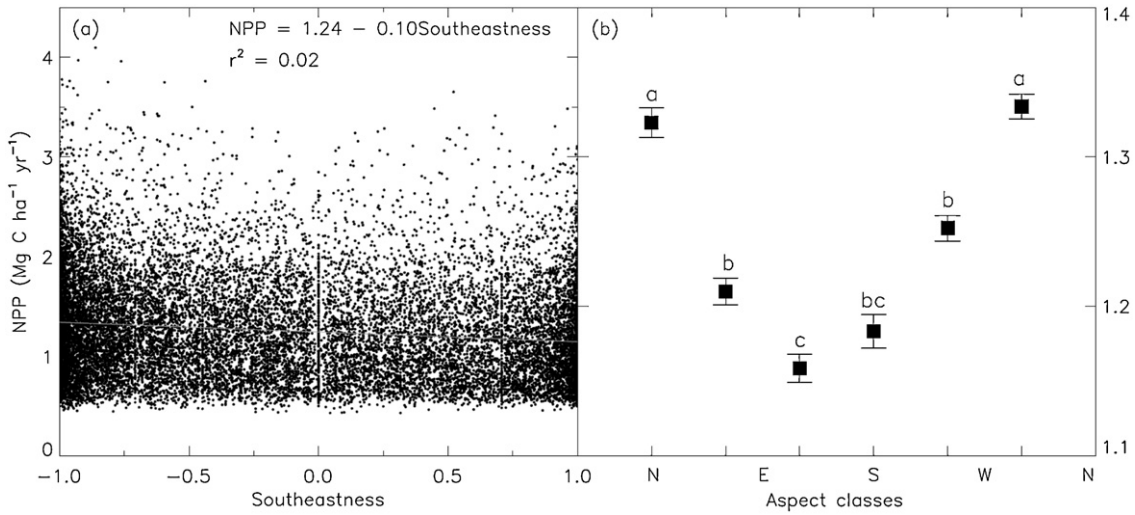


Fig. 9. (a) The relationship between southeastness and modeled annual net primary production (NPP). (b) The Tukey–Kramer multiple comparison of mean NPP in six aspect groups (referring to the x-axis for orientations). Different letters indicate significant differences between groups based upon a significance level (α) of 0.01.

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4.4. NPP and topography: aspect

We computed the dryness indices (Eqs. (6)–(8)) and classified azimuths (a sextile) to indicate the variations of aspect. The dryness index southwestness was a significant variable to predict shrub species distributions or vegetation classes in semi-arid shrublands of southern California (Franklin, 2002; Miller and Franklin, 2002). Nevertheless, it failed ($p = 0.73$) to model the variations of NPP in P–J woodlands in GSENM of the Colorado Plateau region. In fact, P–J woodlands in southwest-facing aspect did not produce the lowest of NPP (Fig. 9b). Two other dryness indices (southeastness and southness) were merely explaining about 1–2% of NPP variations (Fig. 9a). The outcome suggests that environmental dryness based on azimuths may vary locally, and/or dryness indices may not be sensitive enough to delineate the variations of NPP in P–J woodlands of the Colorado Plateau.

A distinct pattern of NPP relative to azimuth was observed on a general nominal classification scheme (Fig. 9b). Overall, P–J woodlands on the north and northwest-facing classes produced the highest level of NPP, which were in contrast to the south-facing ones. Aspect has direct and indirect influences to solar radiation, surface temperature, evaporation, soil moisture and precipitation of an area. Field ecologists have long recognized that north-facing aspects would generate wetter and cooler micro-climate locally in the Northern Hemisphere (Whittaker, 1956, 1960). In contrast, south-facing aspects form harsh environments for plant communities with drier and hotter climate (Haase, 1970). The effect of this prevailing topographic factor is also clearly revealed in this study, which would have pronounced influence to the spatial dynamics of net C uptake in P–J systems.

4.5. Long-term grazing

Managed grazing practices could significantly alter drylands through desertification (defined as decrease of grass cover and/or increase of bare soil surface or shrub cover [Schlesinger et al., 1990]), or woody encroachment depending on the aridity of environments (Archer et al., 2001). A very high spatial resolution study integrating field and remote sensing observations by Harris et al. (2003) was conducted in the same grazed and control sites in GSENM. It revealed that woody cover has increased in both sites. However, Deer Springs Point (the grazed site) produced significantly higher level of remote sensing PV estimates. Although grass was less abundant in the grazed site according to the field records, the apparent trend of shrub proliferation was observed. They concluded that managed grazing had reduced grass cover, and induced shrub encroachment and thickening in these sites. Overall, green vegetation cover increased in the grazed site, which was not observed in the tree overstory (Barger et al., 2009; Guenther et al., 2004; Harris et al., 2003). Therefore, two grazing induced "syndromes" (Asner et al., 2004): Desertification and woody proliferation may be observed in the selected sites (Guenther et al., 2004).

Following the previous studies, we found that modeled NPP at Deer Springs Point (the grazed site) was significantly higher than that of No Man's Mesa (the control site) with lower spatial variation (Fig. 7b) after controlling topo-edaphic variables (Table 2) and bioclimatic conditions. The additional NPP of the grazed site might be contributed from shrub growth in the understory or inter-canopy spaces (Guenther et al., 2004; Harris et al., 2003). Synthesis of the findings from this study and the previous research efforts may facilitate the understanding of C dynamics of the P–J systems revealing evidence of managed grazing evoking woody encroachment and generating a homogenous woody species dominated landscape (Fig. 7b). These phenomena may amplify woody abundance and NPP subsequently in the systems. This information is crucial for understanding the global terrestrial C cycle since the majority of world's drylands are grazed by livestock (Asner and Archer, 2009).

4.6. Potential for future research

This study demonstrates the feasibility of utilizing the new version of CASA to model the productivity of P–J woodlands at high spatial resolution. Only a minimum amount of public domain spatial (vegetation cover [Landsat], climate [PRISM] and soil texture [SURRGO]) and flux (solar radiation, possibly from AmeriFlux [http://public.ornl.gov/ameriflux/] and NEON [http://www.neoninc.org/] in the future) input data with the field knowledge of the PV-GAP relationship are needed to run the model, which facilitates regional NPP studies where field data are often lacking. With the availability of seasonal cloud free Landsat images, the model may also be able to assess C net uptakes of systems of apparent phenological patterns such as desert grasslands and deciduous forests, which may imply the possibility of high resolution measuring of terrestrial ecosystem production across biomes through time at the global scale. Establishment of a simple and systematic remote sensing assessment protocol to estimate contemporary and to predict future C fluxes in response to climate changes would greatly facilitate planning and management of terrestrial C budgets.

In arid and semi-arid systems of the southwestern United States, recent projections of future climate suggest that this region will experience increasingly arid conditions (Overpeck and Udall, 2010; Seager et al., 2007). These changes may amplify perturbations such as wildfire, bark beetle infestation and drought related tree die-off (Breshears et al., 2005; C. Huang et al., 2010; N. Huang et al., 2010) that are important disturbance regimes which dramatically alter NPP across P–J woodlands of the Colorado Plateau. Integrating CASA with possible future climate scenarios (e.g., Kurz et al., 2008) would permit investigating the ramifications of climate change on this dominant dryland vegetation type of North America.

5. Conclusions

This study demonstrated the feasibility of utilizing the high spatial resolution CASA to estimate regional NPP under mean climate conditions in P–J woodlands of the Colorado Plateau by integrating fine resolution Landsat PV and substrate data, and long-term climate records. With the availability of detailed NPP information, we can explore the influences of topography and managed grazing on NPP at the regional scale. CASA-estimated NPP was generally comparable to validation data obtained from the K–S model and field observations. Our regional analysis revealed a positive relationship between elevation and NPP, which is may be explained by increasing water availability in the higher elevation areas. The relationships between slope and dryness indices and plant growth in this mountainous region were complicated, which hindered these variables from predicting the variation of NPP. Partitions of NPP based upon a general sextile grouping of aspect classes revealed that north-facing aspects produced higher NPP because of cooler and wetter climate, and vice versa. Utilization of the topographic factors – elevation, slope and a dryness index – yielded the highest predictability for modeled NPP. A comparison of NPP acquired from the grazed and ungrazed highland mesas in GSENM showed that higher NPP occurred on the grazed site. Combining the results from this study and previous research, we conclude that grazing may facilitate the proliferation of woody plants and boost net C uptake in P–J woodlands of the Colorado Plateau. The findings indicate that terrain variation and managed grazing may significantly enhance spatial heterogeneity of NPP in this dryland region.

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