

Modeling annual grassland phenology along the central coast of California

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Abstract. Grassland phenology is an important component of terrestrial biophysical models, with substantial differences in the cycling of energy, carbon, water, and nutrient fluxes between periods of growth and dormancy. Modeling the phenology of moisture-driven annual grasslands in Mediterranean-type ecosystems (MTEs) remains challenging because although soil moisture is often a direct control on green-up, high rainfall variability during MTE wet seasons makes predicting the optimal time for senescence problematic. For this study, we developed a Mediterranean grassland phenology model (MGPM) to model green-up and senescence for coastal California annual grasslands. Mediterranean grassland phenology model was embedded in an ecohydrologic model, Regional Hydro-Ecologic Simulation System, and simulations of ecosystem fluxes were compared to a simpler fixed-date (i.e., photoperiod) phenology model. Results indicated that a soil water potential threshold was an accurate predictor of grassland green-up initiation. Annual cumulative net primary productivity (NPP_{cum}) was observed to be a good predictor of senescence initiation, with higher levels of NPP_{cum} associated with delayed senescence initiation. We also observed that photoperiod acts as an additional control on senescence initiation, restricting the window of time during which senescence may occur. Long-term peak NPP_{cum} was noted as a potential control on the timing of this photoperiod window. Inclusion of MGPM into biophysical models is expected to improve the representation of annual grasslands and more accurately simulate ecosystem fluxes.

Key words: California; grassland; green-up; model; net primary productivity; phenology; Regional Hydro-Ecologic Simulation System; senescence.

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INTRODUCTION

Vegetation phenology is a key component of terrestrial biophysical models, with the timing of green-up and senescence affecting modeled energy, carbon, water, and nutrient cycling (Richardson et al. 2013). In seasonally dry Mediterranean-type ecosystems (MTEs), phenology is primarily driven by water availability (Ma et al. 2007, Vico et al. 2015). However, modeling green-up and senescence for drought-deciduous and/or annual

vegetation types remains challenging in these ecosystems because soil moisture is frequently only a direct control on green-up. The controls on senescence, on the other hand, are more complicated because high rainfall variability during MTE wet seasons makes forecasting the optimal length of the growing season for maximizing reproduction and/or productivity unfeasible. Instead, MTE vegetation must optimize the long-term balance between senescencing too early, which limits reproduction and productivity, and

senescencing to late, which risks vegetation stress and physiological damage from low soil moisture levels (Vico et al. 2015).

In California, grasslands make up over 10% of the landscape and provide many ecosystem services such as carbon sequestration and habitat for threatened plant and animal species (Jackson et al. 2007, Stromberg et al. 2007). California grasslands are composed primarily of non-native annuals from Europe that became established in the 1800s (D'Antonio et al. 2007) and are expected to continue to expand in extent with climate change (Lenihan et al. 2008). The phenology of California grasses is moisture driven, with germination occurring shortly after the first substantial rains of the wet season, usually in fall or early winter (Slade et al. 1975, Chiariello 1989). Grass senescence occurs in the spring near the end of the wet season and coincides with reproduction (Ma et al. 2007). Both reproduction and senescence have been shown to be potentially subject to multiple influences, including temperature, rainfall amount and timing, CO₂ concentrations, and photoperiod (Slade et al. 1975, Savelle 1977, Ewing and Menke 1983*a, b*, Jackson and Roy 1986, Zavaleta et al. 2003, Cleland et al. 2006). However, given that phenology may vary by location based on species, meteorological conditions, soils, etc., there is no consensus on the relative importance of these individual controls on senescence timing.

Biophysical models are often used to estimate the responses of land surface processes and resource use to climate and land use/land cover change at watershed to global scales. Biogeochemical cycling of grasslands in these models is likely to be sensitive to how phenology is represented because of substantial differences in cycling between periods of growth and dormancy (Xu and Baldocchi 2004). Phenology timing may be modeled either statically using fixed dates that do not vary from year to year or dynamically using environmental cues to predict the dates of phenological transitions (Richardson et al. 2012, Yang et al. 2012). For the latter approach, some phenological models in seasonally dry ecosystems rely on a soil moisture threshold for green-up initiation and begin senescence once soil moisture drops below this threshold (Vico et al. 2015). Grasses in California, however, do not senesce in response to

mid-wet season droughts (Chiariello 1989), suggesting that senescence cannot be modeled using a simple soil moisture control.

Despite the importance of modeling grassland ecosystems in California, we are not aware of any models available for simulating annual grassland phenology and its impact on grassland water or carbon fluxes. Xin et al. (2015) simulated green-up for multiple North American grasslands, but excluded grasslands with an autumn green-up such as those in California. Dahlin et al. (2015) and Vico et al. (2015) developed global-scale phenology models for drought-deciduous vegetation; however, these models do not capture the nuances needed to effectively model phenology in California grasslands. For this study, our two primary research objectives were to (1) develop and evaluate a phenology model for coastal California annual grasslands which uses soil moisture availability as the primary control on green-up and net primary productivity (NPP) as the primary control on senescence, and (2) examine differences in ecosystem model fluxes using the phenology model vs. a simpler fixed-date (i.e., photoperiod) phenology model. We hypothesized that NPP, which integrates the effects of multiple controls that are known to affect senescence (e.g., radiation, temperature, water stress, CO₂), may be a good predictor of the timing of senescence initiation. The experiment was conducted using a coupled carbon and hydrologic cycling model, Regional Hydro-Ecologic Simulation System (RHESSys) combined with 14 yr of phenological data derived from the Moderate Resolution Imaging Spectroradiometer (MODIS).

STUDY SITES

Two grassland sites were selected along the central California coast, the first located to the west of the city of Santa Barbara (lat: 34.447, long: -119.941) and the second to the northeast of the city of Morro Bay (lat: 35.373, long: -120.814; Fig. 1). Both sites are located less than 5 km from the ocean and are characterized by rolling hills with elevations ranging from 35 to 110 m at the Santa Barbara site and from 20 to 160 m at the Morro Bay site. Soils at the Santa Barbara site consist of a mixture of Ayar, Diablo, and Zaca clays, while soils at Morro Bay are a mixture of Cibo clays, Diablo clays, and Los Osos loam (Soil

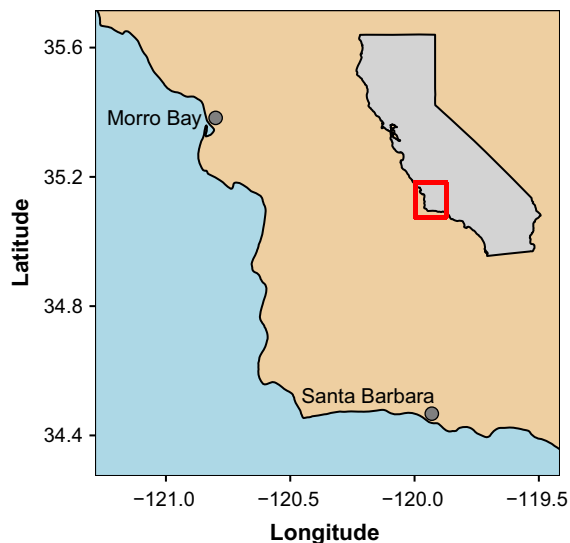


Fig. 1. Map of study locations along California central coast.

Survey Geographic database [SSURGO], <https://websoilsurvey.nrcs.usda.gov/>). A mix of non-native annual grass and forb species is dominant at both sites, including *Bromus* spp, *Avena barbata*, and *Brassica nigra*. No wildfires have been recorded at either site (Fire Resource and Assessment Program, <http://frap.fire.ca.gov/>); however, the grasslands may be subject to occasional grazing.

Water availability during Central California's winter wet season is highly variable, with annual rainfall totals varying by an order of magnitude. The timing of initial wet season rainfall events can range from October to January, and extended mid-season drought periods following germination are not uncommon (Reever Morghan et al. 2007). Most rainfall is completed by March and April, which commences the summer drought period of six or more months of no rainfall. Proximity to the ocean moderates the temperatures year-round at both sites. Foggy and overcast conditions, particularly at the beginning of the dry season during the late spring, can limit evaporative demand of the grasses.

Daily precipitation and temperature data for the two sites were acquired from NOAA's National Centers for Environmental Information (<http://ncei.noaa.gov>). For the Santa Barbara grassland site, a meteorological station located at the Santa Barbara Municipal Airport (USW00023190), 9 km east of the study site, was used. For the Morro Bay

grassland site, a nearby meteorological station in the city of Morro Bay (USC00045866; 3 km distant) was used. Gaps in the Morro Bay record were filled using a monthly regression between the Morro Bay station and a meteorological station located 16 km inland at San Luis Obispo Polytech (USC00047851).

APPROACH

Remote sensing

A remote sensing time-series of MODIS normalized difference vegetation index (NDVI) was used for the development, calibration, and validation of the phenology model. Remote sensing data have frequently been used in the development of vegetation phenology models for other ecosystems and regions (Yang et al. 2012, Dahlin et al. 2015, Xin et al. 2015, Melaas et al. 2016). Normalized difference vegetation index provides a relative measure of vegetation greenness, based on reflectance in red and near-infrared bands (Rouse et al. 1974). Vegetation green-up leads to an increase in NDVI values, while senescence results in reduced NDVI values that persist through the summer and into fall (Reed et al. 1994, Hardy and Burgan 1999, Schwartz and Reed 1999). An average NDVI value was calculated for each site for 16-d periods based on the MODIS Terra MOD13Q1 version 5 product (Huete et al. 1999). This product has a spatial resolution of 250 m, and provides 16-d composites that are corrected for directional reflectance effects and are screened for cloud, cloud shadow, and heavy aerosol scattering (Huete et al. 1999). For each site, grass cover within 250-m pixels was examined using high-resolution imagery provided by ArcGIS (ESRI, Redlands, California, USA). High-resolution imagery was acquired in 2014 and had spatial resolutions of 1 and 0.15 m for the Santa Barbara and Morro Bay sites, respectively. Moderate Resolution Imaging Spectroradiometer pixels were selected based on grass cover (visually at least 85%) and topographic position (excluding sub-pixel scale valleys). Nine pixels were selected for the Santa Barbara site and eleven pixels were selected for the Morro Bay site for the period from 2000 to 2014. For each composite date, pixel NDVI values were screened based on a quality data layer and then averaged to provide a single NDVI value for each site.

TIMESAT version 3.2 (Jönsson and Eklundh 2004) was used to calculate the green-up and senescence initiation day from the NDVI time-series for each site. The NDVI time-series was filtered using Savitzky-Golay filtering with a three-period window (Chen et al. 2004). The green-up initiation day was determined using the 20th percentile of NDVI amplitude in each year, while the senescence initiation day was determined using the 80th percentile.

RHESys

A new phenology model was incorporated into RHESys, a spatially distributed ecohydrologic model that simulates vegetation growth and watershed hydrology (Tague and Band 2004). As RHESys is under continuous development, version 5.19 was used in this study. Regional Hydro-Ecologic Simulation System couples daily carbon, water, and nutrient fluxes, with most canopy processes represented at the patch (highest resolution) scale. Patches are typically defined as 30-m grids. Incoming radiation is computed as a function of location, terrain, and atmospheric variables and radiation absorption and transmission is tracked through each leaf layer to the surface. Net primary productivity is calculated as the difference between daily carbon assimilation through photosynthesis and daily respiration. Photosynthesis is computed using the Farquhar model (Farquhar and von Caemmerer 1982), which replicates a C3 grass, and respiration is computed following Ryan (1991). Daily net photosynthate is allocated to leaves, roots, and storage for the following year using a fixed partitioning strategy (Thornton 1998). Regional Hydro-Ecologic Simulation System does not model the growth of individual grass species but rather a representative grass functional type. As such, the model is unable to capture year-to-year differences in species composition. Parameters for the grass function type were based on RHESys parameter libraries.

Vertical moisture fluxes include interception, infiltration, and drainage through the rooting zone and unsaturated layer to a local water table. Aerodynamic conductance is calculated using a model developed by Haddeland and Lettenmaier (1995), while canopy interception is computed as a function of vegetation type and vegetation size. Canopy, surface, and litter fluxes

to the atmosphere are modeled using Penman-Monteith (1965).

Previous versions of RHESys have relied on a fixed-date model or utilized the Growing Season Index (GSI) approach (Jolly et al. 2005). The GSI approach uses running averages of temperature, day length, and vapor pressure deficit (VPD) as controls on green-up and senescence. In this study, we modified the GSI approach, retaining the temperature and VPD controls, but disabling the day length control since vegetation green-up occurs during the fall and winter, rendering the control ineffective. Although temperature and VPD controls were retained, they had little impact on the results of this study. The day length control was replaced with the Mediterranean grassland phenology model (MGPM) described below.

Mediterranean grassland phenology model

The MGPM is composed of two sub-modules; the first determines the timing of green-up and the second determines the timing of senescence (Fig. 2). Green-up is initiated in response to an increase in soil moisture within the rooting zone. This is modeled as an increase (i.e., less negative) in soil water potential (ψ_{soil}) above a wetness threshold (ψ_{thr}). Soil water potential in RHESys is calculated as a function of the percent saturation (S) within the rooting zone,

$$\psi_{\text{soil}} = \min[\psi_{\text{open}}, -0.01\phi_{\text{ae}}(S^{-p})] \quad (1)$$

where ψ_{soil} is the predawn soil water potential (MPa), ψ_{open} is the soil water potential at which stomata fully open, ϕ_{ae} is the soil air-entry pressure, and p is the pore size index (Clapp and Hornberger 1978). Green-up is triggered when a 15-d running average of ψ_{soil} exceeds a ψ_{thr} of 1.0 MPa.

Green-up initiation is followed by a period when stored carbon is expressed to initialize leaves and roots. The length of this green-up period was fixed in the model at 15 d. The total amount of carbon expressed during the green-up period reflects the carbon stored in grass seed pools. We discuss estimates of seed pool carbon in the next section. We assume a decreasing proportion of this total stored carbon is expressed as the green-up period progresses. Thus, the amount of carbon expressed at each time-step is

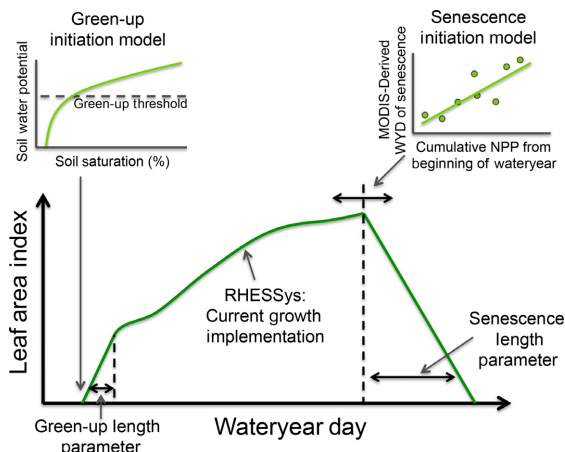


Fig. 2. Conceptual model for Mediterranean grassland phenology model. WYD, wateryear day.

based on a fixed percent reduction of the amount transferred at the previous time-step,

$$C_{\text{tran}} = \frac{2 \times C_s}{L - t + 1} \quad (2)$$

where C_{tran} is the amount of carbon transferred at time t , C_s is the amount of stored carbon available for expression at time t , L is the total length of carbon transfer (days), and t is the current time-step. Following expression of grass carbon stores, grass growth dynamics during the active growth phase (period of time between green-up and senescence) are based on the current growth (NPP and allocation) sub-models within RHESSys.

The day of senescence initiation is related to the net productivity of the grasses, with years of higher productivity during the wet season producing a later senescence than years of lower productivity. The threshold wateryear day (WYD) for senescence initiation (SEN_{thr}) was modeled as a function of NPP accumulated from the beginning of the wateryear (NPP_{cum}),

$$\text{SEN}_{\text{thr}} = a \times \text{NPP}_{\text{cum}} + b \quad (3)$$

where a and b are parameters derived from calibration using remote sensing data (see *Model calibration, cross-validation, and simulation*). Senescence is triggered when the WYD is equal to or greater than SEN_{thr} ; otherwise, the grasses remain in an active growing phase. This differs from the use of

NPP by Jolly and Running (2004), who predicted senescence when 7-d trends of NPP and soil moisture were negative. Upon senescence initiation, carbon in the leaves and roots is transferred to litter pools based on the carbon transfer model in Eq. 2. Exploratory analysis of phenology patterns in the remote sensing data found that the length of senescence was not related to any predictor variables. Consequently, the carbon transfer length parameter, L , was fixed at the mean difference between the MODIS-derived senescence start and end day.

Model calibration, cross-validation, and simulation

For each study site, RHESSys was run as a single patch under the assumption of no lateral moisture fluxes into the patch. Annual grasses produce more seeds in a given year than are necessary for reproduction in the following year, leading to a buildup of seed banks over time in the absence of disturbance (e.g., fire; Young and Evans 1989). Regional Hydro-Ecologic Simulation System does not have an explicit reproduction module although a proportion of daily NPP (NPP_{nsc}) is allocated to a non-structural carbohydrate pool that would ultimately reflect carbon reserved for seed production. The remaining daily NPP is expressed as shoot and root carbon. For this paper, carbon and nitrogen stores were reset at the beginning of each wateryear (1 October) to the same initial values. This resetting of the carbon stores in the model is equivalent to assuming that the same number of seeds germinates each year. Initial carbon store values were selected manually in order to provide a reasonable range of leaf area indexes (~1–2; Xu and Baldocchi 2004) and rooting depths (~30 cm; Holmes and Rice 1996) during the growing season. Future work will expand the RHESSys carbon cycling model to include allocation and turnover of seed pools.

The phenology model was calibrated using a Monte Carlo simulation for parameters that were expected to directly affect soil water potential or NPP. These parameters included soil air-entry pressure (ϕ_{ae}), pore size index (p), percent of rainfall that bypasses the soil matrix to a deeper groundwater store, and proportion of NPP allocated to new daily growth (NPP_{gwth}). 5000 parameter sets were selected and calibrated over a 14-yr period from wateryear 2001 though 2014. In addition, for each wateryear, the model was

run with senescence inhibited in order to compute NPP for each day of a possible growing season. Other controls on NPP, such as specific leaf area, carbon–nitrogen ratios, and relative proportion of NPP allocated to roots vs. shoots, were derived from White et al. (2000).

Each calibrated parameter set was evaluated using a two-step process. First, the modeled green-up initiation day was compared to the MODIS-derived green-up initiation day using root-mean-square error (RMSE). All parameter sets with an RMSE value <125% of the lowest RMSE value were considered behavioral and included in the second part of model evaluation, the fit of senescence initiation. Since the calibration model was run with senescence inhibited, a linear regression was developed between the WYD of MODIS-derived senescence initiation and the modeled value of NPP_{cum} on the same day in order to estimate parameters a and b in Eq. 3. The parameter set associated with the highest coefficient of determination (R^2) for the relation was selected as the top parameter set for modeling grassland phenology.

A leave-one-out cross-validation approach was used to provide an estimate of how well the model predicts grassland phenology and to guard against over-parameterization (Kohavi 1995). Leave-one-out cross-validation was implemented by removing one of the 14 yr of remote sensing data from calibration. The remaining year was used for validating the top calibrated model. This procedure was then repeated for all years. The cross-validation approach is feasible with the modeling framework in this study because initial storage conditions are reset each year, eliminating annual temporal autocorrelation between carbon and hydrologic stores. Unlike during calibration, the senescence model was not inhibited during validation. The fit of model predictions to each of the 14 individual validation years was evaluated collectively using RMSE for both green-up and senescence. Fit using MGPM was compared to that of a simpler fixed-date phenology model. This fixed-date phenology model was based on the mean green-up and senescence initiation day from each calibration group.

Simulations in RHESSys using the MGPM and the fixed-date phenology model were conducted to evaluate differences in two ecosystem fluxes, annual evapotranspiration (ET) and annual NPP.

The simulations incorporated a 50-yr record (wateryears 1945–1994) for Santa Barbara and a 30-yr record (wateryears 1960–1989) for Morro Bay.

RESULTS

The remote sensing time-series of NDVI confirms that green-up in California grasslands is highly variable from year to year, with most green-up initiation dates spread over a ~100-d period stretching from the beginning of October through early January (Fig. 3). For the extremely dry wateryear of 2014, green-up was delayed until February at both sites. On average, green-up occurs about five days earlier in Santa Barbara (WYD 67, 6 December) than at Morro Bay (WYD 72, 11 December). Following green-up, NDVI increases at a variable rate throughout the vegetation growth phase, peaking shortly before senescence initiation. Senescence, however, is not triggered during this phase, despite the presence of mid-season droughts that produce periods of negative NPP (Fig. 3).

Senescence initiation is less variable than green-up initiation, extending over a 52-d period from the beginning of April to the end of May (Fig. 3). The mean senescence initiation day occurs on WYD 213 (1 May) for Santa Barbara and on WYD 214 (2 May) for Morro Bay. The mean length of senescence for Santa Barbara is 51 d compared to 46 d for Morro Bay, while the mean date for the end of senescence is WYD 264 (21 June) for Santa Barbara and WYD 260 (17 June) for Morro Bay.

The calibration results for MGPM are presented in Table 1. The model captured green-up initiation similarly for both study sites, with a RMSE of 22.09 for Santa Barbara and 19.93 for Morro Bay. The relation between the MODIS-derived and modeled green-up initiation day shows that MGPM captured much of the inter-annual variability in green-up initiation (Fig. 4). The modeled green-up initiation day was generally delayed compared to the MODIS-derived green-up initiation day, particularly when green-up initiation occurred before WYD 75. This delay, or bias, in the modeling of green-up initiation accounts for approximately a third of the calibration RMSE values and may be related to the 15-d running average for soil moisture potential.

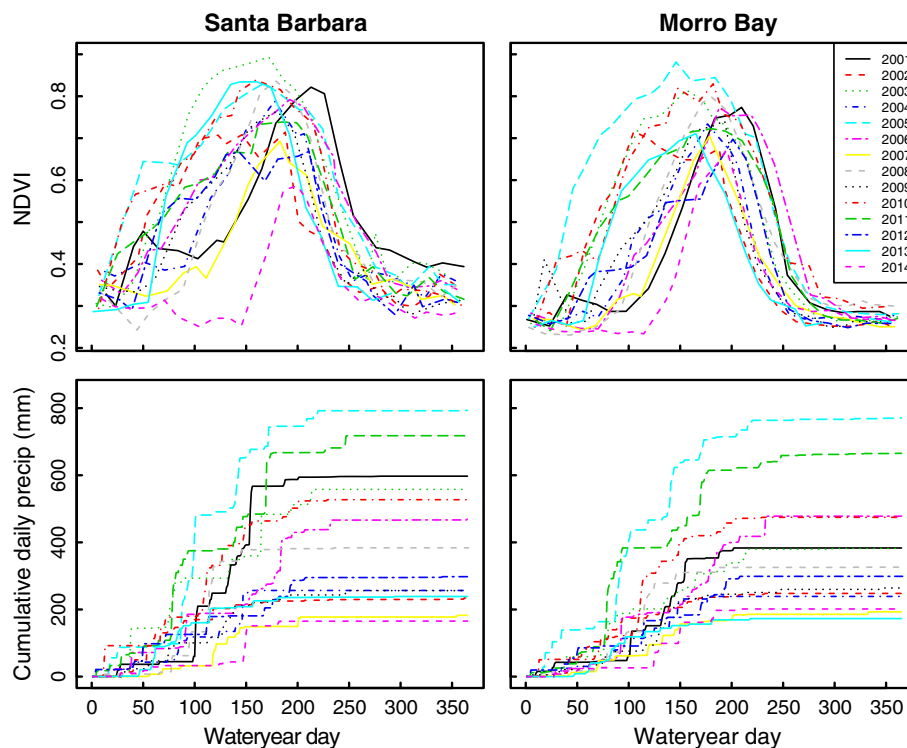


Fig. 3. Normalized difference vegetation index (NDVI) time-series and cumulative daily precipitation, separated by wateryear. Wateryear begins on 1 October.

For cross-validation, MGPM was better at representing green-up initiation at both grassland sites than the fixed-date phenology model. In Santa Barbara, MGPM was able to predict green-up initiation with a RMSE value of 24.17, while the RMSE value (44.59) for the fixed-date phenology model was 84% higher. In Morro Bay, MGPM produced a cross-validation RMSE of 26.55. The cross-validation RMSE value of the fixed-date phenology model was 46% higher at 38.68.

For grassland senescence, the calibration results showed that higher grassland productivity during

the wet season was associated with a later senescence, though model estimates were not as strong as for green-up (Fig. 5). The R^2 for the positive relation between the MODIS-derived WYD of senescence initiation and NPP_{cum} on that same day was 0.605 for Morro Bay and 0.373 for Santa Barbara (Table 1). The top parameters for the senescence model (Table 2) showed that both study sites had similar intercept values (parameter b in Eq. 3), WYD 198 and 200 for Morro Bay and Santa Barbara, respectively. This day is approximately two weeks earlier than the mean

Table 1. Calibration and validation results for the Mediterranean grassland and the fixed-date phenology models.

Site	Model	Calibration			Cross-validation	
		Green-up	Senescence		Green-up	Senescence
		RMSE (d)	R^2	RMSE (d)	RMSE (d)	RMSE (d)
Santa Barbara	Med. grassland	22.09	0.373	11.75	24.17	14.55
	Fixed-date				44.59	14.90
Morro Bay	Med. grassland	19.93	0.605	10.82	26.55	15.28
	Fixed-date				38.68	15.74

Note: RMSE, root-mean-square error; Med., Mediterranean; d, day.

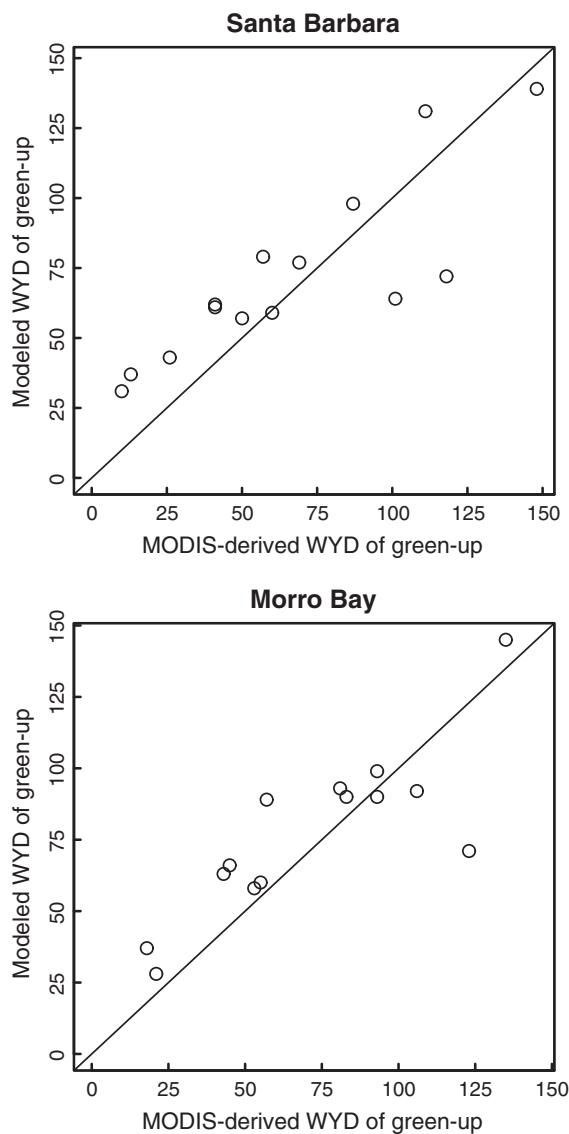


Fig. 4. Relation between Moderate Resolution Imaging Spectroradiometer (MODIS)-derived wateryear day (WYD) for green-up initiation and the modeled WYD for green-up initiation using the Mediterranean grassland phenology model. Line represents 1:1 line.

MODIS-derived senescence date. The increase in senescence WYD with NPP_{cum} (parameter a in Eq. 3) was slightly lower for Santa Barbara than for Morro Bay. During cross-validation, MGPM was better at predicting senescence initiation than the fixed-date phenology model; however, the absolute difference in performance between the phenology models was small (Table 1). In Santa Barbara, MGPM had a RMSE value of 14.55 vs.

14.90 for the fixed-date phenology model. In Morro Bay, MGPM had a RMSE value of 15.28 vs. 15.74 for the fixed-date phenology model.

In light of the validation results for senescence, a hybrid phenology model incorporating a dynamic green-up day and a fixed senescence initiation day was included in simulations along with MGPM and the fixed-date phenology model.

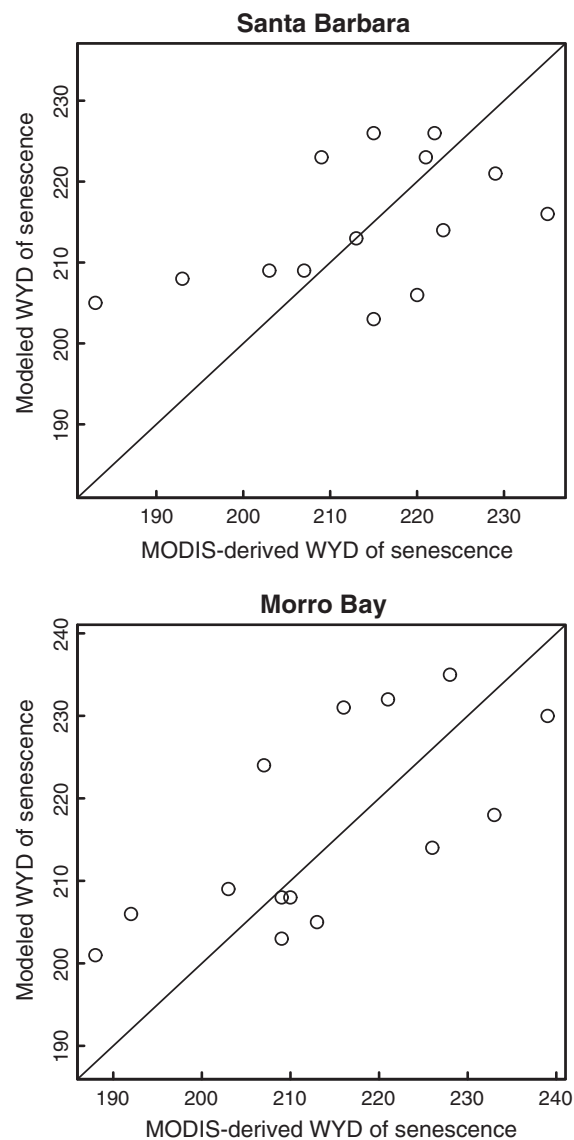


Fig. 5. Relation between Moderate Resolution Imaging Spectroradiometer (MODIS)-derived wateryear day (WYD) for senescence initiation and the modeled WYD for senescence initiation using the Mediterranean grassland phenology model. Line represents 1:1 line.

Table 2. Top parameter values for senescence component of the Mediterranean grassland phenology model.

Site	a (WYD/[kg C/m ²])	b (WYD)
Santa Barbara	206	200
Morro Bay	225	198

Note: WYD, wateryear day.

The effect of these three models on annual ET and annual NPP is shown in Fig. 6. For both Santa Barbara and Morro Bay, the magnitude and variance of simulated annual ET and NPP were similar for both the MGPM and the hybrid phenology model. This implies that there was little difference in simulated fluxes using NPP_{cum} as a predictor for senescence compared to using a fixed date. On the other hand, simulations using the fixed-date phenology model in Santa Barbara produced

mean annual ET and NPP values that were 9.8% and 12.8% higher than with MGPM. In addition, the variance of annual ET was smaller using the fixed-date phenology model. This decrease in variance was due to the fixed-date phenology model not having a dynamic range of green-up dates, as MGPM has. Wateryears with a very early green-up are more likely to be associated with the highest levels of annual ET, whereas wateryears with a very late green-up are more likely to be associated with the lowest levels of annual ET. The fixed-date phenology model was not able to capture these extremes. For Morro Bay, mean annual ET and NPP values produced by the fixed-date phenology model were not substantially different from values produced by MGPM and the hybrid model; however, a decrease in variance was observed for both annual ET and annual NPP.

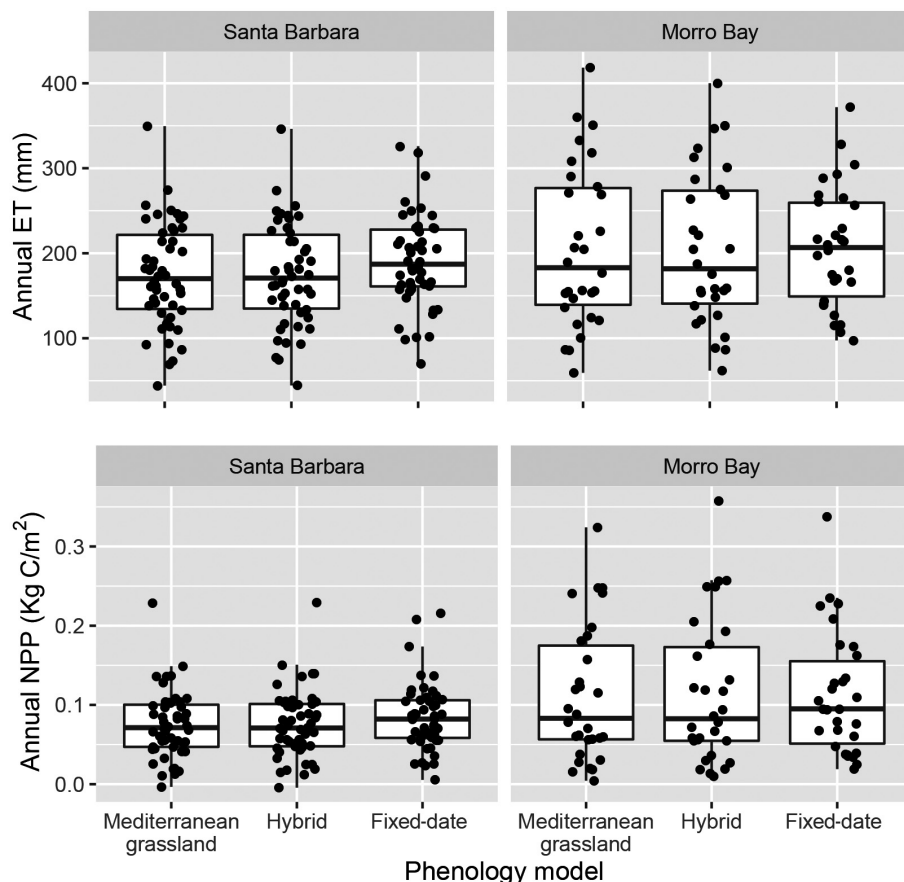


Fig. 6. Simulated differences in annual ET and annual net primary productivity (NPP) for the Mediterranean grassland, hybrid (includes dynamic green-up but fixed-date senescence), and fixed-date phenology models.

DISCUSSION

The MGPM developed in this study was used to model the timing of green-up and senescence initiation in California annual grasslands. The study results demonstrated that a soil water potential threshold can be an accurate predictor of grassland green-up initiation, a finding that is consistent with phenology models for other vegetation types in seasonally dry regions (e.g., Jolly and Running 2004). Still, with RMSEs in the cross-validation predictions as high as 26.55, the predictions for grassland green-up along the central coastal of California were slightly higher than those predicted by Xin et al. (2015) for grasslands in North America that have a spring green-up (Table 1). This suggests that some controls on green-up initiation remain unaccounted for. A potential source of this uncertainty may have been due to year-to-year differences in the composition of grass species, which may vary based on the timing, amount, and duration of rainfall that initiates germination (Bartolome 1979). The soil water potential threshold for green-up initiation may not be constant among grass species. For example, the threshold may be higher for species that germinate early in the wet season when the likelihood of near-term succeeding precipitation is relatively low compared to species that germinate near the middle of the wet season. There is also uncertainty in the rainfall estimates used to drive the ecohydrologic model and determine soil water potentials, as storm precipitation can be spatially variable along coastal California (Shields and Tague 2012).

For senescence, NPP_{cum} showed a positive relation with the day of senescence initiation. Physically, this relation may represent increased levels of reproduction during years with high NPP_{cum} . Ewing and Menke (1983a) observed greater seed generation during wetter (and presumably more productive) conditions than during drier conditions. This increase in seed generation may postpone senescence. The relation between NPP_{cum} and WYD of senescence initiation may also reflect the implicit relation between NPP_{cum} and wetness levels; years with higher NPP_{cum} are likely to be wetter and soil conditions during wet years are likely to persist further into the dry season, allowing senescence in grasses to be delayed.

While NPP_{cum} was able to account for some of the inter-annual variability of senescence initiation, the short time-period over which senescence typically occurs, as well as the comparable effectiveness of the fixed-date phenology model at predicting senescence initiation, indicates an element of photoperiod control on senescence initiation. This photoperiod control appears to limit senescence initiation to a window of time between early April and late May, while NPP_{cum} affects the timing of senescence within this window. Other studies have noted this photoperiod control. For example, Jackson and Roy (1986) observed that additional watering during flowering postponed grass death by less than a week. Nilsen and Muller (1981) found photoperiod length to be the primary control on senescence for a drought-deciduous shrub species near Santa Barbara.

If photoperiod is a control over the window of time that senescence initiation occurs, a natural follow-up question is to ask how photoperiod controls are set by vegetation. To explore this question, the annual WYD of peak NPP_{cum} was identified from the calibration output for the top calibrated parameter set. Since senescence was inhibited during calibration of MGPM, the WYD of peak NPP_{cum} represents the near-optimal day for senescence. These results were plotted next to the annual MODIS-derived days of senescence initiation in Fig. 7 and show that the range of MODIS-derived wateryear days for senescence initiation is contained within the range of peak NPP_{cum} . Thus, while it is not possible for grasses to forecast when the ideal time to senescence will be a priori, it appears that grasses senesce during a window that corresponds to the long-term peak NPP_{cum} . This suggests a long-term adaptation and that photoperiod controls on phenology could be altered under climate change.

Simulations of ecosystem fluxes with RHESSys revealed that the representation of grassland green-up affects both the magnitude and variance of annual ET and annual NPP estimates. The observed difference in long-term flux magnitude (up to 12.8%) has the potential to overwhelm changes due to climate change (Jung et al. 2010) and highlights the importance of accurately modeling grassland green-up in biophysical models. The reduced range of annual variability produced by the fixed-date green-up

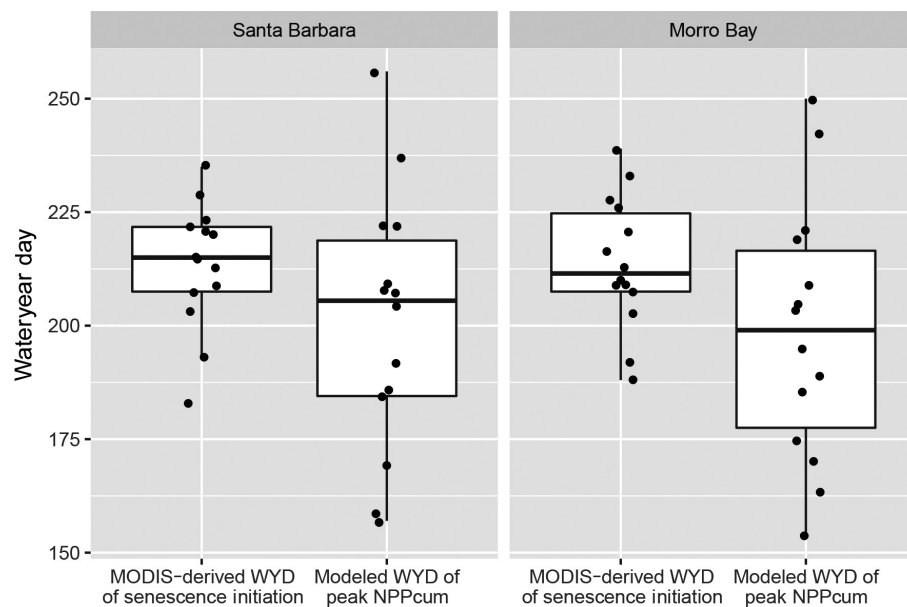


Fig. 7. Comparison of the Moderate Resolution Imaging Spectroradiometer (MODIS)-derived wateryear day (WYD) of senescence initiation with the modeled WYD of peak NPP_{cum} using the Mediterranean grassland phenology model with senescence inhibited.

model lessens the sensitivity of extreme conditions (e.g., drought) on ecosystem fluxes, which may underestimate ecosystem stress.

There was little difference in simulated ecosystem fluxes using the dynamic NPP_{cum} control on senescence compared to a fixed-date, photoperiod control. These results indicate that either control may be appropriate for modeling senescence initiation for annual grasslands along the central coast of California. The more parsimonious fixed-date senescence model may be advantageous for simulations when the controls on NPP (e.g., temperature, climate) are stable, as the fixed-date senescence model performs similarly to the NPP_{cum} model under stationary conditions (Table 1). However, in simulations where the controls on NPP change over time, such as when assessing the effects of climate change, the more complex, dynamic NPP_{cum} control may perform better. As temperatures warm and water availability for grasslands changes, grassland productivity is likely to be altered, potentially affecting the timing of grassland senescence (Cleland et al. 2007). The sensitivity of the NPP_{cum} senescence model to changes in productivity makes it more likely to capture these phenological changes compared to fixed-date model.

One of the challenges with modeling senescence in California grasslands is that senescence cannot be modeled using only external drivers (e.g., soil moisture, temperature, VPD). Instead, senescence is physiologically driven (Chiariello 1989). We have shown that senescence can be modeled as a function of NPP, which likely acts a surrogate for grassland reproduction (Chiariello 1989). Since including a full reproduction sub-model is prohibitive due to a substantial increase in model complexity, NPP provides a reasonable semi-mechanistic approximation of ecophysiological processes that underlie senescence. In order to establish a relation between NPP_{cum} and the WYD of senescence initiation, a preliminary calibration run may be necessary since NPP is an internally derived model variable, adding another source of uncertainty in the application of this model. Still, the model parameters for senescence at both sites were similar to one another, suggesting that a single calibrated senescence model may be suitable along the California central coast.

Grasslands throughout much of California have a similar phenology to the central coast, with green-up occurring early in the wet season and senescence at the end of the season (Ma et al.

2007). Although MGPM was applied to only two sites along the central coast of California, we expect that the soil moisture component of the model to be robust and a good predictor of green-up throughout the state, as soil moisture is well established as the primary control on green-up (Slade et al. 1975, Chiariello 1989, Ma et al. 2007). Additional research will be needed to determine the applicability of the NPP_{cum} component of the model for other parts of California, as well as for other MTE regions. The NPP_{cum} senescence model may also be a potential predictor on phenology for drought-deciduous shrubs in MTEs.

In conclusion, we found the MGPM, consisting of a dynamic green-up initiation based on a soil moisture threshold combined with a NPP_{cum} control on senescence initiation, to be the best predictor of phenology in California annual grasslands. We also observed that photoperiod acts as an additional control on senescence initiation, restricting the window of time during which senescence may occur. Long-term peak NPP_{cum} was noted as a potential control on the timing of this photoperiod window. Inclusion of MGPM into biophysical models is expected to improve the representation of annual grasslands and more accurately simulate ecosystem fluxes.

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DATA ACCESSIBILITY

Data in this study are available from the figshare repository <https://doi.org/10.6084/m9.figshare.4635118>.