Nitrogen cycling and export in California chaparral: the role of climate in shaping ecosystem responses to fire

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Abstract. Climate change models predict that interannual rainfall variability will increase in California over the next several decades; these changes will likely influence how frequently California ecosystems burn and how they respond to fire. Fires uncouple N mobilization from uptake by destroying plant biomass and increasing nitrification. Following fire, autumn and winter rains can leach N into streams from slopes that have been denuded. The amount of N exported depends on how rapidly soil microbes metabolize it into mobile forms such as NO_3^-, and the rate that recovering plants take up available N. However, the long-term effects of a changing climate on postfire N dynamics remain unknown. We used the ecohydrologic model RHESSys (regional hydro-ecologic simulation system) to evaluate how interannual climate variability may affect the magnitude of N mineralization, nitrification, N export, and plant recovery following fire. N export was highest when fire was followed by drought; even though there was less water moving through the system, dry conditions prolonged the period during which N mobilization was decoupled from plant uptake. We also found that the effects of drought on N export were magnified in stands dominated by obligate seeders, which initially recovered more slowly than resprouters. These findings suggest that climate may regulate N balance most powerfully by influencing how quickly plants "turn on" and begin to immobilize N.

Key words: chaparral; climate change; ecohydrology modeling; leaching; mechanistic model; Mediterranean-type ecosystems; mineralization; nitrification; plant–soil–water interactions; regional hydro-ecologic simulation system; semiarid; wildfire.

INTRODUCTION

Wildfires are a major pathway for nitrogen (N) export from terrestrial to aquatic ecosystems. This pathway is especially prevalent in Mediterranean-type ecosystems such as California chaparral, where cool wet winters support rapid shrub growth but are followed by extended summer droughts that promote recurrent fires (Meixner et al. 2006). These ecosystems also typically occur in steep mountainous terrain where overland flow can move mobile elements downslope. Wildfires amplify seasonal N pulses to streams that occur at the onset of autumn rain by converting complex, insoluble, organic N into forms that readily dissolve or leach, and by destroying plant cover and suppressing microbial biomass that might otherwise immobilize this newly available N. The size of the postfire N pulse, and the amount of N that is exported over time, can vary in response to climate conditions surrounding a fire event. While the immediate effects of fire and rain on N cycling and retention are straightforward to quantify, decadal-scale responses to climate variability are not, especially in semiarid ecosystems such as chaparral, where N dynamics are also driven by rainfall

seasonality (Austin and Vitousek 1998, Homyak et al. 2014).

Fires denude chaparral landscapes, consuming most aboveground biomass and surface soil organic matter, and releasing some N to the atmosphere. At the same time, fires supply ash that is rich in ammonium (NH_4^+) and easily decomposable organic N (Marion et al. 1991, Bodí et al. 2014). Decomposable N, combined with postfire pH increases, can enhance mineralization and nitrification during the first years of recovery (Hanan et al. 2016b). However, loose and exposed soils immediately after fire make burned slopes vulnerable to leaching and erosion (De Koff et al. 2006), especially at the onset of autumn rains before recovering plants and microbes gain access to available N (Hanan et al. 2016a). Severe fires can therefore promote substantial N leaching from chaparral (Mooney and Rundel 1979), and recur on average every 40–60 years in the Santa Barbara region (Moritz 2003).

N is also exported from chaparral on an annual basis, due to the seasonal nature of rainfall (Homyak et al. 2014). While most biological activity shuts down during the prolonged dry season in Mediterranean-type ecosystems (Stark and Firestone 1995), some basal mineralization still occurs, allowing NH_4^+ to accumulate in soil microsites that remain hydrologically disconnected

through the summer (Parker and Schimel 2011). Upon wet-up, NH_4^+ can then diffuse to nitrifiers, which respond within hours to rewetting (Placella and Firestone 2013). Thus, early autumn storms can generate a flush of nitrate (NO_3^-) to streams while plants are still relatively dormant (Mooney and Rundel 1979, James and Richards 2006, Homyak et al. 2014). Because chaparral fires typically occur during summer (Keeley and Fotheringham 2001), they can magnify the early wet season N flush by further decoupling N mineralization from uptake. However, the amount of N that is exported during this period likely varies with climate and weather patterns surrounding a given fire. Rainfall can influence N export directly by driving postfire leaching and erosion, or indirectly by regulating fuel loads, fuel moisture, and, as a consequence, how much N fire can make readily available. Rainfall also regulates how quickly plants recover and take up mobilized N. These factors may feed back to influence long-term recovery trajectories; however the effects of climate patterns on postfire N dynamics are not well understood.

Chaparral ecosystems are often water-limited; therefore hydrologic processes regulate biogeochemical cycling, and N balance may be sensitive to changes in water availability. While N may limit plant productivity during the growing season, water constrains growth during the dry season and when rainfall is low. Although total rainfall might not change substantially in southern California in the coming years, climate models project that precipitation will become more sporadic, with more dry days, and larger storms occurring during a shorter rainy season (Pierce et al. 2012). Southern California already experiences strong rainfall seasonality; most storms correspond with extratropical cyclones that pass between October and May, and the majority of annual precipitation falls in just a few large events (Beighley et al. 2005). A shorter rainy season (with more runoff), and increasing temperatures (with higher evapotranspiration [ET] rates) will likely reduce available water in chaparral.

In addition to the projected increase in rainfall seasonality, interannual rainfall patterns are expected to become more variable over the next several decades, which may alter fuel characteristics and fire regimes in chaparral (Westerling et al. 2006). For instance, woody biomass might accumulate over a series of wet years, promoting more severe fires during droughts (Swetnam and Betancourt 2010). Over time, changing climate may therefore intensify N export to streams, which could alter net primary productivity. To understand how seasonal precipitation and climate patterns regulate the effects of fire on N dynamics, it is necessary to assess not only the mechanisms controlling the immediate postfire N flush, but also the longer-term processes that correspond with ecosystem recovery.

Postfire N balance can vary depending on how fire alters the physical environment, as well as the rate and trajectory of plant recovery. Simulation modeling is a useful tool for linking patterns and processes that occur over different spatial and temporal scales, and for exploring the feedbacks that control N cycling and export as ecosystems recover. In semiarid regions, such as chaparral, modeling tools that incorporate interactions between vegetation and hydrology are critical because ET can account for more than 70% of annual water use (Poole et al. 1981), and because hydrology is a dominant control over microbial activity, nutrient dynamics, and NO_3^- export (Miller et al. 2005).

We developed a modeling experiment to evaluate the role of precipitation patterns in shaping ecosystem responses to fire using the mechanistic ecohydrologic model RHESSys (Tague and Band 2004). RHESSys employs a hydrologic model that is fully coupled with a biogeochemical model, allowing it to account for feedbacks among vegetation, hydrology, and soils over time in a watershed (Tague and Band 2004). RHESSys is therefore ideal for evaluating the effects of fire in semiarid systems because ecosystem processes in these systems are also tightly coupled with moisture conditions (Tague et al. 2004, 2009, Miller et al. 2005, Shields and Tague 2012). We addressed the following questions: (1) How does interannual climate variability affect the magnitude of postfire N export? Specifically, does total export change when fires occur during years with average precipitation, during prolonged (multi-year) drought, or during climatic transitions (e.g., dry to wet, or wet to dry periods)? (2) Do the effects of precipitation patterns in the years before or after fire extend over time to influence decadal scale plant recovery and N dynamics?

METHODS

Study site

We simulated stand-level climate–fire interactions in Rattlesnake Canyon, which is a 7-km^2 subcatchment of the Mission Canyon watershed (31 km^2), located in the Santa Ynez Mountains in southern California, USA (34°28′ N, −119°40′ E; Fig. 1). The Santa Ynez Mountains are located along the western boundary of the east-west trending Transverse Ranges. Climate in the region is Mediterranean, with cool wet winters and hot dry summers. Mean annual precipitation ranges from 500 mm/yr at lower elevations to 850 mm/yr near the mountain tops, 80% of which typically falls between December and March (Beighley et al. 2005). Temperatures vary from 0°C in winter to 40°C in summer. Elevations in Rattlesnake Canyon range between 270 and 1262 m, and slopes are generally somewhere between 20% and 50%, though they can reach 100% in some areas. Soils in the region are rocky, nutrient-poor, sandy loams, classified as Typic Dystroxerepts from the Maymen series (NRCS 2015), though soil characteristics vary with elevation. These soils are shallow, well-drained, acidic, and highly erodable (NRCS 2015). Infiltration capacity is generally high in chaparral, and therefore, most hydrologic
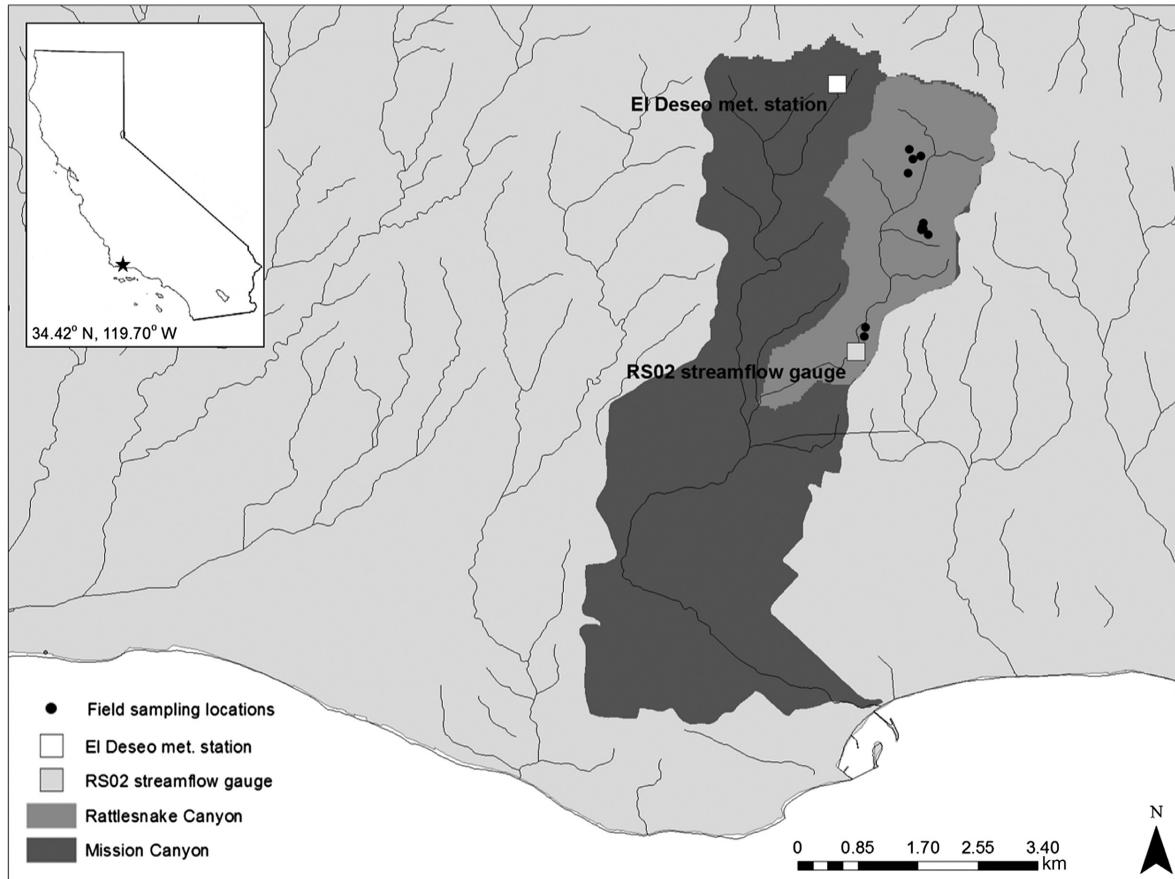
FIG. 1.   Study site in the Santa Ynez Mountains in Santa Barbara County, California, USA. The Rattlesnake Canyon catchment is nested within the upper reach of the Mission Canyon watershed.

transport occurs through shallow subsurface flow. Two related empirical studies were conducted in Rattlesnake Canyon to evaluate the controls over N cycling and retention following a landscape fire that occurred in 2009 (Hanan et al. 2016*a, b*). In this fire, burn severity was high across upland ecosystems, and low in riparian areas, which is typical of the crown-fire regime in chaparral.

Vegetation on the slopes of Rattlesnake canyon includes sclerophyllous evergreen shrubs, dominated by *Ceanothus megacarpus* (big pod ceanothus), *Adenostoma fasciculatum* (chamise), and *Arctostaphylos* spp. (manzanita). *Heteromeles arbutifolia* (Toyon), *Cercocarpus betuloides* (Mountain mahogany), and other mesic chaparral species are also present. These species are well adapted to severe crown fires. Following fire, chaparral shrubs employ three major reproductive and recovery strategies: (1) obligate seeders are killed by fire and reestablish through seed germination cued by heat, smoke, or char (e.g., *C. megacarpus*); (2) obligate resprouters survive fire and regrow from basal lignotubers (e.g., *Rhamnus californica*); (3) facultative resprouters can regenerate by a combination of both strategies (e.g., *Adenostoma fasciculatum*; Keeley et al. 2005). Obligate seeders and facultative resprouters dominated the study

area. Postfire herbs such as *Calystegia macrostegia* (coast morning glory), and suffrutescents (i.e., sub-shrubs) such as *Acmispon glaber* (deerweed) also establish rapidly after fire with the onset of autumn rain, and play an important role in nutrient retention and cycling during the early stages of recovery (Rundel and Parsons 1984, Hanan et al. 2016*a*). *C. megacarpus* and *A. glaber* are both symbiotic N-fixers and can increase ecosystem N-storage in both plant biomass and litter (Nilsen 1982). While ephemeral herbs dominate the immediate postfire landscape, sclerophyllous shrubs tend to recover closed canopies and displace herbaceous and suffrutescent vegetation within 10 years (Gray and Schlesinger 1981).

RHESSys model

RHESSys is a coupled ecohydrologic-biogeochemical model that has been run successfully in Mission Canyon and other chaparral-dominated watersheds in California to capture interactions among climate, soils, vegetation, and hydrology (Tague et al. 2004, 2009, Tague and Pohl-Costello 2008, Shields and Tague 2012). RHESSys requires climate inputs in the form of temperature and precipitation, and then uses topographic data from

digital elevation models to extrapolate spatial variation in these inputs as well as solar radiation over mountainous terrain using the MTN-CLIM approach (accounting for orographic effects; Running et al. 1987, Tague and Band 2004). RHESSys models rainfall interception by plants, infiltration into the soil, evaporation, and transpiration (using a Penman-Monteith approach), and vertical drainage. Water fluxes interact with several vegetation and soil parameters to generate time series outputs of both hydrologic and biogeochemical dynamics. Tague and Band (2001, 2004) provide a detailed description of the hydrologic and ecophysiological algorithms used to estimate each of these processes.

RHESSys considers multiple canopy layers by partitioning sunlit and shaded leaves, and attenuating water and energy downward through the canopy (Tague and Band 2004). Photosynthesis is calculated using the Farquhar model (Farquhar and Von Caemmerer 1982), and net-photosynthate is allocated to leaves, stems, and roots for each vegetation layer using the Dickinson partitioning strategy, which accounts for changes in allocation that occur as a plant matures (Dickinson et al. 1998). Because canopy layers compete for light, water, and nutrients, RHESSys can simulate the development of an herbaceous layer immediately after fire that declines in productivity as shrubs more slowly recover and intercept incoming solar radiation. Transpiration and photosynthesis both respond to stomatal conductance in the model, which declines with soil water availability, thereby linking vegetation growth and productivity with climate and hydrology. An important component of this linkage is that plant access to water varies with root C, which varies with C assimilation. This allows us to distinguish between resprouters, which retain some root carbon after fire, and seeders, for which root carbon (and therefore access to water) must develop over time.

Decomposition routines are modified from BIOME-BGC and CENTURY-NGAS, which model litter and soil C and N dynamics at a daily time step as a set of pools and fluxes among those pools (Parton 1996, Tague and Band 2004, Nemani et al. 2005; Fig. 2). RHESSys represents these fluxes (e.g., decomposition, microbial turnover, mineralization, immobilization, etc.) as first-order kinetics. To account for decelerating decomposition rates over time, RHESSys divides litter and soil organic matter into four compartments each, based on their varying recalcitrance. Each compartment is characterized by a unique decomposition rate constant, substrate use efficiency (regulating the amount of carbon respired), and C:N ratio (determining the amount of nitrogen mineralized or immobilized at each time step). Microbes are considered part of the fast cycling SOM pool (soil 1; Fig. 2). Rates are further modified by temperature and moisture.

Nitrification is calculated based on the CENTURY N-GAS model as a function of available substrate (i.e.,
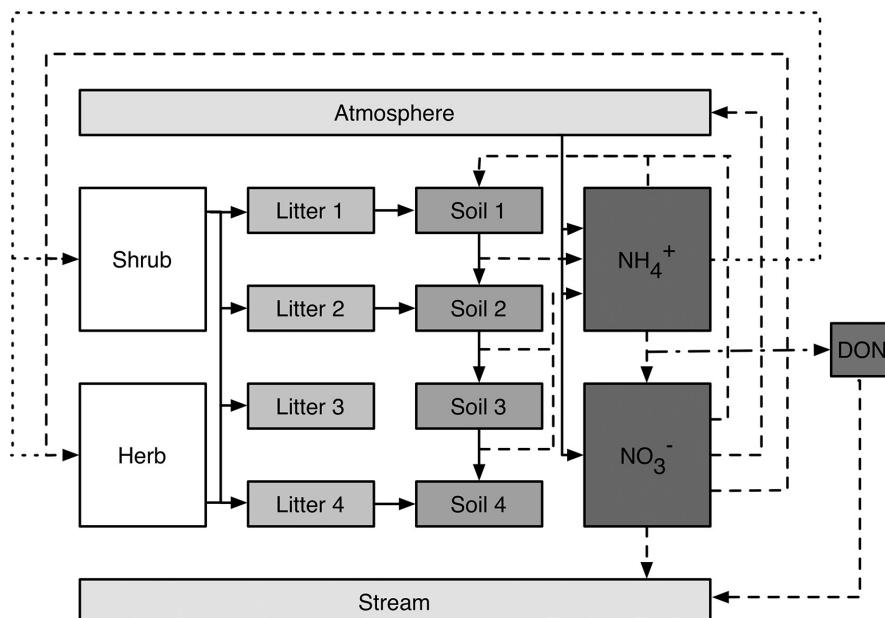

Fig. 2. Conceptual model for RHESSys (regional hydro-ecologic simulation system) N cycling: soil C and N dynamics are modeled at a daily time step as a set of pools and fluxes. As plants turn over, organic C and N are divided into four litter and four soil compartments, each regulated by unique substrate use efficiencies (regulating the amount of carbon respired), and C:N ratios (determining the amount of N mineralized or immobilized at each step). Litter pool 3 is considered shielded cellulose and does not decompose into soil 3. Two pools are used to represent inorganic N (NH_4^+ and NO_3^-). C and N budgets are calculated for each organic compartment, and N budgets are calculated for the NH_4^+ and NO_3^- pools. A fraction of mineralized nitrogen is lost from the system as dissolved organic nitrogen (DON) at each stage N cycling.

mineralized soil NH_4^+), soil temperature (T), and moisture (H_2O; Parton 1996). Nitrate can then be taken up by plants or lost from the soil through flushing and denitrification. Also, a fraction of mineralized N is lost as dissolved organic N (DON) at each step of N cycling.

Although RHESSys can be applied as a spatially distributed model, we used a single patch to represent a typical chaparral stand (i.e., aggregated landscape tessellation strategy), in order to focus on the specific mechanisms regulating interactions between climate and fire over time, while minimizing uncertainty associated with lateral redistribution of both moisture and N within the watershed. Using an aggregated model allows us to generate hypotheses about which mechanisms are most important in regulating stand-scale ecosystem responses to fire as climate continues to change. It also allows us to refine our understanding of those mechanisms, which can then be used to drive more realistic whole-watershed predictions of water and N-export under different fire regimes and climate scenarios. We present results from a biologically active soil layer for an upslope chaparral stand with a west-facing aspect and a relatively steep slope of 28.55°. Because aspect influences soil temperature and moisture (Miller 2012) as well as rates of plant regeneration (Black 1987), we repeated our simulations for patches with north- and south-facing aspects. We use these patch-scale simulations to explore how in-situ N cycling, retention, and export respond to climate and fire. Because RHESSys was run with one patch, embedded within one hillslope, in one basin, N-export reflects N-leaching below the rooting zone and lateral transport out of the patch; thus potential N-contribution to the stream. However, some of this exported N might otherwise be used by downslope vegetation, including riparian woody plants that occur in narrow corridors around streams, which typically do not burn.

Daily precipitation and temperature data were taken for water years 2001 to 2007 from a nearby National Climate Data Center (NCDC) monitoring site near the top of Rattlesnake Canyon (El Deseo; Fig. 1). Streamflow was recorded at Gauge no. RS02, monitored by the Santa Barbara Coastal Long Term Ecological Research Network (SBC-LTER; Fig. 1), and Chen et al. (2016) used streamflow data to calibrate the soil parameters controlling vertical and lateral flow rates in Rattlesnake Canyon. He also found that RHESSys estimates of basin-scale N export match well with rates measured by the SBC-LTER. RHESSys assigns soil and vegetation parameters according to soil and vegetation type; details describing this approach are provided by Tague et al. (2004). Soil and vegetation parameters were assigned based on literature (Ackerly 2004, Vourlitis et al. 2007, Hanan et al. 2016a) and existing spatial data layers (White et al. 2000, Tague et al. 2009). We initialized soil and plant C and N stores using a two-step spin up approach. First, we ran a 1000-yr spin up simulation to allow soil C and N pools to reach steady state. Then to initialize plant C and N (in leaves, stems, and roots), we reset existing pools to zero, and then ran a 50-yr spin up simulation. We generated climate data for these simulations by repeating the available 7-yr meteorological record.

We ran paired simulations for stands dominated by obligate seeders and for stands dominated by resprouters. Vegetation parameters were identical in both sets of simulations (parameterized to represent typical sclerophyllous evergreen shrubs) with one exception: resprouters allocated 5% of their annual assimilated C to belowground storage. Our representation of fire effects on biomass also differed between resprouters and reseeders (see details below). We incorporated an ephemeral herbaceous stratum that interacted with recovering shrubs in the immediate postfire landscape. This stratum was parameterized to generally represent short-lived perennial herbs, using data for *C. macrostegia* where available. We used N deposition rates of 0.05 g·m^{-2}·yr^{-1} for NH_4^+, and 0.15 g·m^{-2}·yr^{-1} for NO_3^- (Schlesinger et al. 1982, Bytnerowicz and Fenn 1996). While these rates are low, they are appropriate in the Santa Ynez mountains, which are not downwind of major urban or agricultural areas (unlike many other chaparral ecosystems in southern California; Weiss 2006).

Fire

Chaparral typically burns under a crown fire regime (i.e., high severity across upland ecosystems), so to introduce fire in our simulations, we removed 98% and 99.5% of all aboveground vegetation and litter C and N pools, respectively, corresponding to observations by Debano and Conrad (1978) following a severe wildfire in chaparral. For obligate seeders, we also removed root C and N as above, while, for resprouters, we removed 25% of root C and 44% of root N to account for fire-caused mortality that sometimes occurs (Keeley and Keeley 2000). To account for pH effects on nitrification following fire, we adjusted the nitrification process model in RHESSys to account for the effects of pH, such that

$$N_{nitrified} = f NH_4^+ f T f H_2O f pH \qquad (1)$$

where the pH scalar on nitrification was calculated following Parton (1996) as

$$pH_{scalar} = \frac{0.56 + \arctan(pi \times 0.45 \times (-5 + pH))}{pi} \qquad (2)$$

We created a pH time series using monthly field measurements collected over two years in Rattlesnake Canyon following a large wildfire (Hanan et al. 2016a). Baseline pH values were set to 5.45. Finally, we added 2.1 g NH_4^+/m^2 to soil surfaces to represent ash inputs (Christensen and Muller 1975), and reduced vertical hydraulic conductivity from 1.0 to 0.1 to account for postfire hydrophobicity, with a logistic return to prefire levels over a period of four years (DeBano 2000).

Simulations

To evaluate the effects of fire timing on nitrogen fluxes in chaparral, we ran 30 simulations: 15 for obligate seeders and 15 for resprouters. Each simulation spanned 40 years and experienced a single fire during one of the middle 15 years of simulation, allowing us to compare the effects of fire under various climate scenarios. For each simulation we ran the model for at least 15 years, prescribed a fire on 20 May 20 for one of the second 15 years of climate data (i.e., years 16–30), and then allowed the model to continue running for the duration of the timespan. Thus, each simulation encompassed at least 15 years prefire and at least 15 years of recovery. We focused on the first decade of recovery because plant growth and N uptake decline within 10 years postfire as nutrients become immobilized in plant biomass (Black 1987). The date 20 May was selected as the fire date to correspond with the timing of a large landscape fire that occurred in the region in 2009 (Hanan et al. 2016a). To generate our 45-yr climate sequence, we used 7 yr of climate data from the NCDC monitoring site near the top of Rattlesnake Canyon (water years 2001–2007; Table 1). Data were looped to generate the 45-yr time series. The 2001–2007 climate sequence covered some very wet years (e.g., water year 2005), however total annual precipitation can fall below 265 mm in Santa Barbara during extreme drought (Michaelsen et al. 1987), while our two driest years had 403 and 368 mm of rainfall (at El Deseo), respectively. Although these values do not represent the most extreme drought conditions, they are still relatively dry, especially when considering that these precipitation measurements were taken near the top of Rattlesnake Canyon, where there are strong orographic effects (Beighley et al. 2005).

To evaluate the impacts of climate, we classified each of the 15 simulated fire years as dry, intermediate, or wet, according to modeled ET using a mature chaparral stand (in the absence of fire), and years with intermediate ET were further subdivided according to rainfall (Fig. 3). Although real climate data only spanned 7 years (2001–2007), these climate years were shuffled and looped to span the 15-year period during which fires were simulated. Doing so provided different ET projections for

TABLE 1. Total precipitation for water years 2001–2007.

Water year	Total precipitation (mm)
2001‡	1271.4
2002†	403.0
2003	994.6
2004	485.6
2005‡	2306.9
2006	1134.2
2007†	368.0

Notes: The years 2001–2007 were looped to generate a 45-year climate sequence (1991–2036). The years covered by real climate data are also listed.

† Two driest years used for restructured rainfall scenarios.

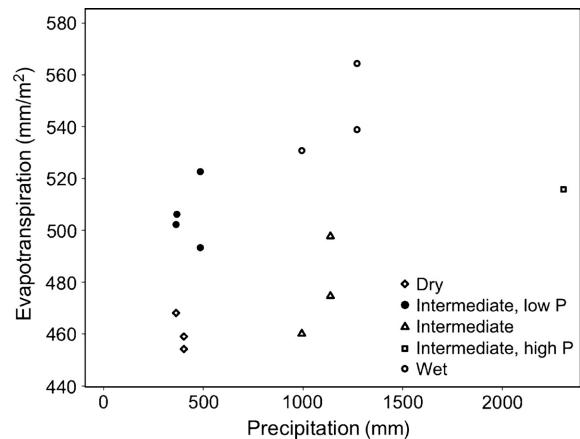‡ Two wettest years used for restructured rainfall scenarios.

Fig. 3. Annual precipitation and modeled evapotranspiration (ET) for each of the years used to simulate fire. Values were modeled in the absence of fire. ET values were used to classify years as dry, intermediate, or wet. Years with intermediate ET were further subdivided according to precipitation.

each simulation year since ET is also a function of antecedent conditions. Also, in semiarid areas, where rainfall is dominated by highly episodic, high-intensity events, water availability for plants is determined as much by the temporal distribution of rainfall as by total annual precipitation (Shields and Tague 2012). Using ET to classify climate conditions allowed us to integrate the effects of that year's precipitation as well as antecedent conditions on water availability. When a given year followed a wet year, transpiration could be high even when total precipitation was low for that year (e.g., water year 2011). However, if rainfall in the wet year came in just a few large events (generating high runoff and promoting longer dry-down periods), ET might still be low the following year (e.g., water years 2009 and 2016). Water years 2009, 2016, and 2021 had the lowest simulated ET and were therefore considered dry; years 2008, 2010, and 2015 were considered wet, and all other years were considered intermediate (Fig. 3).

To evaluate how more extreme climate variability might impact N dynamics, we restructured our climate sequences by looping the two driest years (based on rainfall) and the two wettest years (forming a 4-year sequence for each; Table 1). Using this restructured rainfall, we generated four climate sequences: (1) DFD, four years of drought, followed by fire, then four more years of drought; (2) DFW, four years of drought, fire, then four wet years; (3) WFW, four wet years, fire, then four more wet years; and (4) WFD, four wet years, fire, followed by four dry years. Each of these scenarios was embedded in the 45-yr climate sequence (outlined above) by replacing years 16–23 with our restructured rainfall data, and simulating fire in year 20. Although precipitation patterns for much of the western United States are often strongly correlated from one year to the next (due to El Niño and La Niña cycles), this is not the case in Santa Barbara County where interannual rainfall

variability can be extremely high (Michaelsen et al. 1987). Therefore, it is reasonable to sample from the historical climate record to create example scenarios that may occur with climate change. Then to evaluate the effects of these example scenarios we modeled mineralization, nitrification, N leaching, and plant uptake. Because these simulations were parameterized for an idealized average patch, our results illustrate how fire timing can influence potential N-export from an average upland chaparral ecosystem.

RESULTS

Leaf area index (LAI) is an indicator of growth and recovery, and is a critical variable in photosynthesis, respiration, transpiration, and rainfall interception. LAI tended to recover to its prefire state within 10 years for all RHESSys simulations regardless of rainfall although plants recovered slightly faster when fires occurred during wet years (Table 2). Model estimates are consistent with observations of the time it takes for chaparral to form a closed canopy (Keeley et al. 1981). In the first few years of recovery, shrub LAI recovered more slowly for obligate seeders than it did for resprouters, which is also consistent with field observations (Guo 2001). Slower shrub recovery allowed ephemeral herbs to grow more extensively and persist longer in stands dominated by seeders (Fig. 4a, b; Table 2).

Effects of current climate variability on postfire N flush

N cycling and export patterns were similar among simulations with north-, south-, and west-facing aspects, though the magnitude of N losses varied slightly among simulations; in simulations with a north-facing aspect, drought increased N export to a greater extent than it did in simulations with a south- or west-facing aspect. Because patterns were similar, however, we only show results from the neutral (west-facing) patch. RHESSys simulations captured seasonal NO_3^- export to streams, though fluxes were low, which is consistent with observations by Riggan et al. (1985) for relatively unpolluted chaparral watersheds. NO_3^- export increased by several orders of magnitude after fire and returned to baseline conditions within the first few years of recovery (Fig. 5).

Postfire N balance varied between obligate seeders and resprouters; less N was nitrified over the recovery period

TABLE 2. Average number of years for leaf area index (LAI) to recover to its prefire condition (within 0.2) for dry, intermediate, and wet years; and for seeders vs. resprouters.

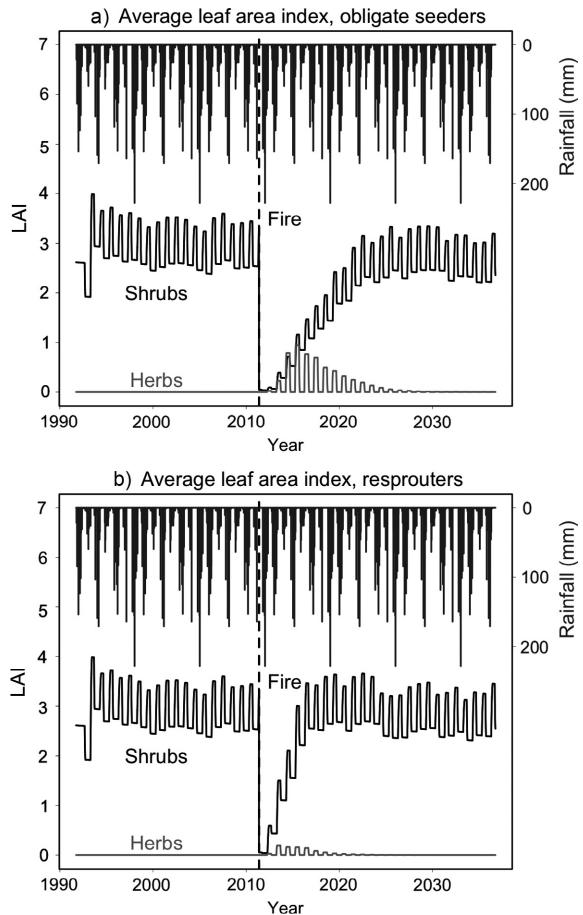| Moisture conditions (fire year)	Years to recover	
	Obligate seeders	Resprouters
Dry	10	5
Intermediate	10	5
Wet	9	5

FIG. 4. Precipitation and recovery of leaf area index (LAI) for both shrubs and ephemeral herbs averaged over all simulations for (a) obligate seeders and (b) resprouters. Annual fluctuations are due to seasonality of leaf production.

in stands dominated by resprouters because more mineral N was taken up by recovering plants (Fig. 6). NO_3^- production and accumulation were higher for obligate seeders after fire due to initially slower plant recovery, which corresponded with higher rates of denitrification after fire.

To further explore the effects of climate variability on these fluxes, we evaluated cumulative nitrification, NO_3^- export, and N uptake for each of 15 climate–fire scenarios (Fig. 7). Nitrification rates were extremely low prefire, and then increased by several orders of magnitude immediately after fire for all simulations; they were highest during the first two years of recovery, and then returned to prefire rates within three years (Fig. 7a, b), which is consistent with field observations (Hanan et al. 2016a). Postfire nitrification was almost doubled in stands dominated by obligate seeders compared to resprouters. Also, for stands dominated by seeders, nitrification increased slightly more when fires occurred during dry years (Fig. 7a). For both plant types, the total amount of N nitrified over the postfire recovery period was generally
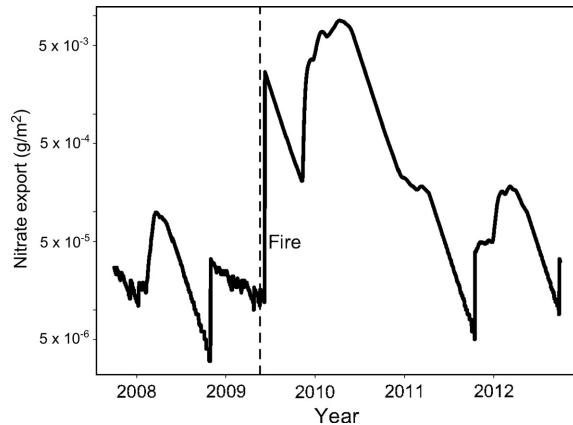
FIG. 5. Example of N export over five years of simulation with a fire occurring on 20 May of the second year. N export includes NO_3^-, NH_4^+ and dissolved organic N (DON). Results are illustrated on a log scale.
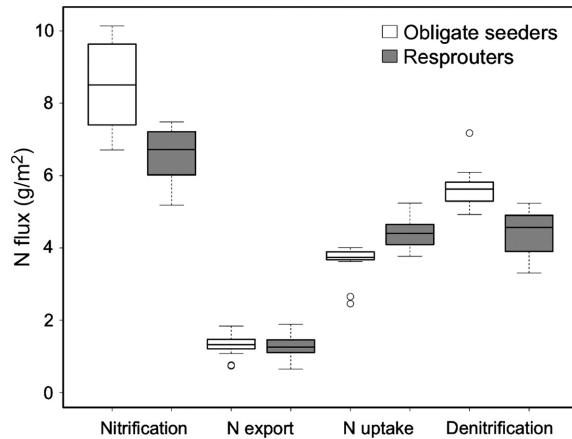

FIG. 6. Cumulative N fluxes after one year of recovery for all simulations for obligate seeders (white boxes) and resprouters (gray boxes). Boxplots show the upper and lower quartile for each variable, heavy lines inside each box are the mean values, upper and lower whiskers are the minimums and maximums for each variable (excluding outliers), and point are outliers.

larger when fires occurred during either drought or periods of high rainfall compared to when fires occurred during average years (Fig. 7a, b).

Cumulative NO_3^- export varied more substantially with climate than nitrification; export was up to an order of magnitude higher when fire occurred during dry years (i.e., cumulative export was as low as 0.25 g/m^2 in an average year, and as high as 1.9 g/m^2 during drought; Fig. 7c, d). NO_3^- export was generally low when fire occurred in wet years, and more variable during average years. Drought increased NO_3^- export more intensely in stands dominated by obligate seeders than in stands dominated by resprouters (Fig. 7c, d). Recovering plants immobilized some of the NO_3^- produced postfire, and plant growth varied most among simulations for resprouters (Fig. 6a, b).

Effects of more-extreme climate variability on postfire N flush

When precipitation patterns were restructured to simulate greater interannual rainfall variability, climate effects on recovery rates became more pronounced. When fire was followed by drought (i.e., DFD and WFD simulations), obligate seeders' LAI recovered more slowly than when fire was followed by higher-than-usual rainfall (Table 3). For resprouters, on the other hand, the prefire conditions were more important in regulating postfire recovery: LAI recovered more slowly when fire was preceded by drought (i.e., DFD and DFW simulations). Similar to simulations using current climate data, recovery rates were more rapid for resprouters than for obligate seeders, which allowed herbs to thrive over a longer period of time in stands where shrubs had to regrow from seeds than in stands where they resprouted (e.g., Fig. 8a, b; Table 3).

In extreme climate simulations, NO_3^- production also became more divergent among simulations (Fig. 9a, b). Nitrate accumulated most in soils when fire was followed by drought: the DFD and WFD treatments both accumulated more NO_3^- than either treatment that was followed by a wet period (DFW, WFW). The greatest NO_3^- accumulation, however, occurred in the middle of a drought (DFD simulations; Fig. 9a, b). Also, soil NO_3^- accumulated more, and over a longer period postfire, in WFD simulations when stands were dominated by obligate seeders (Fig. 9a, b).

NO_3^- export also varied with climate; in DFD and WFD simulations, the initial flush lagged behind DFW and WFW simulations, but the amount exported was more substantial (Fig. 9c, d). DFD and WFD simulations generated two separate NO_3^- pulses when stands were dominated by obligate seeders (Fig. 9c), while only the DFD simulation generated a second pulse when stands were dominated by resprouters (Fig. 9d). The periodic turnover of postfire herbs (which were more prevalent in stands dominated by seeders) may have contributed to the second NO_3^- pulse observed in the DFD and WFD simulations.

When considering an entire decade of recovery, the total amount of N nitrified was larger when fire occurred during drought (or was followed by drought); total nitrification was higher in DFD and DFW than in WFW and WFD simulations (Fig. 10a, b). Similarly, NO_3^- export was higher in DFD and WFD simulations. The effect of postfire drought was stronger (i.e., export was greater) in stands dominated by obligate seeders than in stands dominated by resprouters (Fig. 10c, d), because plant recovery (and therefore N uptake) was more rapid for resprouters (Fig. 8a, b).

DISCUSSION

Potential N export was sensitive to the climate conditions occurring in the first few years after fire, such that
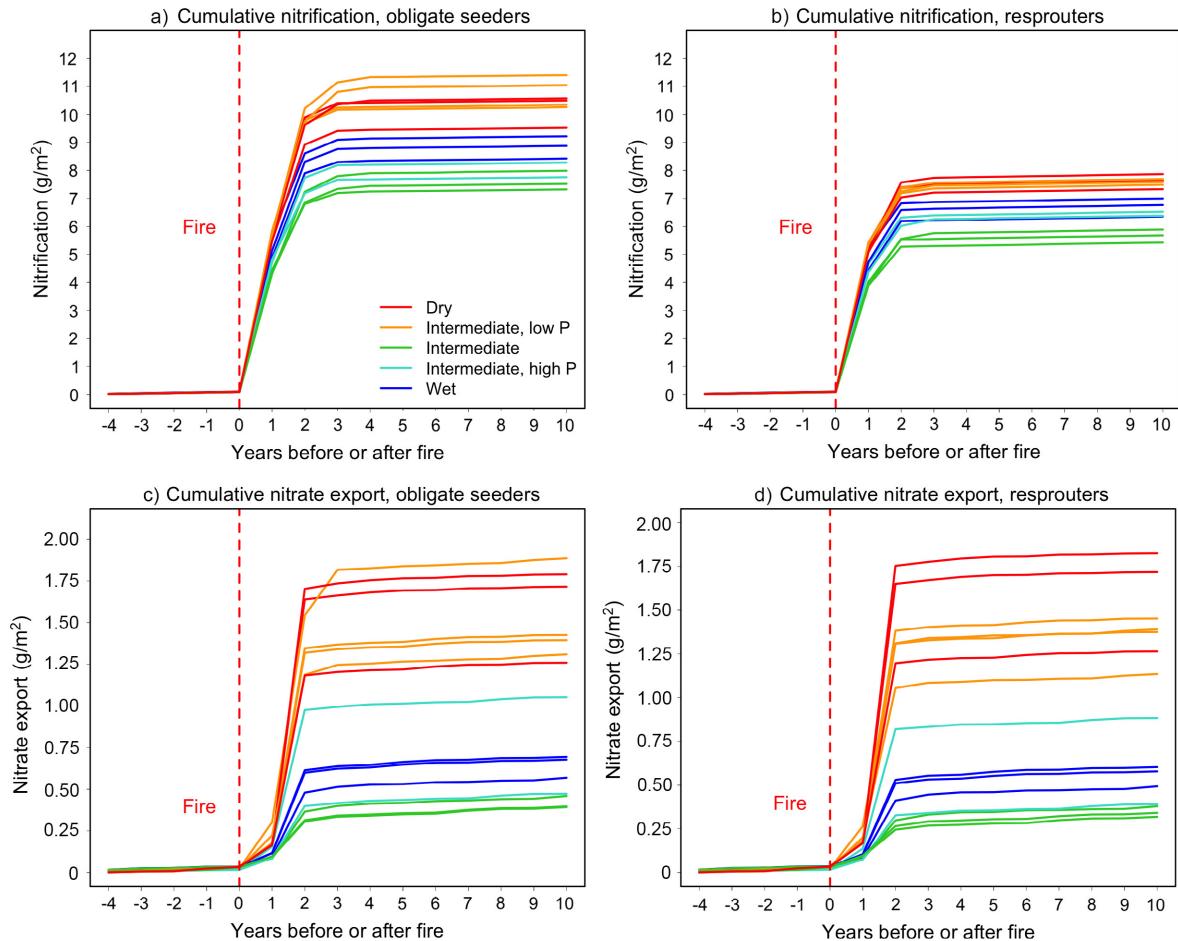
Fig. 7.   Results from simulations using current climate data: (a) cumulative nitrification for each of the 15 simulations for stands dominated by obligate seeders, (b) cumulative nitrification for stands dominated by resprouters, (c) cumulative nitrate export for stands dominated by obligate seeders, and (d) cumulative nitrate export for stands dominated by resprouters. Each of the 15 simulated fire years were classified as dry, intermediate, or wet, according to modeled ET, and years with intermediate ET were further subdivided according to precipitation (*P*).

cumulative N-export from an upland chaparral patch varied by more than an order of magnitude across climate sequences derived from historic data. Surprisingly, export was highest when fire was followed by drought; even though there was less water moving through the system, plant recovery and nutrient uptake were slower

Table 3.   Number of years for LAI to recover to its prefire condition (within 0.2) for each of the restructured rainfall scenarios; and for seeders vs. resprouters.

Climate scenario	Time to recover (yr)	
	Obligate seeders	Resprouters
DFD	11	7
WFD	11	5
DFW	9	7
WFW	9	6

Note: Climate scenarios are DFD, dry, fire, dry; DFW, dry, fire, wet; WFW, wet, fire, wet; WFD, wet, fire, dry.

under drought. Dry conditions also prolonged the period during which N mineralization and nitrification were decoupled from plant uptake, which allowed mineral N to accumulate and be subsequently flushed from soils upon wetup. The effects of drought on N export were magnified in stands dominated by obligate seeders. Seeders have less biomass and a smaller root network than resprouters during the early stages of recovery, which make them more susceptible to dry conditions following fire.

Fires intensify N export by increasing mineral N supply (through ash deposition), by reducing plant and microbial demand for N, and by reducing plant demand for water and increasing water flux. Globally, N export generally increases with increasing precipitation (Gallo et al. 2015). Our model results illustrate how a combination of greater drought effects on plant uptake relative to drought effects on microbial processes, combined with sporadic high-intensity rainfall, can lead to the higher N export following drought in Mediterranean environments. These
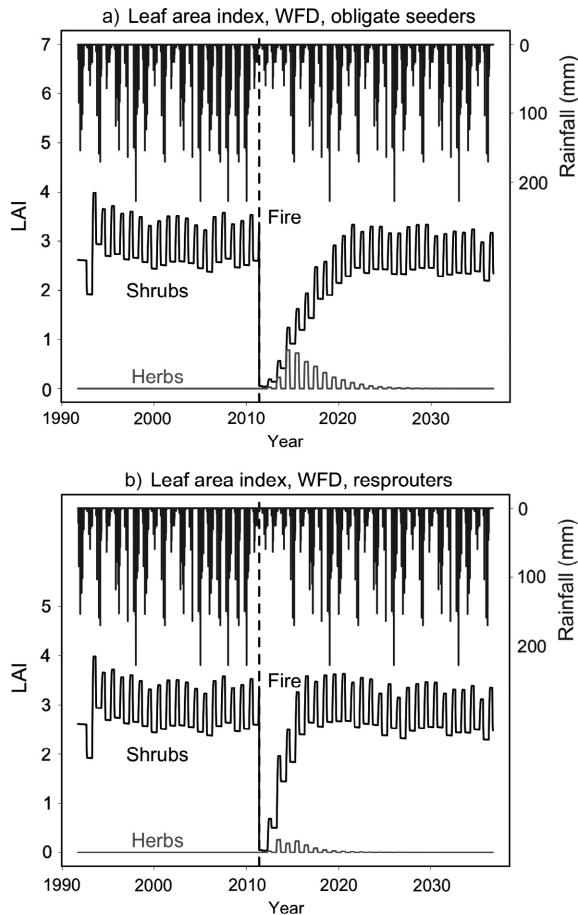
FIG. 8. Precipitation and recovery of leaf area index (LAI) for both shrubs and ephemeral herbs for DFW (dry, fire, wet) simulation: (a) obligate seeders, (b) resprouters.

findings suggest that Mediterranean-type climate may regulate N balance most powerfully by influencing how quickly plants "turn on" and begin to take up N.

Previous field-based studies also suggest that chaparral and other semiarid ecosystems naturally leak N and that this occurs because soil microbes are generally less sensitive than plants to low soil water potential and can metabolize N in hydrologically disconnected microsites when plants are still dormant or senescent (Jackson et al. 1988, Austin 2002, Austin et al. 2004, Parker and Schimel 2011). Although RHESSys does not explicitly model soil microsites with a patch, it does account for the empirical relationships between soil moisture and nitrification, hydraulic conductivity, and plant growth. Therefore, model results are consistent with this general understanding, and also show how the magnitude of these effects following fire is likely to vary with inter-annual climate variation and with plant functional type. In addition to elevated N export during drought, we found that NO_3^- was also more vulnerable to leaching when fires occurred during wetter than average years because soil moisture increased nitrification rates relative to plant

uptake. Thus N loss is greater during both extreme wet and extreme dry years (drought), although the impact of drought is much greater than the impact of increased rainfall in the postfire environment. These results suggest that projected increases in interannual climate variability may increase N loss in chaparral by enhancing nitrification relative to plant uptake during wet years, or by decreasing uptake relative to nitrification during drought.

Effects of climate on postfire biogeochemical processes

RHESSys simulations suggest that when fires occur during relatively dry years, NO_3^- accumulates to a greater extent than it does under other climate scenarios. This occurs because fires supply NH_4^+ in ash and reduce plant cover, which might otherwise take up soil mineral N (Fenn et al. 1993). Dry conditions then allow nitrification to proceed at low rates over prolonged periods of plant dormancy. Fires also consume litter and surface soil organic matter, thereby suppressing heterotrophic microbial activity and corresponding N immobilization (Hanan et al. 2016a). Although RHESSys does not explicitly model microbial dynamics, heterotrophic microbes are considered part of the fast cycling SOM pool, which competes with plants and nitrifiers for NH_4^+. Therefore, RHESSys implicitly represents the reduced competition with heterotrophs and so allows NO_3^- to accumulate after fire and during drought. In addition to promoting NO_3^- accumulation, dry conditions surrounding fire also allowed NH_4^+ to accumulate and rapidly nitrify in later storm events, which enhanced total nitrification over the simulation period (Fig. 7a, b). The amount of N ultimately exported each day depends on the mineral N content in soil, and how much of that N is taken up by plants. Plant N demand depends on photosynthesis requirements each day. Because vapor pressure deficit is zero on rainy days, net photosynthesis and ET are low. And because, plant growth and N uptake are limited by water availability, N can accumulate in the soil during drought, and be rapidly flushed upon wetup. However, some of the N that accumulates in soils may also be denitrified. Denitrification rates were higher when fires occurred in the wettest vs. driest years; though intermediate years varied the most substantially (data not shown). Thus, elevated denitrification also helped constrain N leaching under the wettest conditions.

It is also worth noting that under current climate conditions, wet environments during the time of fire ultimately increased nitrification and NO_3^- accumulation relative to moderate conditions (Fig. 7a, b). This occurred because soil moisture promoted nitrification, and though plant uptake was also enhanced in wet years, recovering plants were not able to immobilize all of the NO_3^- produced. Hence, rainfall efficiently exported excess NO_3^-. While this mechanism increased NO_3^- export in wet years (relative to moderate but not dry years), export was still dampened by the rapid growth of postfire herbs. Herbs such as *C. macrostegia* can rapidly take up ash-deposited
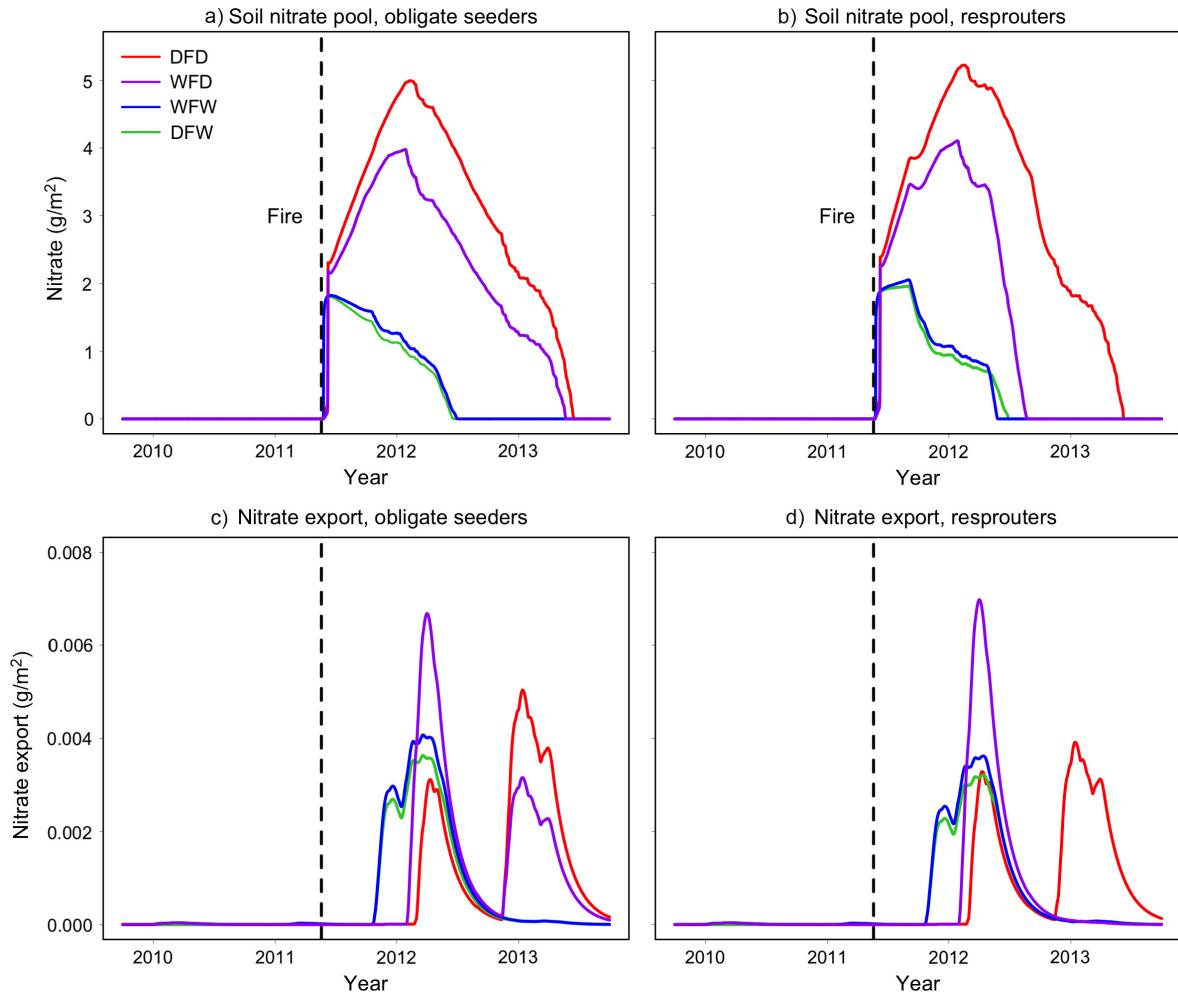
Fig. 9. Short-term results from simulations using repackaged climate data; DFD, dry, fire, dry; DFW, dry, fire, wet; WFW, wet, fire, wet; WFD, wet, fire, dry. (a) Nitrate accumulation for each of the four simulations for stands dominated by obligate seeders, (b) nitrate accumulation for stands dominated by resprouters, (c) nitrate export for stands dominated by obligate seeders, and (d) nitrate export for stands dominated by resprouters.

N, and gradually return it to the soil as they die back and decompose annually. Because herbs contain less lignin and other carbon-rich phenolic compounds such as tannins, their N-rich litter decomposes quickly and can release mineral N into the soil (Christensen and Muller 1975, Schlesinger and Hasey 1981); rapid herb growth following fire can suppress immediate leaching losses, while supplying nutrients to shrubs over subsequent growing seasons as herbs die and decompose (Rundel and Parsons 1984).

In extreme climate simulations there was greater total N export when fires were followed by drought than when fires were followed by heavier rainfall (Fig. 7c, d). Even under extreme conditions, rates of N export appear to be driven more by how much N is available to be leached than by the amount of water available to leach it. This reinforces the importance of plant uptake in constraining the amount of N available to be leached in these infertile soils (McMaster et al. 1982). For example, in the DFD

simulation, more NH_4^+ accumulated before fire, contributing to a larger postfire N flush and greater export. Heavy autumn/winter precipitation in WFW and DFW simulations on the other hand helped recovering plants take up mineral N and grow more quickly, thereby reducing leaching.

Species differences in postfire plant recovery and N uptake

Net primary productivity and N uptake can vary with life history strategy. For example, resprouting requires resources (especially C) to be allocated to belowground lignotubers that might otherwise be allocated to leaves and photosynthetic machinery (Pratt et al. 2012). While these physiological trade-offs may cause resprouters to grow more slowly than obligate seeders, resprouters can capture resources more rapidly after fire because their belowground C reserves support rapid shoot recovery
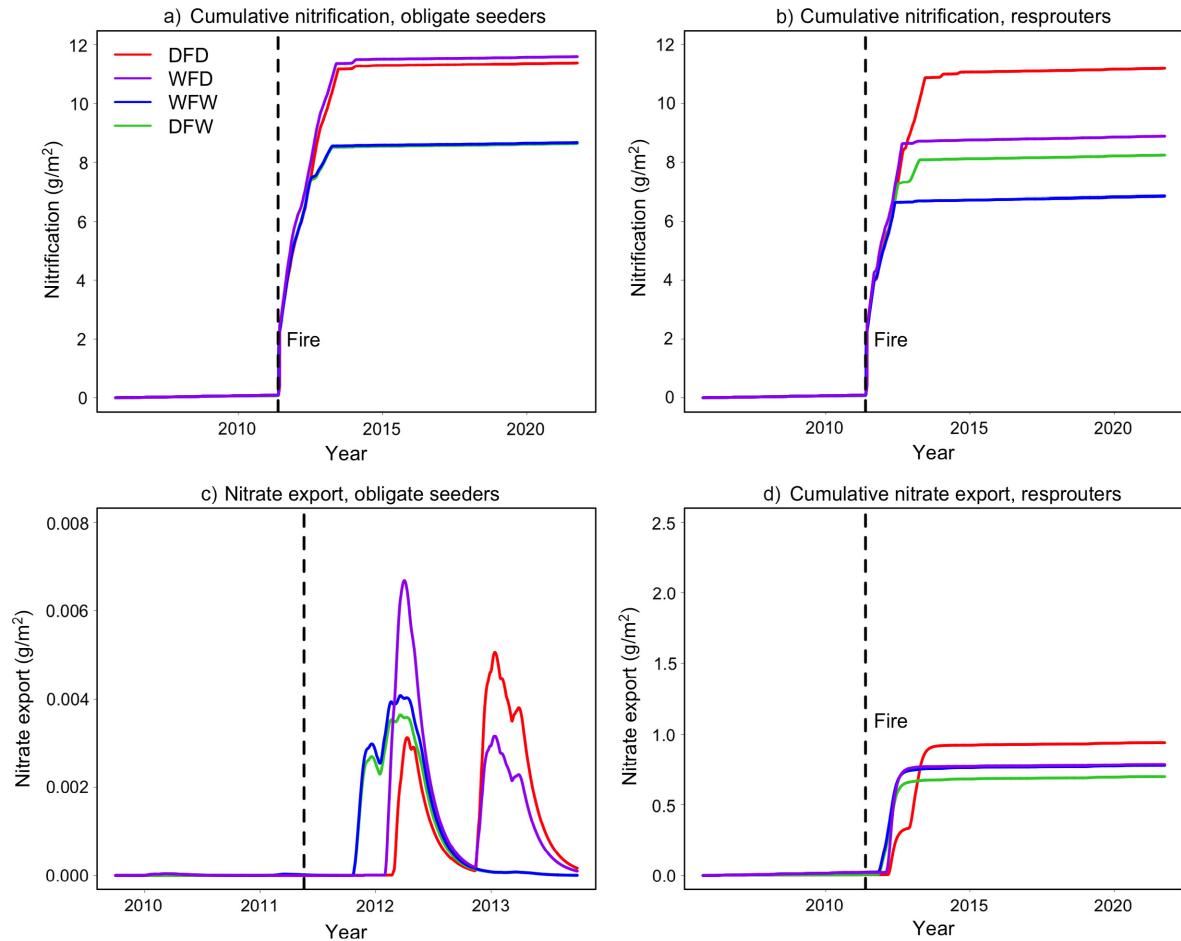
FIG. 10. Longer-term (cumulative) results from simulations using restructured climate data; DFD, dry, fire, dry; DFW, dry, fire, wet; WFW, wet, fire, wet; WFD, wet, fire, dry. (a) Cumulative nitrification for each of the four simulations for stands dominated by obligate seeders, (b) cumulative nitrification for stands dominated by resprouters, (c) cumulative nitrate export for stands dominated by obligate seeders, and (d) cumulative nitrate export for stands dominated by resprouters.

and their existing root network can readily capture soil resources (Bond and Midgley 2001, Davis et al. 2002). In our model scenarios, when fire was followed by drought, resprouters recovered and immobilized N more quickly than obligate seeders (Table 3), even though seeders are well adapted to water stress (Pratt et al. 2008). This led to a larger and more prolonged NO_3^- flush in DFD and WFD simulations for obligate seeders (Fig. 9c, d).

When fire was preceded by drought, on the other hand, resprouters recovered more slowly, suggesting that if conditions are unfavorable prior to burning, resprouting shrubs are likely to have smaller non-structural carbohydrate pools and less root biomass, which can slow recovery. Recovery to prefire LAI was also slightly slower for resprouters when conditions both before and after fire were wetter than average (WFW relative to WFD simulations; Table 3). Although wet conditions prior to fire in this case helped sustain belowground resources, prolonged rainfall, cooler temperatures, and increased cloudiness postfire slightly reduced

net photosynthesis and ET. In addition to recovering shrubs, ephemeral herbs can help prevent postfire N loss (Hanan et al. 2016a), however their growth is also sensitive to soil moisture, so like shrubs, herbs did not immobilize N as rapidly during drought.

The time lag between rainfall and plant response can vary with plant phenology (Baker et al. 1982), however for some chaparral shrubs (e.g., *C. megacarpus*), phenology is more connected to photoperiod than to moisture conditions (Gill and Mahall 1986), so the timing of rainfall can play an important role in the amount of N that is taken up or exported. In the current study, a delayed onset of rainfall in drought simulations meant that N was lost in winter when shrubs were not actively growing, which may have contributed to the enhanced NO_3^- export we observed for both growth forms when fire was followed by drought. Nevertheless, the asynchrony between N mobilization and plant uptake clearly plays an important role in how much N is exported at the onset of autumn rain.

Longer term impacts

While clearly climate can generate large differences in biogeochemical fluxes over short timescales (0–3 years postfire) due to difference in postfire weather patterns and hydrology, we were also interested in whether the climate surrounding a fire event would influence recovery trajectories at decadal timescales, which is the time it takes for recovering shrubs to form a closed canopy. The strongest differences in N export occurred during the first 2–3 years of recovery, which fixed varying patterns upon the simulated ecosystems. For example, cumulative NO_3^- export was up to an order of magnitude higher when fire occurred during drought than when fires occurred during average years (Fig. 7c, d). However, following the initial 3 years of recovery there were few legacy effects (i.e., the patterns set up in the first three years persisted). These findings are consistent with streamflow observations in the region, which show that following an initial postfire flush, N export can rapidly return to baseline conditions (Coombs and Melack 2013, Verkaik et al. 2013). The role of climate in driving plant recovery and N immobilization may be even more pronounced in watershed subject to high rates of N deposition, where N export can outstrip plant recovery and N uptake for prolonged periods following fire (Vourlitis and Hentz 2016).

Conclusions

Models are an essential tool for exploring future scenarios given the uncertainty associated with climate change (Loehman et al. 2011). Using a coupled hydrological-biogeochemical model, we explored the differential effects of moisture on postfire nutrient cycling, balancing changes in plant growth against changes in soil nutrient mobilization. Our patch-scale simulations characterized potential N-export from an average upland chaparral ecosystem. We found that the extent of postfire nitrification and potential NO_3^- export can differ by up to an order of magnitude with current climate variability. N-export can be further modified by spatial processes occurring at the catchment scale, including downslope consumption of mobile N, N-inputs from adjacent patches, and N-export from riparian areas.

At the ecosystem scale, our model results demonstrate how N-export may be greatest when fire is followed by drought in this Mediterranean climate region, because plant recovery is more sensitive than microbial processes are to drought. Results also suggest that the effects of drought are likely to be amplified in stands dominated by obligate seeders. Although climate patterns prior to fire can set the stage for recovery, particularly for resprouters by influencing root C, the first few years after fire are the most critical for defining plant regrowth and consequently the magnitude of N losses. Our simulations project additional increases in N-export for more extreme (multi-year) drought scenarios. Further, because N loss can increase in chaparral during both relatively wet or dry years, our analysis suggests that projected increases interannual climate variability may generate a tipping point, where plants are no longer able to recover N that is lost due to export following fire.

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DATA AVAILABILITY