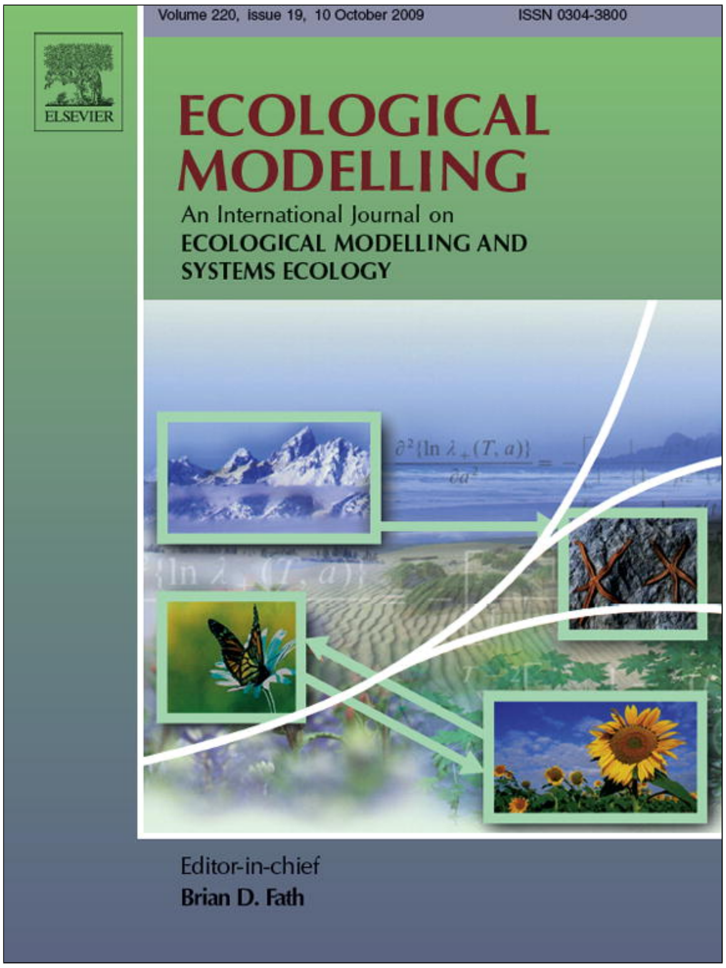
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Modeling the influence of precipitation and nitrogen deposition on forest understory fuel connectivity in Sierra Nevada mixed-conifer forest

Matthew D. Hurteau[a,*], Malcolm North[b], Theodore Foin[c]

[a] National Institute for Climate Change Research, Western Region, Northern Arizona University, PO Box 6077, Flagstaff, AZ 86011, United States
[b] USFS Sierra Nevada Research Center, 1731 Research Park Drive, Davis, CA 95618, United States
[c] Department of Plant Sciences, University of California, Davis, CA 95616, United States

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Climate change models for California's Sierra Nevada predict greater inter-annual variability in precipitation over the next 50 years. These increases in precipitation variability coupled with increases in nitrogen deposition from fossil fuel consumption are likely to result in increased productivity levels and significant increases in forest understory fuel loads. Higher understory plant biomass contributes to fuel connectivity and may increase future fire size and severity in the Sierra Nevada. The objective of this research was to develop and test a model to determine how changing precipitation and nitrogen deposition levels affect shrub and herb biomass production, and to determine how often prescribed fire would be needed to counter increasing fuel loads. Model outputs indicate that under an increasing precipitation scenario significant increases in shrub and herb biomass occur that can be counteracted by decreasing the fire return interval to 10 years. Under a scenario with greater inter-annual variability in precipitation and increased nitrogen deposition, implementing fire treatments at an interval equivalent to the historical range of 15–30 years maintains understory vegetation fuel loads at levels comparable to the control.

1. Introduction

General circulation models predict a range of climatic changes for California over the next 50 years depending on different emission scenarios. These model outputs indicate a general trend of increased warming, especially during summer months (Cayan et al., 2008; Hayhoe et al., 2004). Precipitation projections vary depending on the GCM-Emissions scenario stipulated, but range from a 9% decrease to a 13% increase for northern California (Cayan et al., 2008). Increased warming will accelerate snowmelt, amplify drought stress, and increase fire frequency and intensity (Cayan et al., 2008; Westerling and Bryant, 2008; Miller and Urban, 1999). The western United States has already experienced climatic shifts that correlate with increased fire size and severity (Westerling et al., 2006) and is expected to experience continued drying, resulting in an increase in the number of days with high fire danger (Brown et al., 2004) and increased forest fire activity (Flannigan et al., 2000). Concurrent with these climate changes is an increasing input of atmospheric nitrogen from automobile and industrial burning of fossil fuels (Bytnerowicz et al., 1998). Although tailpipe emission standards are becoming more restrictive, California's population continues to increase and commensurate with population increase is an increase in tailpipe emissions. These policy changes are likely to result in a slowing of the rate of increase in nitrogen deposition, however population growth will likely ensure continued nitrogen pollution increases. Water and nitrogen are the two most limiting resources in most western forests (Fenn et al., 1998; Witty et al., 2003). Increases in their availability are likely to produce increases in understory productivity, resulting in an even greater increase in fuel connectivity and potential fire size than linear model predictions (Miller and Urban, 1999).

Most fuel treatment models simulate fire behavior based on a range of weather scenarios using current climate conditions. Years of climate research and recent trends, however, indicate current weather scenarios are unlikely to remain constant (Cayan et al., 2008; Hayhoe et al., 2004; Melack et al., 1997; Field et al., 1999; Knowles et al., 2006). While climatologists have developed more sophisticated models, ecological models of changes in forest communities and fuel dynamics resulting from climate change are still rare. One of the few models to simulate climate change effects on fire (Miller and Urban, 1999) focused on a linear burn–behavior response to eight scenarios of differing temperature and precipitation. Climate change scenarios, however, all emphasize that annual variability will increase and this increased amplitude may produce synergistic effects on fuels. Studies in the summer monsoonal conditions of southwestern ponderosa pine have suggested large fires often occur in a dry year preceded by a wet year, because

* Corresponding author. Tel.: +1 928 523 0497; fax: +1 928 523 0565.
E-mail addresses: Matthew.Hurteau@nau.edu (M.D. Hurteau), mnorth@ucdavis.edu (M. North), tcfoin@ucdavis.edu (T. Foin).

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higher soil moisture increased grass biomass and subsequent fuel continuity (Swetnam and Betancourt, 1990). If precipitation variability increases in the Sierra Nevada this fire size response might occur. However, with the Sierra's Mediterranean climate, a fire occurring in a dry year followed by several years of below-average precipitation levels could impede understory recovery. This interannual variability and its interaction with pollution inputs and fire have never been modeled for a western forest. What are the likely effects of this greater amplitude in year to year climate on understory fuel production? How can these changes be effectively incorporated into existing fire models to improve forecasting?

2. Background information

The mixed-conifer forests of the Sierra Nevada historically experienced frequent, low-intensity fires that burned approximately every 15–30 years (Kilgore and Taylor, 1979; Caprio and Swetnam, 1995; McKelvey and Busse, 1996) but with fire suppression, the current fire return interval has been estimated at over 600 years (McKelvey and Busse, 1996). Currently, fire managers are attempting to re-introduce fire into these forests approximating historic intensity and frequency. The historic forest structure was characterized by a patchy understory community and surface fires were carried primarily by dead fuels (litter, duff, tree branches) that had accumulated on the forest floor (van Wagtendonk and Fites-Kaufman, 2006; Stephens et al., 2008). The historical fire return interval was longer than other dry western forest types, such as ponderosa pine, which had a fire return interval ranging from 2 to 12 years (Covington and Moore, 1994). The more frequent historical surface fires in ponderosa pine forests resulted from high understory fuel continuity due to nearly continuous plant cover (Covington and Moore, 1994). In the Sierra Nevada, the majority of fuel loading is produced by needle litter and woody material (van Wagtendonk and Fites-Kaufman, 2006). These woody inputs may not immediately be affected by changing climate and pollution conditions. Fuel continuity, however, and its potential effect on fire size may more rapidly change as herbs and shrubs respond to altered growing conditions.

Determining how altered precipitation levels and increased nitrogen will affect understory biomass production and fuel continuity is important for prioritizing fuel treatment units within a fire management area. Forecasting fuel continuity changes in areas of concern, such as around nest trees of sensitive species such as the California spotted owl (*Strix occidentalis occidentalis*), allows land managers to prioritize their limited resources, such as short burning windows and fire personnel. Prior to constructing this model, we met with land managers to determine a suite of possible quantitative model inputs that could be supplied by existing data. We determined that annual precipitation and nitrogen deposition data are readily available and fuels data are collected prior to all prescribed burns as part of burn plan development.

Climate change research in the Sierra Nevada has focused on how shifting climatic patterns will influence processes at the landscape scale (Brown et al., 2004; Lenihan et al., 2008; Westerling and Bryant, 2008). Prescribed fire management decisions are typically made at the stand or burn unit scale. The objectives of this study were to model how altered precipitation levels and increased nitrogen deposition affect understory fuel production and continuity in California mixed-conifer forests. Such a model could provide fire managers with a planning tool allowing them to make informed decisions about fuel accumulations and burn frequency. We constructed a computer simulation model using STELLA®7 (isee systems inc.) and set model parameters and validated model predictions using data from a field experiment manipulating snowpack, nitrogen, and fire (Hurteau and North, 2008). We used this validated model to examine the effects of altering the fire return interval and to determine if fuel levels that are commensurate with current conditions can be maintained under a range of forecasted conditions.

Most models of forest response to climate change have focused on forest overstory species and their contribution to fuel loads. Understory communities, however, can substantially influence fire spread because shrubs and herbs provide fuel paths across forest gaps connecting litter and slash, which are concentrated in tree clusters.

3. Model

3.1. Overview of model structure

To assess fuel dynamics in these fire corridors, we constructed and parameterized a deterministic model in STELLA®7 (isee systems inc., 2001), using pre- and post-treatment data from a 4-year field experiment. The model incorporates the influence of precipitation and nitrogen deposition on two forest functional groups, shrubs and herbs, for fire planning (Fig. 1, supplementary data). The model's herbaceous plant and shrub components were segregated to account for the different biomass turnover rates associated with each group, as well as how each group responds to a fire event. The model was developed to run for a 50-year planning horizon with a 1-year time-step based on predicted precipitation and nitrogen deposition values used in the field experiment.

3.2. Herb and shrub growth

Herb and shrub growth are calculated as

$$\text{Herb growth} = (\text{rH} - \text{HS}) \times \text{HB tracker} \quad (1)$$

$$\text{Shrub growth} = (\text{rS} - \text{SS}) \times \text{SB tracker} \quad (2)$$

where rH and rS are the growth rates for herbs (rH) and shrubs (rS) at time *t* determined by the water and nitrogen inputs, and fire occurrence at time *t*. HS and SS are the growth suppression coefficients for herbs and shrubs, respectively, and HB tracker and SB tracker are the state variable values at time $t-1$. HS and SS only influence growth if the herb or shrub biomass meets or exceeds the equivalent of 100% cover. Suppression coefficients are invoked via a logic statement driven by the herb and shrub biomass trackers (SB and HB tracker). The growth suppression coefficient is a constant, specific to herbs (170 g plot^{-1}, equivalent to 20.9 kg ha^{-1}) and shrubs (1484 g plot^{-1}, equivalent to 183.1 kg ha^{-1}), which was determined from plots in the field experiment that had 100% understory plant cover. The growth suppression coefficient incorporates competition for growing space into the model by constraining maximum herb and shrub biomass. Growth is asymptotically modeled as biomass approaches the empirically derived maximums. Herb and shrub growth do not explicitly interact because of the timing of growth in the field (Hurteau and North, 2008). Shrub and herb biomass can remain in the stock, be consumed by fire, or in the absence of a fire event be transferred to the fuels stock.

3.3. Influences on growth

There are three parameters that determine herb and shrub growth rates for a given time-step. Nitrogen is input in kg ha^{-1} year^{-1} deposition. Precipitation values for each time-step can be determined by either standardized values or via a random algorithm. Standardized values for precipitation can be input as above average (>0), average (0), or below-average levels (<0). The model user can also run a random algorithm that outputs annual precipitation levels with a normal distribution. The model user

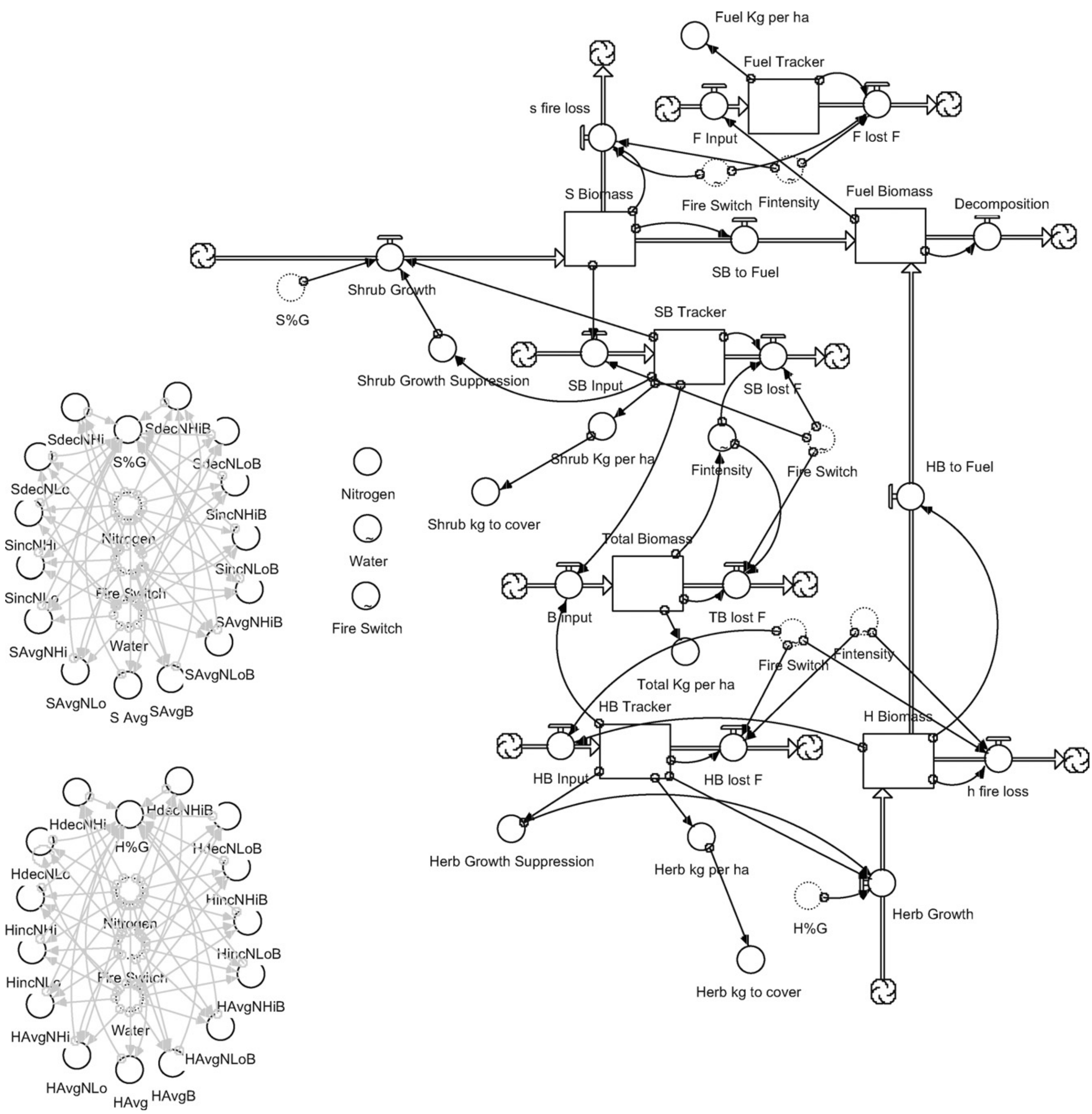

Fig. 1. The graphical representation of the mixed-conifer understory response model constructed in STELLA®7, isee systems inc.

selects the mean and standard deviation for the distribution, allowing them to examine the system response to annual precipitation fluctuations occurring around higher, lower, or mean precipitation values. The random algorithm, by using Gaussian variation, allows the precipitation distribution to be user determined above or below-average means and standard errors. Fire events can be set to occur at specific time-steps or randomly with a user input likelihood of occurrence.

The nitrogen, precipitation, and fire parameters influence herb (Eq. (1)) and shrub (Eq. (2)) growth by summing the treatment-specific growth rates that are output from a series of if-then-else statements to determine the rH and rS parameters, respectively (see supplementary data). These treatment-specific growth rates were determined from field results (Table 1).

3.4. Biomass

Initial herb and shrub biomass (kg ha^{-1}) are calculated based on initial percent cover estimates from field sampling as

Herbs:

$$y = 0.448368x - 0.440583, \quad r^2 = 0.79 \tag{3}$$

Shrubs:

$$y = 1.372014x + 2.576618, \quad r^2 = 0.80 \tag{4}$$

where y is equivalent to biomass in kg ha^{-1} and x is equivalent to the field measured percent cover. The y values are then used as the initial state variable values for shrub and herb biomass. The model operates on a first-in-first-out principle. Initial biomass is calcu-

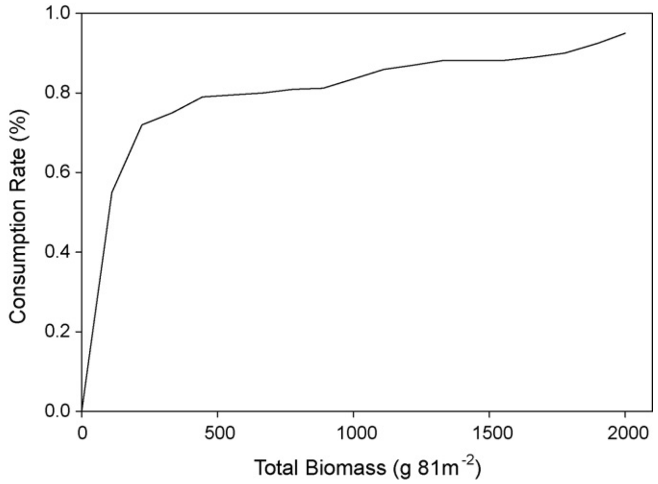

Fig. 2. Graph of the model's fire consumption relationship where the percent consumption is a function of available biomass. Graph values were calculated from pre- and post-fire fuel biomass measured in the field study.

lated using Eqs. (3) and (4). In a given time-step, growth is added to both the shrub and herb model stocks via Eqs. (1) and (2) as a function of the nitrogen and water values and the biomass from time $t-1$. If a fire event is slated to occur during a given time-step, that event occurs following the addition of growth for that time-step. The transfer of live biomass to fuel occurs following the growth addition for a given time-step in the absence of fire and following the fire event in the presence of fire because not all live biomass is consumed by fire. The occurrence of a fire event results in the loss of biomass at a rate of biomass (t) multiplied by the fire consumption. Fire consumption is a graphical representation of consumption rate (percentage) dictated by the amount of consumable biomass (Fig. 2). The fire consumption graph was created based on empirical pre- and post-treatment dead fuels measurements and live biomass consumed per unit area converted to kg ha^{-1}. The fire consumption graph does not equate to fire intensity at the stand or forest level, nor does it incorporate weather or topography, it is strictly the relationship between understory biomass present pre- and post-fire. In the absence of a fire event, shrub biomass is transferred to fuels at the rate of 40% per year and herb biomass is transferred at a rate of 85% per year. These leaf turnover values were calculated for the species composition of the field sites based on values used by White et al. (2000) in the Biome-BGC Terrestrial Ecosystem Model. Fuel biomass remains in the stock and is subject to a 20% per year decomposition rate or is consumed by fire using the same equation as shrubs and herbs. We selected the 20% decomposition rate based on work by Stohlgren (1988) involving tree leaf litter decomposition in Sierran mixed-conifer forest.

The remaining model components, referred to as "tracker" components provide information for the growth suppression logic statements (herb and shrub growth suppression). If herb and/or shrub biomass is ≥100% cover, the logic statement subtracts the growth suppression coefficient from the growth rate (rH or sH).

Table 1
Treatment-specific growth rates in percentage growth per year determined from the field experiment.

Precipitation	Nitrogen	Fire	Herb	Shrub
Average	0		1.50	2.00
Average	0	Burn	0.50	0.10
Average	12		3.60	1.50
Average	12	Burn	2.50	0.05
Average	24		1.30	2.20
Average	24	Burn	1.40	0.50
Decrease	12		1.55	0.70
Decrease	12	Burn	2.00	2.00
Decrease	24		1.20	1.90
Decrease	24	Burn	2.00	0.65
Increase	12		3.50	2.70
Increase	12	Burn	2.50	0.75
Increase	24		1.60	2.40
Increase	24	Burn	3.00	0.20

4. Model evaluation

4.1. Field study

The field study used for model parameterization and validation was conducted over a 4-year period at the Teakettle Experimental Forest and Yosemite National Park (Fig. 3). The specific results of the field study can be found in Hurteau and North (2008). California has a Mediterranean climate with most of the precipitation falling as snow in the winter months. For the field study, we used a full factorial design that included three levels of snowpack (ambient, increase, decrease), two levels of nitrogen addition (ambient, increase), and two levels of prescribed fire (no burn, burn) (Fig. 3). Specific treatment levels were tailored to each site based on variation in climate and nitrogen deposition monitoring stations. We increased and decreased snowpack by 30% at Teakettle and 60% at Yosemite and added nitrogen at a rate equal to 24 kg ha^{-1} $year^{-1}$ at Teakettle and 12 kg ha^{-1} $year^{-1}$ at Yosemite to bracket the range of observed differences between sites from comparing Western Regional Climate Center data and air sampling stations (Hurteau and North, 2008). With the differences in treatments, the two sites were not treated as replicates but were used to bracket a larger range of treatment effects and potential responses.

4.2. Model parameterization and sensitivity analysis

We parameterized growth rates for the model using a randomly selected subset of plots, equivalent to 50% of the data, from each treatment in the field experiment. The remaining field experiment data were then used to evaluate model performance. Pre-treatment cover values were entered in conjunction with the appropriate water, nitrogen, and fire values. Paired t-tests indicated there were no significant differences between field experiment results and model outputs (Table 2) for any of the snowpack and N manipulations.

Parameter sensitivity analysis was focused on the water and nitrogen parameters of the model, as these parameters directly affect herb and shrub growth and are likely to vary in a more continuous manner than the treatment levels applied in the field experiment. Nitrogen inputs were varied across the range of possible values from 0 to 24 kg ha^{-1} $year^{-1}$, based on current deposition rates for California (Fenn et al., 1998). Standardized water inputs were varied from one standard deviation below average to one standard deviation above average. We also examined the synergistic effects of all nitrogen–water combinations. We calculated mean absolute percentage differences from baseline values for all possible nitrogen and water values, and their combinations. Herb and shrub biomass sensitivity to water and nitrogen varied considerably (Table 3). Herb biomass was most sensitive to nitrogen, particularly at the 12 kg ha^{-1} $year^{-1}$ level (209% mean absolute change), and water–nitrogen combinations (WIncN12 185% mean absolute change). Shrub biomass was sensitive to all levels of nitrogen, water, and their combinations.

No Burn				Burn			
	Water:				Water:		
Nitrogen:	None	Addition	Reduction	Nitrogen:	None	Addition	Reduction
None	Control	+ H_2O	- H_2O	None	Burn only	+ H_2O	- H_2O
Addition	+ N	+ H_2O + N	- H_2O + N	Addition	+ N	+ H_2O + N	- H_2O + N

	Treatments:		
Location:	Snowpack reduction	Snowpack addition	Nitrogen
Yosemite	-60%	+ 60%	+ 12 kg/ha
Teakettle	-30%	+ 30%	+ 24 kg/ha

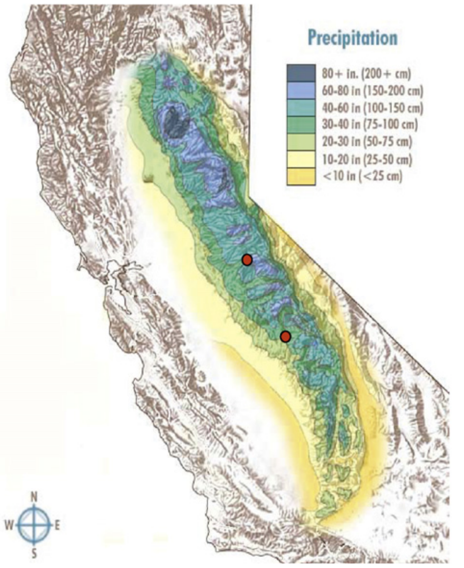

Fig. 3. Field experiment locations (indicated by circles) of Yosemite National Park (northern site) and Teakettle Experimental Forest (southern site), and the experimental design and treatments for the manipulation study used to parameterize the model.

Table 2
Means (g/81 m^2 plot) and standard errors (in parentheses) for model validation comparisons between empirical field data and model outputs for herbs and shrubs.

Treatment	Herb			Shrub		
	Model	Field	*p*-value	Model	Field	*p*-value
Control	30.5 (13.8)	43.5 (24.1)	0.394	182.7 (53.1)	261.3 (133.6)	0.459
Nitrogen	19.2 (10.4)	28.9 (10.6)	0.347	223.3 (76.1)	287.0 (127.8)	0.568
Water increase nitrogen	14.9 (8.4)	16.1 (7.3)	0.481	293.4 (144.5)	297.7 (170.5)	0.951
Water decrease nitrogen	13.8 (4.4)	14.4 (5.5)	0.892	135.2 (61.3)	141.8 (58.7)	0.794
Nitrogen burn	4.5 (2.2)	13.7 (12.3)	0.457	21.5 (12.0)	21.5 (17.5)	0.999
Water increase nitrogen burn	7.5 (3.4)	12.2 (6.4)	0.354	17.7 (6.7)	19.7 (6.4)	0.836
Water decrease nitrogen burn	13.3 (7.0)	29.1 (17.1)	0.317	48.2 (18.1)	126.1 (82.3)	0.409

5. Model application

To examine differences in biomass production related to increasing, decreasing, and average trends in precipitation, we conducted two model experiments that crossed the range of precipitation and nitrogen combinations with and without fire. Model runs were made with a random water component that fluctuated annually, around a mean value that was either above, below, or equal to the current mean annual precipitation. We used three different fire return intervals (10, 15, 30 years) to address the question of whether altering fire return interval can maintain fuels at their current levels under future conditions. To examine the influence of inter-annual variation in precipitation on the understory, we conducted another model experiment that varied precipitation levels between below average and above average values. We set precipitation levels to be above average for 1 and 3 years preceding a fire event and below average for the 5 years following a fire event and used the 15- and 30-year fire return intervals. These precipitation values were set manually using a graphical function in the model. Model outputs were analyzed using repeated measures ANOVA (SAS).

Table 3
Sensitivity analysis results for water and nitrogen inputs in percent mean absolute change from baseline values.

Parameter	Description	Mean absolute change (%)			
		Herb		Shrub	
N12	Nitrogen 12 kg ha^{-1} $year^{-1}$	+	209.2	+	5.6
N24	Nitrogen 24 kg ha^{-1} $year^{-1}$	–	4.2	+	20.2
W-1	Water decrease	–	4.5	–	55.7
W1	Water increase	–	9.0	–	65.1
W-1N12	Water decrease nitrogen 12 kg ha^{-1} $year^{-1}$	+	9.0	–	44.4
W-1N24	Water decrease nitrogen 24 kg ha^{-1} $year^{-1}$	+	0.3	–	8.8
W-1N12	Water increase nitrogen 12 kg ha^{-1} $year^{-1}$	+	185.0	+	89.5
W-1N24	Water increase nitrogen 24 kg ha^{-1} $year^{-1}$	+	19.2	+	44.5

Mean absolute change from baseline values was calculated at each time-step and averaged across the 50-year planning horizon to calculate table values. A +/– value indicates the direction of the change.

5.1. Model results without fire

Using random water inputs that had average, increasing, or decreasing trends to simulate annual precipitation variation, we found that varying water and nitrogen levels produced significantly different responses from the control (average water–nitrogen 0) for herbs, shrubs, and fuels when no fire events were simulated. Nitrogen level was the primary driver in herb cover response when fire was not included in the model runs. Both water increase–nitrogen 12 and water decrease–nitrogen 12 resulted in greater percent herb cover than the control (Table 4). Neither water increase–nitrogen

Table 4
Means and *p*-values for comparison with control for model runs without fire.

Treatment	Herb		Shrub		Fuels	
	Mean	*p*-value	Mean	*p*-value	Mean	*p*-value
Control	10.5		49		2259.7	
Water increase nitrogen 12	17.8	0.0001	63.9	0.0001	4582.9	0.0001
Water increase nitrogen 24	11.5	0.14	57.1	0.0001	3298.8	0.0001
Water decrease nitrogen 12	13.4	0.0001	41.3	0.0001	1657.6	0.0009
Water decrease nitrogen 24	9.9	0.38	48.7	0.77	2211.5	0.6913

24, nor water decrease–nitrogen 24 had significantly different cover values from the control (Table 4).

Water level was the primary driver in shrub cover response when fire was not included in the model runs. Water increase coupled with both nitrogen 12 and 24 produced greater percent shrub cover than the control. Water decrease–nitrogen 24 did not produce shrub cover that was significantly different from the control, while water decrease–nitrogen 12 had significantly less shrub cover than the control (Table 4). In the absence of fire, dead fuels followed the same response pattern as shrub cover. The water increase treatments at both the nitrogen 12 and nitrogen 24 levels produced more fuels (kg ha^{-1}) than the control (Table 4).

The results of these model runs suggest significant changes in herb and shrub cover, and fuel biomass accumulation with increasing precipitation and nitrogen deposition. Model outputs indicate that nitrogen level is more important for driving changes in herb cover and precipitation level is more important for driving changes in shrub cover. Changes in fuel accumulation are driven primarily by precipitation level, as shrub biomass is the largest contributor to fuels. Nitrogen deposition at a rate of 12 kg ha^{-1} year^{-1} coupled with above-average precipitation produced the largest increase in herb cover. Model outputs suggest that lower levels of deposition produce greater amounts of herb cover than higher levels of deposition. For shrubs, nitrogen deposition at 12 kg ha^{-1} year^{-1}, coupled with above average precipitation, produced the greatest mean average difference (89.5%) from baseline. Without a change in precipitation level, nitrogen deposition at 24 kg ha^{-1} year^{-1} resulted in a greater mean average difference for shrub cover than nitrogen deposition at 12 kg ha^{-1} year^{-1} (Table 3). Overall the model suggests that increases in nitrogen deposition and precipitation will likely result in significant increases in herb and shrub cover and fuel biomass accumulation, while decreasing precipitation will result in decreasing cover, particularly for shrubs. An increase in cover equates to increased fuel continuity resulting in the potential for greater fire spread.

5.2. *Model results with fire*

To examine the effect of fire return interval on herb and shrub cover, and fuels accumulation under a range of precipitation/nitrogen scenarios, we used the same water and nitrogen levels as the no fire model runs and varied the fire return interval (FRI) between 10, 15, and 30 years. Fifteen and 30 years represent the minimum and maximum values for the average range of historical FRI for Sierran mixed-conifer forests. We added the 10-year FRI to examine its effect on fuels accumulation and biomass production because shortening the FRI is a treatment option available to land managers. Model run results that included fire are shown in Table 5. Model runs that included both a 15- and 30-year fire return interval produced similar results to the no fire model runs. Water increase–nitrogen 12 and water decrease–nitrogen 12 produced significantly greater herb cover than the control for both the 15- and 30-year fire return intervals (Fig. 4). For shrubs, the water increase with both nitrogen and nitrogen 24 produced significantly higher cover values and fuels accumulation than the control

Table 5
Means and *p*-values for comparison with control for model runs with fire return intervals at 10, 15, and 30 years.

	Herb		Shrub		Fuels	
	Mean	*p*-value	Mean	*p*-value	Mean	*p*-value
Treatment – FRI 10						
Control	8.1		24.9		2481.8	
Water increase nitrogen 12	10.7	0.0001	28.7	0.0001	2536.8	0.887
Water increase nitrogen 24	7.1	0.0001	25.7	0.179	2191.2	0.462
Water decrease nitrogen 12	6.5	0.0001	22.3	0.002	2929.4	0.268
Water decrease nitrogen 24	6.6	0.0001	24.1	0.224	2201.0	0.477
Treatment – FRI 15						
Control	7.3		33.4		1053.6	
Water increase nitrogen 12	17.4	0.0001	44.8	0.0001	2402.3	0.0001
Water increase nitrogen 24	8.3	0.06	39.6	0.0001	1556.3	0.0001
Water decrease nitrogen 12	10.2	0.0002	30.6	0.0009	1114.4	0.331
Water decrease nitrogen 24	6.8	0.2551	34.1	0.224	1113.0	0.341
Treatment – FRI 30						
Control	9.3		43.3		1635.1	
Water increase nitrogen 12	19.1	0.0001	58.3	0.0001	3648.2	0.0001
Water increase nitrogen 24	10.4	0.0001	51.6	0.0001	2467.3	0.0001
Water decrease nitrogen 12	12.1	0.0001	38.2	0.0008	1339.8	0.004
Water decrease nitrogen 24	8.7	0.0001	43.3	0.964	1618.2	0.827

for both the 15- and 30-year fire return intervals (Fig. 4). Decreasing the fire return interval to 10-year resulted in only the water increase–nitrogen 12 scenario producing greater herb cover and shrub cover than the control (Fig. 4). The increase in herb and shrub cover prior to the last fire event in the 10-year FRI scenario is a result of higher precipitation values present in the string of random precipitation values used for the model runs. There were no significant treatment effects on fuels accumulation with the 10-year FRI. Manipulating the time between prescribed fire applications is one of the primary tools available to forest managers. Our findings indicate that under a future condition of increasing precipitation, forest managers will likely need to decrease the time between fires. If there is a general decreasing trend in precipitation patterns, using the historical fire frequency will maintain herb and shrub cover and fuels at levels we currently observe in the forest. However, a more likely precipitation scenario will involve greater inter-annual variability.

5.3. *Model results with varying precipitation levels*

To examine the influence of large annual fluctuations in precipitation we conducted model runs with above-average precipitation for the 1 and 3 years preceding a fire and below-average precipitation for the 5 years following a fire event. These scenarios have both fire management and ecological implications. Above average precipitation tends to increase plant cover and thus fuel loads in the understory (Westerling and Bryant, 2008), while recent work at the Teakettle Experimental Forests indicates that more heavily disturbed sites are drier and have reduced cover and diversity (Wayman and North, 2007) suggesting below-average precipitation following a fire event may increase plant recovery time. Model runs with 1 year above average precipitation prior to the fire event were driven largely by the nitrogen deposition level. Nitrogen 12 produced greater herb cover than nitrogen 24, with the opposite trend for shrubs (Fig. 5). Fuel biomass accumulation followed the shrub pattern, since it is largely driven by inputs from shrubs. However, fuels in the nitrogen 24 treatment did not differ substantially from the control. The results were similar for both the 15- and 30-year fire return interval. Model runs with 3 years above average precipitation preceding the fire event showed a similar response. However, shrub cover and fuels at the nitrogen 24 level surpassed control shrub cover and fuels values prior to the last fire event (Fig. 5) as a result of the variation in precipitation levels.

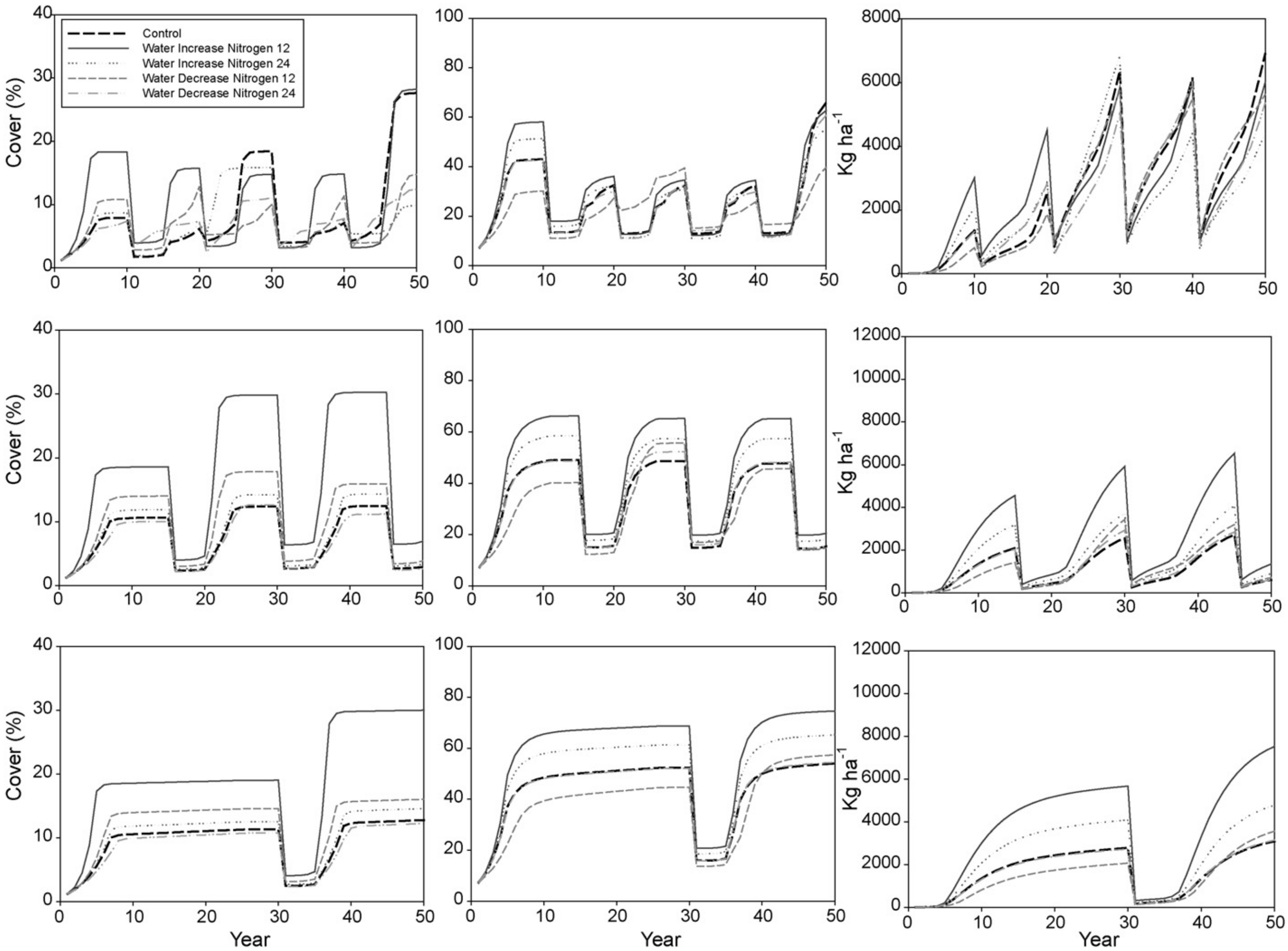

Fig. 4. Model outputs for herb (left column), shrub (center column), and fuels (right column) responses to average precipitation/no nitrogen increase, increased precipitation/increased nitrogen and decreased precipitation/increased nitrogen for 10- (top row), 15- (middle row), and 30-year (bottom row) fire return intervals.

6. Discussion

While there is some uncertainty in the direction of change for precipitation under increasing greenhouse gas concentrations (Cayan et al., 2008; Hayhoe et al., 2004), inter-annual variability is likely to increase. Our model experiments indicate that if the general precipitation trend is downward, punctuated by above average precipitation years preceding a fire event, herb and shrub cover may diminish over time as a result of decreasing water availability post-fire. However, the response varies depending on the inter-annual variability. Having a greater number of above-average precipitation years prior to the fire event resulted in greater herb cover values at the nitrogen 12 level. The potential for increased inter-annual variability and its associated effects on forest understory plants will require increased monitoring efforts to ensure that prescribed fire is applied at a frequency that maintains fuel connectivity within an acceptable range for wildfire risk reduction.

We caution that this model has several limitations that constrain its ability to represent future environmental change. The model is a simplification of the many processes affecting mixed-conifer understory communities. By grouping herbaceous plants and shrubs the model cannot predict species-specific responses to changes in precipitation and nitrogen deposition. Additionally, the impact of warming average temperatures was not included in field experiment manipulations and therefore is not incorporated in the model. However, warming temperatures are likely to influence precipitation form (Melack et al., 1997; Knowles et al., 2006) and snowpack duration (Westerling et al., 2006). The general warming trend and potential shift in precipitation from snow to rain is likely to have some impact on understory growth dynamics, including the potential to decrease soil moisture. While our growth values were calculated using snow amendments and reductions rather than changes in rain water timing and abundance, if the modeled system experiences late winter/early spring precipitation inputs in the form of rain rather than snow, we believe the model predictions may still hold because the shift in precipitation will likely result from an increase in temperature causing plant germination and bud break to occur earlier in the season. The major change would likely be later in the growing season when soil moisture has been exhausted and live and dead fuel moistures are low. Increasing temperatures may accelerate this period leading to an increase in the fire season length (Westerling et al., 2006; Westerling and Bryant, 2008). Low fuel moistures would lead to increased combustion during a fire event.

The model results indicate that we have captured some of the mechanisms driving system behavior at our field experiment sites. The two sites we selected for this study were typical of mixed conifer and had a structure similar to other mid-elevation western forests with patchy overstory and shrub-dominated understory. We believe that the model should capture system dynamics in similarly structured forests if herb and shrub growth responses were parameterized to local changes in precipitation and nitrogen, as well as

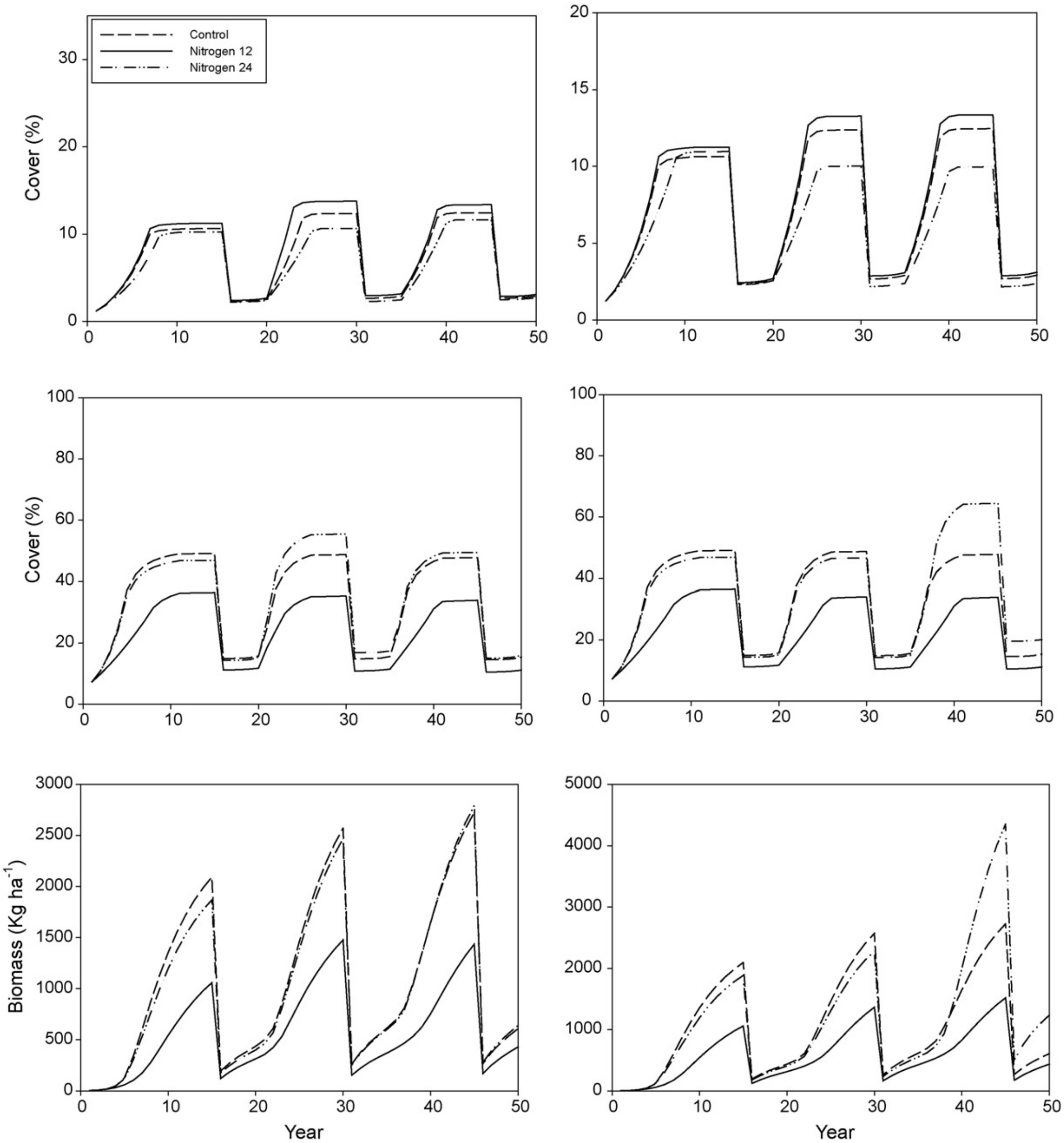

Fig. 5. Model outputs for herb (top row) and shrub (middle row) cover and fuels biomass (bottom row) responses to 1 year above average precipitation (left column) and 3 years above average precipitation (right column) prior to the fire event for the 15-year fire return interval with nitrogen 12 and 24 and the control (average precipitation/no nitrogen).

the fire–fuels consumption relationship.

In our 4-year experiment, we used ammonium instead of nitrate in the nitrogen addition treatment because plants rapidly incorporate it. Nitrogen deposition from increasing air pollution will increase nitrate more than ammonium inputs, but will likely enrich soil nitrogen similar to our field conditions. Our model results indicating increased nitrogen and increased precipitation increase biomass production are in agreement with another study in California. An experiment examining the effects of increased CO_2, temperature, precipitation, and nitrogen (at one level) on an annual grassland in California found that nitrate had the largest effect on net primary productivity of all treatments (Dukes et al., 2005). Increased precipitation resulted in a significant increase in shoot production but a decrease in root production over time.

Our finding that herb cover had a greater increase at the rate of 12 kg ha^{-1} year^{-1} over 24 kg ha^{-1} year^{-1} suggests that growth response to nitrogen deposition crosses some threshold in the system. One possible explanation for N12 producing more biomass in herbs and shrubs with increasing precipitation may be that as nitrogen, currently a limiting nutrient in the system, increases in abundance, herbaceous plants respond by producing more biomass. However, as nitrogen saturates the system at higher deposition levels, soil can become more acidic, increasing the risk of aluminum toxicity and nutrient cation deficiency (Johnson and Lindberg, 1992; Fenn et al., 1998). These soil changes may explain why our field data found that herb biomass is actually lower in the N24 than the N12 treatment. In contrast, shrub biomass increased in the N24 and decreased precipitation treatment possibly because mixed-conifer's perennial shrubs tolerate a wider range of soil conditions than its annual herbs.

Using forest GAP and present general circulation models, Miller and Urban (1999), suggested future wild fires would become larger and more frequent. Lenihan et al. (2008) found that under three climate change scenarios, California's annual burn area increased. Westerling et al. (2006) have suggested shifting climatic patterns are already influencing fire size and severity. Surface fires in Sierran mixed-conifer forest are typically driven by fuel inputs from the forest overstory. Our model outputs suggest that the understory plant community has the potential to alter the importance of surface fuels under changing climatic conditions. A general increasing trend in precipitation has the potential to increase both herb and shrub biomass above current conditions, suggesting that reducing the fire return interval from its historic 15–30-year to a 10-year interval is a viable management option for maintaining lower surface fuel loads needed to manage fuel continuity. When increased interannual precipitation variability is simulated, the herb and shrub communities exhibit different growth responses. While shrub cover does not differ substantially from the control under the nitrogen 12 scenario, herb cover under the nitrogen 12 scenario increased from the control. The potential for increased herb cover suggests that, overall fuel loads may not increase; fine fuels may become a more dominant driver of fire spread than under current conditions because of increased fuel bed continuity. Our model provides a tool for fire managers to track changes and predict responses in the understory plant community to changing precipitation and nitrogen inputs, as well as altered fire frequency. In the future the understory plant community may become a more important fuel source requiring more aggressive fuel reduction treatments, with prioritization given to more mesic areas and areas that experience higher levels of nitrogen deposition.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2009.06.032.

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