Photodegradation accelerates ecosystem N cycling in a simulated California grassland

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Abstract. Photodegradation accelerates litter decay in arid grasslands where plant growth and litter decay are strongly controlled by precipitation and evapotranspiration. However, the effects of photodegradation on ecosystem C and N dynamics are not well understood. We examined the effects using an ecosystem biogeochemical model DayCent-UV with photodegradation explicitly represented and validated. The model was parameterized for a California grassland where photodegradation was documented to release CO2 from litter. The model was parameterized with an inverse modeling approach using an extensive data set of six years of daily observed carbon and water gas exchange (gross primary production, ecosystem respiration, and evapotranspiration), soil temperature, and soil moisture. DayCent-UV correctly simulated the seasonal patterns of the observed gas exchange and closely simulated the inter-annual variation in the gas exchange and biomass production rates. The simulations suggested that the inter-annual variation is driven more by actual evapotranspiration than by precipitation because a large portion of precipitation is lost as runoff during wet years. Photodegradation in DayCent-UV accelerated C and N cycling, decreasing system C and N by 9.2% and 9.5% and C and N residence times by 9.4% and 18.2%. Accelerated N cycling made a greater fraction of system N available for plants, increasing net N mineralization and plant production for a given amount of system N. Increased net N mineralization was due to decreased immobilization by microbes in the aboveground organic matter. Photodegradation did not alter the control on plant production by evapotranspiration. These results suggest that at the ecosystem level, the central effect of photodegradation is to suppress microbial activity. We conclude that photodegradation accelerates N cycling at the expense of microbes in this grassland, making it more efficient in supporting plant growth for a given amount of N in the system.

Key words: biogeochemistry; C and N cycling; DayCent; ecosystem modeling; grassland; litter decomposition; photodecay; photodegradation; solar radiation; ultraviolet radiation.

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INTRODUCTION

Plant litter decay strongly affects ecosystem carbon and nitrogen cycling, but its effects are underestimated by microbial decomposition models in arid grasslands where photodegradation may play a large role (Parton et al. 2007a, Austin 2011). Photodegradation is a process in which solar radiation, in both ultraviolet (UV) and visible ranges, degrades many compounds...
including litter (Pauli 1964, Evans et al. 1992). It may be a substantial driver of litter decay in dry grasslands that receive high doses of solar radiation in the summer when the grasses are senescing or have died and become litter (Foereid et al. 2011). Photodegradation accounted for 60% of carbon lost from aboveground litter in a semi-arid steppe of Patagonia (Austin and Vivanco 2006) and contributed more than half of dry season CO₂ loss in a California annual grassland (Rutledge et al. 2010). In such places, the effect of photodegradation on litter decay likely extends to ecosystem dynamics in ways not captured by microbial decomposition models. Photodegradation may increase litter decay in dry periods when microbial activity is low, decoupling N dynamics from precipitation (Yahdjian et al. 2006), decreasing N uptake by microbes (Brandt et al. 2007), and increasing N released from aboveground litter that can then either be taken up by grasses or be lost from the system (Parton et al. 2007a). These effects may be best examined with ecosystem models, and incorporating photodegradation into the models improves our ability to examine and predict the ecosystem dynamics of dry grasslands.

Previous works have incorporated photodegradation into an ecosystem biogeochemical model CENTURY that simulates both C and N dynamics (Moorhead and Callaghan 1994), and its daily time step version DayCent that includes a photosynthesis submodel (Chen et al. 2016). In a resulting model DayCent-UV, photodegradation is represented by two key mechanisms found in experimental studies (reviewed in King et al. 2012, Barnes et al. 2015). The first is that photodegradation directly degrades litter, including standing dead, to produce CO₂ (Kieber et al. 1999, Brandt et al. 2009, Lee et al. 2012), by acting primarily through lignin (Rozema et al. 1997, Austin and Ballare 2010, Austin et al. 2016) and causing reactions that propagate to other organic compounds (Kieber et al. 1999, George et al. 2005, Cory et al. 2010). The second is that photodegradation directly inhibits microbes, increasing microbial turnover from UV radiation damaging microbial cells (Kielbassa et al. 1997, Johnson 2003, Zenoff et al. 2006, Caldwell et al. 2007), and reducing microbial activity (Johanson et al. 1995, Hughes et al. 2003, Uselman et al. 2011, Lin et al. 2015, Adair et al. 2017). These mechanisms counteract, as direct degradation produces compounds that are more susceptible to subsequent microbial decomposition (Gallo et al. 2009, Liu et al. 2014, Wang et al. 2015, Austin et al. 2016). The mechanisms were incorporated into DayCent-UV, and the model was validated against observations from Long-Term Intersite Decomposition Experiment (LIDET) at three semi-arid sites in the western United States (Chen et al. 2016). By incorporating photodegradation, DayCent-UV was better able to simulate the patterns of mass loss seen in the LIDET data for the semi-arid sites (Chen et al. 2016).

Taken together, these mechanisms of photodegradation affect ecosystem C and N cycling in complex ways that remain unexplored (King et al. 2012, Barnes et al. 2015). Photodegradation accelerates aboveground litter decay, stimulating C loss and likely liberating more N from the litter (Chen et al. 2016). However, the fate of released N remains unknown. It likely depends on the timing of rainfall and the activities of plants and microbes. The released N may be retained in soil organic matter to fuel plant or microbial growth if periods of high photodegradation coincide with moderate rainfall that increases plant and microbial demand for N. However, the released N may be lost from the system through runoff and leaching if rainfall exceeds plant demand, or happens when plant and microbial demand is low. Ultraviolet radiation reduces microbial activity (Gehrke et al. 1995, Pancotto et al. 2003, Brandt et al. 2009), but it remains unclear whether this will slow N immobilization and enhance plant N uptake. Depending on its interactions with rainfall and plant and microbial activities, the effects of photodegradation may extend to ecosystem C and N dynamics, affecting cycling rates, residence times, and ultimately the capacity to store C and N.

California grasslands present a unique opportunity to explore the effects of photodegradation on ecosystem dynamics with DayCent-UV because of their Mediterranean climate, and the wealth of data available to parameterize the model. Unlike continental grasslands with rainfall in the spring and summer when plants are growing quickly, California grasslands experience virtually no rain in the summer months. The annual grasses of California grasslands start growth after the first rain in the fall and continue
until death in late spring when rainfall stops. This affects the relationship between rainfall and plant growth. Annual rainfall and plant production were highly related in continental grasslands of the central United States (Sala et al. 1988), but unrelated in a California grassland (Ma et al. 2007, 2016). Furthermore, aboveground biomass becomes standing dead and surface litter during the dry summer in California grasslands. The summer can last five months, exposing the standing dead and litter to high doses of solar radiation. The effects of photodegradation have been documented at a site, accounting for as much as 92% of total CO₂ released in half an hour during a summer day, and 60% of total CO₂ flux during the summer (Rutledge et al. 2010). In addition, the site has been extensively studied with the eddy covariance technique. The site has been measured for CO₂ and water fluxes in addition to soil moisture and temperature since 2001 (Xu and Baldocchi 2004, Ma et al. 2007). The studies at the site have generated tremendous amounts of data at the site for parameterizing DayCent-UV and to extrapolate the documented effects of photodegradation to the ecosystem.

In this study, we examine the effects of photodegradation on ecosystem C and N cycling in California grasslands, by extrapolating the results of Rutledge et al. (2010) to the ecosystem scale using DayCent-UV that explicitly represents photodegradation. We optimized DayCent-UV using an inverse modeling approach with extensive eddy covariance data from the California grassland site. Our objectives were to simulate the seasonal and annual variation in ecosystem fluxes of California grasslands, and to examine the effects of photodegradation on ecosystem C and N flux rates and pool sizes.

**METHODS**

DayCent-UV

The DayCent-UV model simulates the effects of photodegradation on the exchange of water, C, and nutrients among the atmosphere, soil, and plants. It is based on a version of DayCent that simulates photosynthesis and hence gross primary production (Savage et al. 2013, Chen et al. 2016) using a simplified Farquhar model of SIPNET (Aber and Federer 1992, Braswell et al. 2005). DayCent is a biogeochemical model widely used to simulate the dynamics of various ecosystems, from agricultural fields to grasslands and forests, to examine a variety of topics, including organic matter decomposition, and N cycling and ecosystem responses to climate and land-use change (Gholz et al. 2000, Parton et al. 2007b, 2015, Luo et al. 2008, Bonatti et al. 2009, Harmon et al. 2009, Savage et al. 2013). Day-Cent simulates aboveground litter decay following the traditional first-order decomposition model with five organic matter pools, and Day-Cent-UV adds modifications that represent the mechanisms of photodegradation (Fig. 1). A detailed description and validation of DayCent-UV can be found in Chen et al. (2016), and of DayCent in numerous sources (Parton et al. 1993, 1996, 1998, Del Grosso et al. 2001, 2008, Savage et al. 2013).

DayCent-UV simulates photodegradation as a function of UV (UV-A and UV-B; 280–400 nm) and total solar radiation. Studies on photodegradation historically examined the UV range only, but recent studies have found that blue–green (400–550 nm) range of photosynthetically active radiation is also involved (Brandt et al. 2009, Austin and Ballare 2010, Day et al. 2015, Austin et al. 2016). DayCent-UV assumes that UV radiation is a fixed fraction of total solar radiation at 6% based on the simulations by MODTRAN (version 5.3), a widely used radiative transfer model (Anderson et al. 2009, Berk et al. 2014). MODTRAN simulations for the California site showed that daily UV radiation was correlated with total solar radiation at $r^2$ of 0.99, assuming the atmosphere at the site can be adequately represented by the standard atmospheric profile. This assumption leads to an underestimation of variation in the fraction of UV to total solar radiation among sites since the fraction depends mainly on site location and elevation, cloud cover, total column ozone, surface albedo, and aerosols. However, the variation tends to be relatively fixed at a site at $r^2 > 0.9$ (Escobedo et al. 2011). Future modifications may be warranted for DayCent-UV to be applied across sites, to use shortwave radiation (UV and photosynthetically active radiation) or simulate UV radiation specifically.
DayCent-UV incorporates photodegradation in part by adding mechanisms of direct degradation (Chen et al. 2016). The direct degradation of litter is implemented in the model by increasing the loss of C from two aboveground litter pools (standing dead and structural litter). The rate of loss increases with more litter and solar radiation until litter completely covers the ground. The rate of loss is calculated as a linear function of the sizes of the aboveground litter pools and the amount of solar radiation that the pools absorb until the sizes of the litter pools reach a maximum (at 200 g C/m²), enough to cover ground surface. The amount of solar radiation the pools absorb decreases with shading by plant biomass and is calculated using a standard light extinction coefficient based on the amount of biomass above the litter pools. The C lost from the aboveground litter pools in the model is then either lost to the atmosphere as CO₂ or becomes more labile material, at a constant fraction. The parameters related to the direct degradation were taken from Chen et al. (2016) or were adjusted to reproduce the values of CO₂ produced under photodegradation reported for the site in Rutledge et al. (2010; 16 g C/m² of CO₂ flux from photodegradation during 2007 dry season).

DayCent-UV also incorporates inhibition of microbes under photodegradation, by increasing microbial turnover and reducing microbial decomposition. In the model, microbial turnover increases with solar radiation absorbed by aboveground litter pools that represent microbial biomass, until absorbed solar radiation reaches a maximum value when only a fraction of the microbial pool is killed (those at the surface, exposed to solar radiation). The model also reduces microbial decomposition of metabolic

Fig. 1. Diagram of DayCent-ultraviolet (UV) surface organic matter submodel. Photodegradation was implemented through modifications shown in red. Boxes represent pools, and arrows show fluxes. The numbers near the arrows are the fraction of C flow that is lost to the atmosphere as CO₂ flux. Taken from Chen et al. (2016).
litter (more labile fraction) with increasing solar radiation. Similar to increased microbial turnover, microbial decomposition is not allowed to decline beyond a specific level. The values of parameters involved were taken from Chen et al. (2016).

**California grassland site**

DayCent-UV was parameterized to simulate the ecosystem dynamics of a California grassland site with a significant amount of litter exposed to solar radiation and documented evidence of photodegradation (Rutledge et al. 2010). The site (38.4133° N, 120.9508° W; 129 m elevation) is in the foothills of Sierra Nevada, near Ione California, and has a Mediterranean climate with cool and wet winter and spring when the grasses grow, and dry and hot summer when the grasses die and soil respiration decreases (Baldocchi et al. 2004, Xu et al. 2004, Tang and Baldocchi 2005). From 1926 to 2000, annual rainfall averaged 513 mm/yr and annual air temperature averaged 16.6°C at a weather station 26 km away in Camp Pardee (Ma et al. 2016). The site is grazed, and the grasses mostly grow from November to May. The grasses are mostly C₃ annual species, dominated by *Brachypodium distachyon*, *Hypochaeris glabra*, *Trifolium dubium*, *Trifolium hirtum*, *Dichelostemma volubile*, and *Erodium botrys* (Xu and Baldocchi 2004). The soil is an Exchequer very rocky silt loam (Lithic xerorthents). Rutledge et al. (2010) reported 16 g C/m² of CO₂ flux from photodegradation during 2007 dry season at this site, almost 60% of dry season CO₂ loss from the system.

The site is a part of AmeriFlux network under the site name Vaira Ranch, and the data at the site were collected continuously since 2001 with an eddy covariance system and meteorological and soil sensors (Ma et al. 2007). Data from 2001 to 2011 were used in this study. A full description of instrumentation and measurement calculation can be found in Xu and Baldocchi (2004) and Baldocchi et al. (2004). Briefly, the eddy covariance system consisted of a sonic anemometer and an infrared gas analyzer mounted 2 m above the ground. The raw data collected were converted to half-hourly fluxes of CO₂ by applying standard corrections (spike removal and coordinate rotation), sonic temperature and high frequency loss corrections (Schotanus et al. 1986), and density correction adjustment (Webb et al. 1980). Gaps in the CO₂ flux data were filled with the simple interpolation method for small blocks, with rectangular hyperbolic light response function for larger blocks (Falge et al. 2002), and with observed relationship between CO₂ flux and soil temperature for nighttime data (Xu and Baldocchi 2004). Meteorological sensors measured photosynthetic photon flux density and shortwave solar radiation with a quantum sensor and a net radiometer mounted at 2.5 m, precipitation with a tipping-bucket rain gauge, air temperature, and relative humidity with shielded and aspirated sensors. Soil sensors measured soil temperature and volumetric water content with thermocouple and frequency-domain reflectometer probes placed at 0.02 and 0.1 m depth. The data for weather, CO₂ and water fluxes, and soil temperature and moisture were from 2001 to 2011. They were taken from the AmeriFlux network portal for the Vaira Ranch site (http://ameriflux.ornl.gov, https://doi.org/10.17190/afm/1245984).

We also used measured values of peak aboveground plant biomass and normalized difference vegetation index (NDVI) from the Vaira Ranch site for comparison with simulated plant production values. We used peak aboveground plant biomass from 2000 to 2009 for comparison with the simulated annual aboveground plant production (aboveground net primary production [NPP]). The peak plant biomass was measured as dry mass of aboveground plant clipped in July. We also used NDVI observed weekly by MODIS (data available from the U.S. Geological Survey) to compare with the observed and simulated plant production and other ecosystem variables. The NDVI data from the location of the Vaira site coordinates were used. For the comparison, we corrected the NDVI values during the growing season relative to the minimum value observed during the non-growing season of summer dry period before the start of growing season in October, by subtracting 0.35 from each of the weekly NDVI values. The corrected values were then integrated for the peak growing season by summing the weekly values from March to May.

**Model optimization**

The DayCent-UV model was first partially parameterized with reported values for the site...
taken from literature. The values taken were for soil characteristics and organic carbon content, N deposition, plant production, and CO₂ produced by photodegradation. The values for the site's soil characteristics (sand and clay fractions, bulk density, organic matter fraction, and field capacity) were taken from Xu et al. (2004) and Baldocchi et al. (2004). Soil organic carbon content was set to be ~6000 g C/m², based on a previous modeling study at the site (Grant et al. 2012). Annual N deposition data were taken from National Atmospheric Deposition Program for nearby Davis (http://nadp.sws.uiuc.edu/nadpdata/annualreq.asp?site=CA88). CO₂ produced by photodegradation (0.186 g C·m⁻²·d⁻¹ during 2007 dry season) was taken from Rutledge et al. (2010).

Other parameters in DayCent-UV critical to the simulation were optimized with an inverse modeling procedure using PEST, Model-Independent Parameter Estimation and Uncertainty Analysis software package (Doherty 2015). The PEST package is used in ground water modeling by the U.S. Geological Survey (Doherty and Hunt 2010), is open source, and is available from http://www.pesthomepage.org. It essentially repeats regression with observed data to find a combination of parameter values that best satisfies a criterion. More specifically, PEST estimates model parameters using nonlinear regression based on least-squares minimization. It iteratively runs the model while varying model parameters, and resulting model outputs are evaluated against observations using an objective function based on weighted least squared differences. The objective function is

\[ \phi(b) = (y - y'(b))^TQ(y - y'(b)), \]

where \( y \) is a vector of observations, \( y'(b) \) is a vector of DayCent-UV outputs, \( b \) is a vector of parameters used to produce \( y'(b) \), and \( Q \) is a diagonal matrix assigning weights to observations in \( y \). Superscript \( T \) denotes the matrix transpose operation. The objective function is minimized by linearizing the nonlinear relationship between model parameters and outputs, expanding current best parameter set using Taylor series, and calculating finite difference of the Jacobian matrix that describes how sensitive model outputs are to the parameter set. PEST then selects parameters that minimize the objective function using the Gauss–Marquardt–Levenberg gradient search algorithm. Detailed information on PEST can be found in Doherty (2015).

For the parameter optimization with PEST, we used eddy covariance data from 2006 to 2011 for optimization and data from 2001 to 2005 for validation. The optimization data totaled 17,528 daily values of six types shown in Table 1. We simultaneously optimized a total of 40 parameters, those that controlled photosynthesis, autotrophic respiration, response of growth to drought, decomposition and heterotrophic respiration, and soil moisture. The model performed almost equally between calibration and validation periods for daily values (Table 2), and we

<table>
<thead>
<tr>
<th>Variable</th>
<th>Calibration</th>
<th>Validation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Evapotranspiration</td>
<td>0.71</td>
<td>0.69</td>
</tr>
<tr>
<td>Gross plant production</td>
<td>0.76</td>
<td>0.83</td>
</tr>
<tr>
<td>Net ecosystem exchange</td>
<td>0.46</td>
<td>0.51</td>
</tr>
<tr>
<td>Ecosystem respiration</td>
<td>0.65</td>
<td>0.62</td>
</tr>
<tr>
<td>Soil temp. at 2 cm depth</td>
<td>0.93</td>
<td>0.93</td>
</tr>
<tr>
<td>Soil temp. at 4 cm depth</td>
<td>0.96</td>
<td>0.93</td>
</tr>
<tr>
<td>Soil water content at surface</td>
<td>0.69</td>
<td>0.75</td>
</tr>
<tr>
<td>Soil water content at 10 cm depth</td>
<td>0.71</td>
<td>0.60</td>
</tr>
</tbody>
</table>

Table 2. Coefficient of determination for comparison between variables observed and simulated by DayCent-ultraviolet optimized with PEST, for calibration (2006–2011) and validation periods (2001–2005).

Table 1. Observation data used for DayCent optimization with PEST.

<table>
<thead>
<tr>
<th>Observation group</th>
<th>N</th>
<th>Units</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Net ecosystem exchange</td>
<td>2191</td>
<td>g C·m⁻²·d⁻¹</td>
<td>Eddy covariance technique</td>
</tr>
<tr>
<td>Gross primary production</td>
<td>2191</td>
<td>g C·m⁻²·d⁻¹</td>
<td>Eddy covariance technique</td>
</tr>
<tr>
<td>Ecosystem respiration</td>
<td>2191</td>
<td>g C·m⁻²·d⁻¹</td>
<td>Eddy covariance technique</td>
</tr>
<tr>
<td>Evapotranspiration</td>
<td>2191</td>
<td>kg H₂O·m⁻²·d⁻¹</td>
<td>Eddy covariance technique</td>
</tr>
<tr>
<td>Volumetric soil water content</td>
<td>4382</td>
<td>Volumetric fraction</td>
<td>Soil reflectometer at 0.02 and 0.1 m depth</td>
</tr>
<tr>
<td>Soil temperature</td>
<td>4382</td>
<td>°C</td>
<td>Temperature probe at 0.02 and 0.1 m depth</td>
</tr>
</tbody>
</table>
combined the results for the two periods for the following analysis.

The model simulations were analyzed based on hydrological year. The growth season at the site is dictated by the pattern of rainfall typical to Mediterranean climate, and begins in the fall, extends through winter, peaks in spring, and ends in summer. Hence, the annual values were calculated on hydrological year (1 October to 31 September), not on calendar year, following previous studies at the site (Ma et al. 2007, 2012).

RESULTS

Once optimized, DayCent-UV captured the ecosystem dynamics of this grassland well. Fig. 2 shows the comparison of observed vs. simulated annual values in actual evapotranspiration (AET), gross plant production (GPP), and aboveground NPP, and ecosystem respiration from 2002 to 2011. The observed values of rainfall and AET show that rainfall varied much more than AET across hydrological years (Fig. 2A), and DayCent-UV was able to simulate this discrepancy. The observations show annual rainfall varied considerably, with maximum values of over 900 mm in 2006 and 2011, and <400 mm for 2004 and 2008. However, there was much less year-to-year variability of AET (coefficient of variation was 0.18 for AET compared to 0.43 for rainfall). The fraction of rainfall lost as AET was much larger for the dry years, ranging from 70% to 90% during the two driest years (2004 and 2008), while the fraction was <35% for the two wettest years (2006 and 2011). Actual evapotranspiration was not well correlated with annual rainfall, as demonstrated in 2006 and 2007 with large changes in rainfall (900 mm compared to 400 mm) but similar values of AET (350 mm compared to 360). The model simulated the

![Graphs A, B, C, D](https://example.com/graphs.png)

Fig. 2. Comparison of observed and simulated annual values of (A) actual evapotranspiration, (B) gross plant production (GPP), (C) aboveground plant production, and (D) ecosystem respiration from 2002 to 2011, showing that DayCent-ultraviolet captured the variation in annual values. Actual evapotranspiration (AET) is also compared against rainfall (A), and both GPP (GPP) and aboveground plant production (aboveground net primary production [NPP]) are compared against spring cumulative normalized difference vegetation index (NDVI) (B and C). Spring cumulative NDVI was calculated as the sum of weekly values of NDVI from March to May, multiplied by 200 for comparison with GPP, and by 50 for comparison with aboveground NPP.

(Fig. 2. Continued)
annual variation in AET well, with model vs. observed AET correlation at $r^2 = 0.83$.

Fig. 2B, C compares observed GPP and aboveground NPP to simulated values and to the cumulative March-to-May NDVI, showing that DayCent-UV captured the large variation in annual GPP ($r^2 = 0.72$) and aboveground NPP ($r^2 = 0.78$). The results show that, as expected, aboveground NPP was correlated with GPP, with the correlation of observed aboveground NPP with GPP equal to 0.70, while the correlation of simulated aboveground NPP with GPP was equal to 0.88. The results also show that the spring NDVI was well correlated with both simulated and observed GPP ($r^2 = 0.87$ for simulated and $r^2 = 0.90$ for observed values). These results suggest that spring NDVI can be used to estimate annual GPP.

Simulated values of ecosystem respiration (Fig. 2D) compared well with the observed values ($r^2 = 0.85$), but the model tended to overestimate ecosystem respiration on average by 157 g C m$^{-2}$ yr$^{-1}$. Simulated and observed values of annual net ecosystem exchange (NEE) were poorly correlated ($r^2 = 0.30$) because the model overestimated NEE in 2005 and underestimated in 2008 (Appendix S1: Fig. S1). The years 2005 and 2008 had the highest and lowest GPP and ecosystem respiration (Fig. 2A, D). When excluding these two years, the simulated and observed values correlated well with an $r^2 = 0.78$. Both the model results and observed data show that NEE was poorly correlated with annual changes in AET ($r^2 < 0.30$ for both model results and observed data).

Fig. 2 shows large year-to-year variation in ecosystem variables between the dry 2004 and wet 2005, and this variation was captured in the daily values simulated by DayCent-UV (Fig. 3). Across both years, observed and simulated values were well correlated at $r^2$ of 0.76 for AET, 0.86 for GPP, and 0.64 for ecosystem respiration. Fig. 3 shows that both observed and simulated values of AET, GPP, and ecosystem respiration increased during the first 60 d of the hydrological year (October and November) following the first rainfall events. The values then remained steady during the winter months (days 60–120; December and January), increased rapidly in the spring (days 120–210; February to April), and declined rapidly during late spring and early summer (days 210–270; May to June). Both observed and simulated values show that growth started earlier in the wetter 2005, as indicated by a rapid rise in AET at the beginning of the hydrological year in winter and sustained higher values of GPP through spring into early summer. Both AET and GPP values also show higher peak values and prolonged growth season for the 2005 wet year. The major model discrepancy was a tendency for the model to underestimate AET in the rapid decline phase (days 210–270; May to June), and a tendency to overestimate soil respiration after rain pulse.
Inter-annual variability of AET, GPP, above-ground NPP, and ecosystem respiration followed similar patterns (Fig. 4), suggesting that AET is a major driver of ecosystem dynamics at this site. Observed AET was highly correlated with both simulated and observed GPP ($r^2 = 0.69$ and 0.77), but annual rainfall was not as well correlated ($r^2 = 0.28$ and 0.07). Observed AET was also correlated with both simulated and observed aboveground NPP ($r^2 = 0.67$ and 0.61) and with ecosystem respiration ($r^2 = 0.62$ and 0.89). Annual rainfall was less correlated (NPP $r^2 = 0.35$ and 0.10; ecosystem respiration $r^2 = 0.52$ and 0.46). Compared to observations, the simulated ecosystem variables had consistently higher correlation with annual rainfall and mostly lower correlations with AET. These results suggest that the annual variation in ecosystem dynamics of this grassland is strongly controlled by AET, but much less so by annual rainfall, and that the model is able to simulate the dynamics reasonably well.

To extrapolate the effects of documented photodegradation to the ecosystem, we compared DayCent-UV simulations with and without photodegradation represented. Photodegradation increased ecosystem respiration and decreased the total amount of C and N held in the system (Table 3). On average, photodegradation in DayCent-UV produced 27.0 g C/m$^2$ of CO$_2$ annually, and 15.3 g C/m$^2$ of CO$_2$ during the summer dry period, comparable to 16.0 g C/m$^2$ reported in Rutledge et al. (2010). As expected, photodegradation affected surface organic matter the most (organic matters in standing dead, metabolic, structural, microbial, and slow decomposing pools; all above the surface of soil; Fig. 1), reducing the amounts of C and N in the surface organic matter. This effect also extended down to the soil, reducing the amounts of C and N in soil organic matter (SOM). In the surface organic matter, photodegradation reduced the amount of N more than C, increasing C:N, but photodegradation did not affect C:N in soil (Table 3).

Photodegradation in DayCent-UV reduced the residence times of C and N in the system, partly because it, unexpectedly, did not affect plant production (GPP and NPP) and biomass (Table 3). In this grassland, most plant biomass turns over annually, and thus has much shorter residence time than surface organic matter or SOM. Photodegradation reduced the size of surface organic matter and SOM but not plant biomass, and this shifted the fraction of system C and N held in favor of the plant pool with shorter residence time. These results suggest that photodegradation accelerates C and N cycling in the system by reducing C and N held in litter and soil. Photodegradation had a greater effect in reducing the residence time of N than of C.

Photodegradation in DayCent-UV did not affect plant growth despite reduced N in surface litter and SOM because of increased N mineralization in the surface organic matter pool (Table 3). Photodegradation reduced the amount
of N in SOM, leading to decreased N mineralization in SOM. It also reduced the amount of N in surface organic matter. Despite these reductions in the amounts of N, photodegradation did not change the fluxes and pool sizes associated with plants, including GPP, N uptake, NPP, peak biomass C and N pool sizes, tissue C:N, and autotrophic respiration. For plant N uptake to remain unchanged, N must become available through mineralization, and photodegradation indeed increased N mineralization in the surface organic matter pool. These results suggest that photodegradation allows the system to support similar plant N uptake and NPP with less total N by increasing the rate of N cycling.

Photodegradation changed the N dynamics in favor of plants, at the expense of microbial activity (Fig. 5). In DayCent-UV, plants take up N from the mineral N pool that gets replenished through mineralization of N in soil and surface organic matter pools. The mineralized N (gross N mineralization) is either immobilized by microbes, taken up by plants, or lost from the system through volatilization and leaching. Plants and microbes effectively compete for the mineralized N, and in the simulation of this grassland, plant N uptake decreased as microbes immobilized a greater fraction of mineralized N \( (P = 0.015) \). Less N immobilization resulted in a greater fraction—not absolute rate—of mineralized N available for plant N uptake that sustained the absolute rate of plant N uptake (Table 3). The sustained N uptake allowed NPP

Table 3. Average simulated values for ecological variables with and without photodegradation (PD) by system (total, microbial, plant).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Without PD</th>
<th>With PD</th>
<th>Percentage difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C</td>
<td>6076</td>
<td>5520</td>
<td>−9.2</td>
</tr>
<tr>
<td>N</td>
<td>367</td>
<td>333</td>
<td>−9.5</td>
</tr>
<tr>
<td>System C:N</td>
<td>17</td>
<td>17</td>
<td>0.1</td>
</tr>
<tr>
<td>C residence time</td>
<td>19.4</td>
<td>17.5</td>
<td>−9.4</td>
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<tr>
<td>N residence time</td>
<td>440</td>
<td>360</td>
<td>−18.2</td>
</tr>
<tr>
<td>Ecosystem respiration</td>
<td>834</td>
<td>840</td>
<td>8.0</td>
</tr>
<tr>
<td>Gross primary production (GPP)</td>
<td>794</td>
<td>807</td>
<td>1.7</td>
</tr>
<tr>
<td>Net primary production (NPP)</td>
<td>373</td>
<td>369</td>
<td>−0.9</td>
</tr>
<tr>
<td>Peak plant biomass C</td>
<td>282</td>
<td>281</td>
<td>−0.4</td>
</tr>
<tr>
<td>Peak plant biomass N</td>
<td>5.3</td>
<td>5.2</td>
<td>−0.7</td>
</tr>
<tr>
<td>Peak plant biomass C:N</td>
<td>53</td>
<td>53</td>
<td>−0.1</td>
</tr>
<tr>
<td>Microbial</td>
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<td></td>
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<tr>
<td>Surface OM net N mineralization</td>
<td>1.83</td>
<td>2.40</td>
<td>30.7</td>
</tr>
<tr>
<td>Surface OM C</td>
<td>213</td>
<td>183</td>
<td>−14.2</td>
</tr>
<tr>
<td>Surface OM N</td>
<td>7.46</td>
<td>6.01</td>
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</tr>
<tr>
<td>Surface OM C:N</td>
<td>29</td>
<td>30</td>
<td>3.3</td>
</tr>
<tr>
<td>Soil OM net N mineralization</td>
<td>5.99</td>
<td>5.36</td>
<td>−10.51</td>
</tr>
<tr>
<td>Soil C</td>
<td>5703</td>
<td>5177</td>
<td>−9.23</td>
</tr>
<tr>
<td>Soil N</td>
<td>359</td>
<td>326</td>
<td>−9.21</td>
</tr>
<tr>
<td>Soil C:N</td>
<td>16</td>
<td>16</td>
<td>0.0</td>
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<tr>
<td>N loss</td>
<td>1.89</td>
<td>2.05</td>
<td>8.42</td>
</tr>
<tr>
<td>Heterotrophic respiration</td>
<td>375</td>
<td>345</td>
<td>−7.98</td>
</tr>
<tr>
<td>Plant</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>GPP</td>
<td>804</td>
<td>818</td>
<td>1.64</td>
</tr>
<tr>
<td>Plant N uptake</td>
<td>8.56</td>
<td>8.46</td>
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<tr>
<td>Autotrophic respiration</td>
<td>476</td>
<td>485</td>
<td>1.80</td>
</tr>
<tr>
<td>Aboveground NPP</td>
<td>204</td>
<td>202</td>
<td>−0.99</td>
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<tr>
<td>Belowground NPP</td>
<td>174</td>
<td>173</td>
<td>−0.85</td>
</tr>
<tr>
<td>Peak aboveground plant C</td>
<td>147.3</td>
<td>146.4</td>
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<td>Peak aboveground plant N</td>
<td>3.096</td>
<td>3.094</td>
<td>−0.07</td>
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<tr>
<td>Peak aboveground plant C:N</td>
<td>41</td>
<td>41</td>
<td>−0.63</td>
</tr>
<tr>
<td>Peak belowground plant C</td>
<td>134.7</td>
<td>134.6</td>
<td>−0.18</td>
</tr>
<tr>
<td>Peak belowground plant N</td>
<td>2.20</td>
<td>2.18</td>
<td>−0.71</td>
</tr>
<tr>
<td>Peak belowground plant C:N</td>
<td>54</td>
<td>53</td>
<td>−0.71</td>
</tr>
</tbody>
</table>

Notes: The values are annual sum for fluxes and average for pools for hydrological year (1 October to 30 September), averaged across the 11 yr of simulation (2001–2011). Percentage difference was calculated as with/without −1. The units are g C or N m⁻² yr⁻¹ for fluxes and g C, N m⁻² for pool sizes, and years for residence times.
to remain unchanged under photodegradation. NPP can be maintained by increasing N use efficiency (NPP/N uptake), increased plant C:N, or increased investment in roots that then take up N (increased root-to-shoot ratio; increased allocation of NPP to roots). None of these processes were affected by photodegradation (Table 3). Photodegradation also did not change plant tissue C:N, and thus the C:N of dead plant material that becomes litter (Table 3), suggesting that the direct effect of photodegradation on microbes reduced N immobilization and made more N available for plant uptake.

Though photodegradation increased NPP on a system N basis, photodegradation did not change the relationship between AET and NPP (Fig. 6). The slope of the relationship between NPP on system N basis did not change with or without photodegradation (P = 0.80). This result suggests that photodegradation does not decouple ecosystem dynamics from AET.

**DISCUSSION**

Photodegradation has been hypothesized to slow the accumulation of soil organic matter and reduce the capacity of an ecosystem to immobilize and retain nutrients (Gallo et al. 2009). These hypotheses are supported by the results of this study. Photodegradation in DayCent-UV reduced the amount of C and N held in the system, shortened their residence times, decreased N immobilization, and increased N loss (Table 3). Photodegradation in DayCent-UV also increased net N mineralization in surface organic matter layer, agreeing with the observations that photodegradation decreases N immobilization (Wang et al. 2015) and that in dry systems, litter exposed to solar radiation releases N even though microbial decomposition model predicts immobilization (Parton et al. 2007). Though some of the N mineralized is lost, it also sustained plant N uptake and NPP, supporting the hypothesis that photodegradation releases litter N to fuel plant growth (King et al. 2012). These results are summarized in Fig. 7, and together they suggest that photodegradation accelerates N cycling, increasing the efficiency of the grassland to support plant growth for a given amount of N in the system.

Photodegradation leads to higher net N mineralization and thus higher plant growth for a given amount of N in the system, and this may be analogous to plant growth and N mineralization in sandy soils being higher than expected. In U.S. grasslands, soils with higher water-holding capacity tend to support greater plant growth (Sala et al. 1988). However, in dry grasslands with annual precipitation <370 mm, sandy soils with lower water-holding capacity support higher plant growth than loamy soils with higher water-holding capacity (Sala et al. 1988). The sandy soils also hold much lower soil C content compared to the loamy soils (Parton et al. 1987, Burke et al. 1989) and are less able to stabilize added litter, a key factor that controls the equilibrium soil C and N levels (Parton et al. 1987, 1994). These taken together suggest that in dry grasslands, sandy soils must have higher net N mineralization rate—on gram of soil organic matter basis—as loamy soils to support the higher plant production. This is one of the key assumptions of the DayCent model that soil texture impacts stabilization of soil organic matter, where higher sand content increases the turnover of microbial biomass and thus C loss from soil respiration (Parton et al. 1987, 1994). This assumption resulted in simulations of soil C
dynamics that match the observations from U.S. grasslands across a precipitation gradient (Sala et al. 1988). Similarly, photodegradation increases C loss and lowers equilibrium C and N pool sizes, but increases net N mineralization—on a per-gram organic matter basis—that supports higher plant N uptake and production. Thus analogous to sandy soils, photodegradation lowers the grassland’s ability to stabilize litter, but increases the efficiency of the grassland to support plant growth for a given N in soil organic matter.

This increase in efficiency may be seen in other dry grasslands and may be a feature of dry grasslands that should be included in ecosystem models. The previous modeling study by Chen et al. (2016) also found that in the short-grass steppe of Colorado, photodegradation increases the net N mineralization in the surface organic matter pool. Increased N mineralization is also seen in experimental studies (Lin et al. 2015, Wang et al. 2015). Chen et al. (2016) found that photodegradation maintains NPP with less system N as well.

However, the magnitude of the effects of photodegradation may partly depend on the climate of the California grassland. We found that photodegradation changed the dynamics of N in favor of plants at the expense of microbes, but we do not intend to imply that plants and microbes are in direct competition for N all the time, nor that photodegradation favors plants in the competition. Plants and microbes may avoid
direct competition for N in this system as N uptake and immobilization were staggered in DayCent-UV. Immobilization was primarily in the winter, while plant N uptake was in the spring (Appendix S1: Fig. S2). The consequence of the staggered immobilization and uptake was that the system lost N after the start of the growing season, and the loss increased slightly with photodegradation. During this period, plants may not have enough root biomass to take advantage of increased N availability. Photodegradation may favor plants by reducing N immobilization in the summer and thus make more N available for plant uptake for the beginning of the growing season.

The climate of Mediterranean grassland (Parton and Jackson 1989) is quite different from continental grassland (Sala et al. 1988) with the majority of the rainfall coming during the winter, while continental grasslands have most of the precipitation coming during the spring and summer months. The results from the simulated and observed AET show relatively small inter-annual changes in AET, while there were large inter-annual changes in rainfall with a large % of rainfall lost (>70–80%) as runoff during wet year and a high % of rainfall lost as AET (>70%) during dry years. Continental grasslands generally have a high correlation of AET with growing season rainfall with most of the precipitation lost as AET during the growing season (Chen et al. 2017). The annual water budget results from this study are similar to the Parton and Jackson (1989) results from California which showed large variations in the amount of rainfall lost in stream runoff and low variability in the annual water loss as AET with a low correlation of annual rainfall with annual AET.

Though the low correlation between AET and rainfall may be unique to Mediterranean grasslands, high correlation between AET and plant production is common in many other grasslands. Previous studies show that GPP and ecosystem respiration are well correlated with annual AET in this California grassland site (Ma et al. 2007, 2016). The high correlation of AET with ecosystem respiration, aboveground NPP, and GPP is also well documented in continental grasslands (Morgan et al. 2016, Chen et al. 2017, Del Grosso et al. 2018). In Australian grasslands as well, aboveground NPP is correlated with annual AET (McKeon et al. 1990, Day et al. 1993), and the GRASP model developed by McKeon et al. (1990) for predicting grassland plant production in Australia assumes that one of the major factors which control grassland plant growth is AET and transpiration. Rainfall is well correlated with annual changes and long-term average grassland aboveground NPP in the Great Plains of North America (Lauenroth and Sala 1992, Derner and Hart 2007, Chen et al. 2017), and AET is well correlated with daytime and net plant carbon uptake in a Colorado grassland (Parton et al. 2012, Morgan et al. 2016).

The model results and observed data show that annual changes in GPP and aboveground NPP are well correlated with cumulative March-to-May NDVI (Fig. 2). These results are consistent with recent studies showing that annual changes in grassland GPP and aboveground NPP are correlated with growing season NDVI (Gilmanov et al. 2005, Zhang et al. 2010, Parton et al. 2012, Hermance et al. 2015, Morgan et al. 2016, Chen et al. 2017, Del Grosso et al. 2018). Chen et al. (2017) and Hermance et al. (2015) showed that annual changes in aboveground plant production are well correlated with cumulative growing season NDVI for continental grasslands in Colorado. Del Grosso et al. (2018), Gilmanov et al. (2005), and Zhang et al. (2010) have developed models showing that NDVI is a major indicator of daily GPP. The model developed by Del Grosso et al. (2018) suggests that 70% of the daily changes in GPP are explained by NDVI followed by soil water.

The results demonstrate that DayCent-UV can correctly capture seasonal and inter-annual dynamics in ecosystem variables and can be used to evaluate the effects of photodegradation in this grassland. The model simulations suggest that photodegradation accelerates N cycling that supports greater plant growth for a given amount of N in the system. Photodegradation increased the decay rate of surface organic matter pool in DayCent-UV, releasing more N for plant uptake and growth despite increased N loss and less N in the system. Because it did not change plant growth, photodegradation did not affect the daily fluxes of GPP and evapotranspiration that are strongly if not entirely controlled by plant activity. The plant growth also sustained C inputs into surface and soil organic matter
pools. If photodegradation had indeed reduced plant growth proportionally to the reduction in the amount of N in the surface and soil organic matter pools, the grassland will have less plant biomass, less C input into the organic matter pools, and less daily fluxes of CO₂ and water between the biome and the atmosphere. This is not shown in our results because photodegradation increased the efficiency of the grassland to support greater plant growth for a given amount of N.

The results raise a question on how photodegradation affects microbial activity. The results show that photodegradation reduces N immobilization, but it is unclear how much of the reduction comes from the direct effects of reduced microbial activity or from the enhanced carbon loss from the surface organic matter that reduces carbon available for microbial activity. In a greenhouse study that manipulated litter moisture, photodegradation accelerated litter decay under drier conditions, but under wetter conditions, it instead decelerated litter decay (Smith et al. 2010). The mechanism responsible was speculated to be the reduced microbial decomposition that wetter conditions favored microbial activity that then was suppressed by photodegradation. In a meta-analysis, photodegradation increased litter biodegradability but had very little effect on remaining litter mass, suggesting that the effects of direct degradation were offset by the effects of reduced microbial decomposition (Wang et al. 2015).

**Conclusions**

In this study, we extrapolated the documented effects of photodegradation to ecosystem dynamics of a California grassland using a validated ecosystem model DayCent-UV with photodegradation explicitly represented. We showed that photodegradation reduces the capacity of the grassland to store and retain C and N but increases its ability to cycle N to support plant growth (Fig. 7). Our results suggest that photodegradation suppresses microbial activity, increases N loss, and accelerates N cycling in arid grasslands, making them more efficient in supporting plant growth for a given amount of N. Including photodegradation in ecosystem models will better capture the C and N dynamics of arid grasslands.

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**Literature Cited**


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**Supporting Information**

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2370/full