

VALIDATION OF A LANDSCAPE-LEVEL SIMULATION MODEL FOR ANALYSING BIOMASS MANAGEMENT IMPACTS ON FOREST ECOSYSTEMS

P.J. Weisberg (PI), S. Ganschow, W.W. Miller, and D.W. Johnson

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Summary

Our research addressed the question of how alternative fire regimes have influenced, or have the potential to influence in future, movement of nutrients from uplands to Lake Tahoe through surface runoff. We developed an ecological simulation model for analyzing the effects of varying fire regime, including fire suppression and prescribed fires for fuel management, on nutrient cycling for forests throughout the Tahoe Basin. Our model predicted nitrogen and phosphorus fluxes and pools for soil and litter components, as well as potential nitrogen leachate, for each 1-ha pixel within the Lake Tahoe Basin. Model outputs for carbon, nitrogen and phosphorus were validated using a field sample of soil and litter from over 110 randomly located sites within Jeffrey pine and chaparral ecoregions. Seven model scenarios were simulated, including one scenario representing continuation of fire exclusion practices, three prescribed fire scenarios, and three scenarios of mechanical biomass removal. Scenarios were implemented following an initialization period of 1000 years under the historical fire regime, followed by 120 years of fire exclusion. We used ANOVA and regression analysis methods to compare alternative fire and fuel management regimes, and to partition variance associated with fire severity, site biomass, relative dominance of N-fixing species, and ecoregion. Our research questions addressed: (1) the extent to which modeled nutrient pools differ under historical fire, fire exclusion, and current fire regimes; (2) how alternative management scenarios relating to prescribed fire and biomass removal compare with regard to long-term effects on nutrient pools; (3) the relative importance of fire and microbially-mediated decomposition for overall nutrient cycling dynamics; and (4) realistic ranges of N and P loading in surface runoff and snowmelt.

The hypothesis that N cycling dynamics are dominated by fire events more than by decomposition processes is generally supported, implying that deviations from natural disturbance regimes result in deviations in N dynamics and hence potential N inputs to Lake Tahoe. Fire exclusion in the Tahoe Basin has likely increased litter and total ecosystem N and P above their levels under historical fire regimes, although effects are more pronounced in ecoregions that formerly experienced more frequent fire (such as the Jeffrey pine forest type). However, leachate N has likely decreased due to lack of fire events associated with large pulses in nitrogen availability. Model results provide a means for evaluating the implications of alternative fuel management regimes for sources of N and P in leachate and surface runoff. Management strategies, such as prescribed fire, that reduce litter biomass will potentially reduce N and P in surface runoff. Prescribed fire may be more likely than a similar intensity of mechanical biomass reduction to increase leachate N, although this effect would be outweighed by a greater reduction in surface runoff nutrients. Reductions in nutrient inputs to Lake Tahoe are more likely to

be achieved through fuel treatments in Jeffrey pine and mixed conifer forest types. While treatments in chaparral are also likely to reduce potential nutrient availability to Lake Tahoe, high concentrations of soil organic matter in chaparral imply that treatments in this vegetation type pose a greater risk of nutrient transport associated with soil erosion. Fuel treatments at the currently implemented frequency (641 ha yr^{-1}) have the potential to reduce litter N and P below their levels under fire exclusion, but higher frequencies (approx. $2,089 \text{ ha yr}^{-1}$) would be required to reduce these nutrients to levels predicted for the historic range of variability scenarios.

Introduction

Lake Tahoe is renowned for its natural beauty, and water clarity is central to its high value as a cornerstone of the regional economy. A trend toward decreased water quality over the past several decades has been associated with increased nutrient loading (Jassby et al. 1999). Increases of lake nitrogen (N) and phosphorus (P) concentrations have led to decreases in lake clarity associated with increased algal growth, and an ecologically important shift from N limitation to P limitation of aquatic productivity (Stephens et al. 2004, Murphy et al. 2006). These most recent increases are attributed largely to anthropogenic sources including pollution, atmospheric deposition, and watershed manipulations that increase overland transport of eroded soils, fine sediments, and leached soil nutrients (Rowntree 1998). Clearly, lake water quality is closely coupled to upland watershed processes (Coats et al. 1976).

Miller et al. (2005) suggested that nutrients originating from organic soil horizons are dissolved in surface runoff and eventually deposited in Lake Tahoe. They further postulated that fire exclusion over the past century has allowed buildups of organic horizons and associated nutrients that are outside the range of natural variability, causing increased N and P inputs to Lake Tahoe. Their interpretations extend the hypothesis of Johnson et al. (1998), which states that fire is the dominant control on nitrogen fluxes in semi-arid ecosystems such as the Lake Tahoe Basin, in that the episodic volatilization and establishment of N-fixing plant species associated with fire exceeds in importance the slow processes of decomposition.

According to the paradigm presented by Miller et al. (2005) and Johnson et al. (1998), management of Lake Tahoe water quality needs to encompass management of upslope fire regimes and vegetation dynamics. However, it is difficult to place modern-day vegetation manipulations or even wildfires in a long-term context given that fire effects on nutrient cycling in the Tahoe Basin have always been episodic. Prescribed fires in the Tahoe Basin may have minimal effects on dissolved N and P in streamwater (Stephens et al. 2005), whereas studies of the 2002 Gondola wildfire observed elevation soil solution concentrations of ammonium, nitrate, and ortho-P (Murphy et al. 2006). Although the wildfire exerted important short-term effects on nutrient leaching, important long-term effects were likely dominated by ecosystem-level loss of N that would need to be recovered over time by establishment of N-fixing vegetation. The long-term nutrient cycling effects of ongoing fuels management, that are designed to reduce fire risk through prescribed fires and mechanical treatments, have yet to be determined.

The effect of fire exclusion has been to increase homogeneity of vegetation and fuels structure at lower elevations within the Tahoe Basin, and for Sierran forests in general. However, it remains an open question whether the spatial variability in nutrient

pools and fluxes has been similarly homogenized. Direct effects of fire are associated with short-term volatilization of nitrogen and concomitant increases in nitrate availability. Such short-lived effects, however, need to be juxtaposed with indirect effects that are mediated over long time periods and large areas by ecological interactions, such as the relationship between disturbance regime and relative abundance of nitrogen-fixing chaparral species.

An improved understanding of the historical range of variability (HRV) for nutrient dynamics is needed, such that current conditions and potential future conditions resulting from planned management actions can be placed in a long-term, historical context. Nutrient dynamics generally are not considered in historic reference condition models used to guide management, whereas historical variation of disturbance regimes and forest structure is often reconstructed, modeled, and used to guide landscape management (e.g., Cissel et al. 1999, Wimberly et al. 2000). For the Tahoe Basin, researchers have developed HRVs for forest structure and fire history (e.g., Caprio and Swetnam 1995, Barbour et al. 2002, Taylor 2004), and short-term interactions between fire, vegetation, and nutrient cycling have been studied (e.g., Caldwell et al. 2002, Stephens et al. 2004, Murphy et al. 2006). The goal of this research was to put the two types of studies together to develop an HRV for nutrient cycling in the Tahoe Basin, and so to contribute towards a balanced, long-term perspective for the question of how alternative fire regimes have influenced (or have the potential to influence in future) movement of nutrients from uplands to the lake through surface runoff. In addition to understanding current conditions in the context of historic reference conditions, it was also important to estimate the long-term effects of future restoration management (i.e., prescribed fire, forest thinning, mechanical treatments) on nutrient cycling. These complementary goals, with emphasis on both past and future, required development of a novel modeling approach that links landscape-level natural disturbance and forest management with site-specific nutrient cycling processes.

We have developed an ecological simulation model for analyzing the effects of varying fire regime (including fire suppression) on nutrient cycling for forests throughout the Tahoe Basin. The NuCycling-Succession model includes vegetation, forest floor, and soil nutrient pools sensitive to direct and indirect effects of fire, fuel treatments, and forest succession. This model is integrated as a software extension within a landscape disturbance simulator (LANDIS-II) that simulates fire and forest management. We have applied the NuCycling-Succession model to address the following questions:

- (1) To what extent do modeled nutrient pools differ under historical fire, fire exclusion, and current conditions?

Nutrient pools, including leachate N, litter N and P, and total N and P, may differ in total amount, mean amount, and variance associated with each ecoregion. Differences in mean amount and variance indicate the importance of fire and ecoregion-specific vegetation and nutrient processes, while differences in total amount weight these processes according to the area of the ecoregion. We hypothesize that nutrient pools were lowest under the historical fire regime, highest under fire exclusion, and intermediate under the current prescribed fire regime. We further expect the variance associated with

these nutrient pools to decrease with fire exclusion, meaning that the distribution of nutrients in each ecoregion is more homogeneous.

- (2) How do alternative management scenarios compare with regard to their long-term effects on nutrient pools?

Prescribed fire and biomass removal have quantitatively and qualitatively different effects on forest composition and structure, and therefore may differ in their effects on nutrient pools. Additionally, the intensity of treatment will affect the magnitude and longevity of the effects. We hypothesize that prescribed fire treatments will decrease litter N and P and total N and P, but will increase leachate N relative to biomass removal. More frequent and larger scale treatment will decrease nutrients more than lower amounts of treatment.

- (3) In comparison to microbially-mediated decomposition, how important is fire to nutrient cycling dynamics?

Johnson et al. (1998) hypothesized that fire is the primary agent of decomposition in semi-arid forests. We hypothesize that nutrient fluxes and available N will be greater in the presence of fire. As a corollary, we expect that ecoregions with more frequent fire will have slower microbially-mediated decomposition rates because decomposition is not the primary source of available N.

- (4) What are realistic ranges of N and P loading in surface runoff and snowmelt?

Murphy et al. (2006), Miller et al. (2005), and others have measured the concentration of nutrients in surface runoff and snowmelt, but have not extrapolated their results from the individual sites to the entire basin. Dominant vegetation, forest floor and understory nutrients, and fire and harvesting treatments may affect nutrient loading.

Methods

Our study emphasized development and testing of a novel, landscape-level model that integrates fire disturbance, vegetation dynamics, and nutrient cycling. The model was calibrated and tested using field data on soil and litter nutrient contents collected within the Basin, and water quality data from within the Basin and nearby areas. We then applied the model to our research questions, requiring multiple model scenarios.

Field Methods

Soil and Litter

Soil and litter samples were collected from spatially clustered sites dominated by Jeffrey pine and chaparral (including non-N fixing *Arctostaphylos* and *Quercus* species and N-fixing *Ceanothus* and *Purshia* species). Groups of five sites located within 500 m of each other were randomly selected from the Jeffrey pine and chaparral ecoregions. It was assumed that geographically close sites had similar underlying soil characteristics

and disturbance histories, and evidence of recent disturbance was documented. If a site was not dominated by the expected vegetation type or had obvious signs of recent non-management related human activity (e.g., campfires, cleared litter, cut trees) it was discarded from the analyses.

At each site, litter and soil samples to 15-cm depth were taken from the center and four additional points located 11 m from the center across and perpendicular to the down-slope axis. Litter depth was recorded at each sampling point and depths less than 0.5 cm or discontinuous litter were recorded as negligible. Soil samples were dried at 105°C and litter samples at 55°C for 48 hours, weighed to determine bulk density, and sieved to remove coarse rock fragments. Total C and N were analyzed using a CN combustion analyzer and ortho-P was analyzed using an inductively coupled plasma spectrometer (Robert Blank, Soil Chemistry Laboratory, Nevada Agricultural Research Station). The soil and litter concentrations of C, N, and P were compared with a random selection of modeled concentrations under fire exclusion using paired student t-tests to evaluate model accuracy.

Water Quality

We installed runoff and snowmelt collectors at several sites (Gondola, North Shore, Truckee, and Sagehen; Fig. 1) to quantify runoff and snowmelt amounts and nutrient contents for selected model validation sites. Vegetation at the Gondola site consisted of *Abies concolor*, *Pinus jeffreyi*, and lesser amounts of *P. lambertiana* and *Calocedrus decurrens*, and was classified as mixed conifer. The understory included *Castanopsis sempervirens*, *Ribes* species, and limited amounts of the N-fixing *Ceanothus velutina* and *Purshia tridentata*. Collectors were installed to determine the effects of wildfire on surface runoff and snowmelt nutrients. The North Shore site had similar vegetation and treatments included prescribed fire, mechanical harvesting, and their combination. The Truckee site was located in a pure stand of *P. jeffreyi* with a shrub understory of *Purshia tridentata*, *Ceanothus prostratus*, and *Arcrostaphylos patula*, and was classified as Jeffrey pine. Treatments included prescribed fire and both cut-to-length and whole-tree harvesting. At the Sagehen site, collectors were located in a mixed conifer forest (including *P. jeffreyi*, *P. ponderosa*, and *A. concolor* with an understory of *Ceanothus velutinus*, *C. prostratus*, and *Arctostaphylos patula*), lodgepole pine-meadow ecotone (dominated by *P. contorta*), and a meadow. At all sites, collectors were located in areas with comparable slope aspect, slope position, soil type, and underlying geology.

Runoff collectors consisted of a buried bucket container with a volume slightly larger than 8 L fitted with a collection funnel, vent stack roof flashing, screen, and a high-density polyethylene cover (see Miller et al. 2005 for a complete description). The top of the collection funnel was located approximately 5 cm below the soil surface and the roof flashing was aligned perpendicular to the slope either at the soil surface of bare soil (typically water repellent in summer and early fall) for the collection of overland flow, or at the litter/mineral surface interface for the collection of litter interflow. The excavated hole was backfilled for insulation and to secure the collection bucket assembly. A small V-notch equilateral triangular opening (length = 1.0 cm; area = 0.43 cm²) was cut into a 20x30 cm piece of high-density polyethylene and secured over the roof flashing with the V-notch opening coincident to the opening in the flashing, which was screened to prevent the entry of forest debris. A sufficient length of tubing was attached to the top of each

sample and vent bulkhead fittings to allow for sampling under a 1-m winter snowpack. Snowmelt collectors were of a similar design with a larger opening (see Johnson et al. 1997). Between 16 and 30 surface runoff collectors and between 8 and 12 snowmelt collectors were installed for each selected validation site.

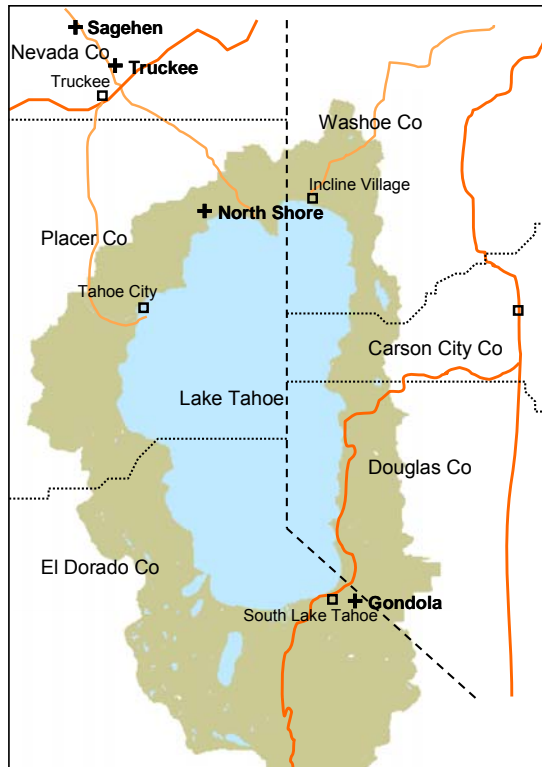


Figure 1. Location of sites for runoff and soil water collections. Major roads are in orange and land within the Lake Tahoe Basin is in green.

Model Description

Model Structure

The NuCycling Succession model represents a tight linkage (i.e. information is transferred each time step) between an existing, widely used model of forest landscape dynamics and fire regimes, LANDIS-II (He and Mladenoff 1999, He et al. 1999, Scheller et al. 2007), and a novel model of landscape-level nutrient cycling that has been developed for this project, NuCycling Succession (Fig. 2). LANDIS-II simulates fire ignition, spread, and succession of forest tree species and, in our case, chaparral and sagebrush shrub communities. Fire reduces biomass and changes species composition in the LANDIS-II model and transfers mass and nutrients between charcoal, litter, soil pools, and the atmosphere in the NuCycling Succession model. This model tracks biogeochemical processes in response to fire, species composition, and climate, provides a feedback to the LANDIS-II model by representing the effects of N uptake from mineral soil on tree growth.

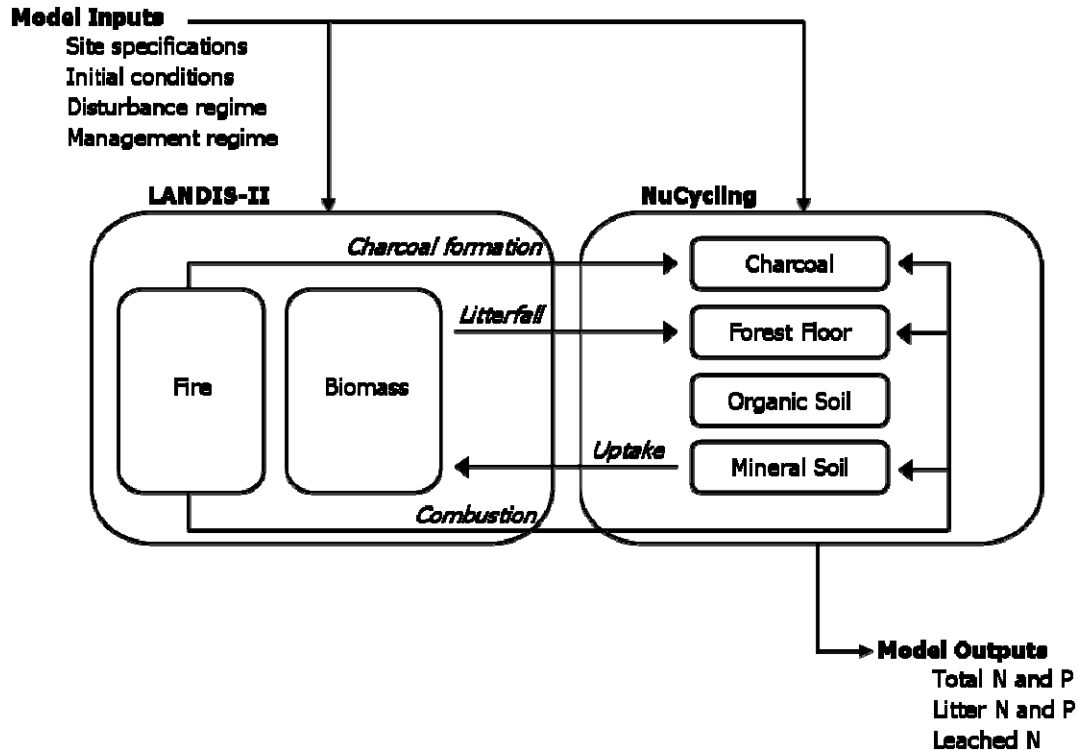


Figure 2. Description of inputs, linkages among modules, and outputs for the NuCycling Succession model.

LANDIS-II forest landscape simulation model

LANDIS-II is a spatially explicit and stochastic simulation model of landscape succession and disturbance dynamics over large landscapes and long time periods. Individual modules describe key ecosystem processes, including succession, biomass accumulation, and fire and harvest events, with different time steps and spatial extents. Multiple paths of succession are driven by disturbance regimes, available seed sources, life history attributes of potential species, and site conditions. The time step and spatial resolution of the model are alterable; we chose to use an annual time step and a resolution of one hectare (a cell size of 100m by 100m).

A landscape is represented as a grid of sites that are linked spatially through seed dispersal and disturbance. The landscape is divided into user-specified “ecoregions” of assumed homogeneous environmental conditions (e.g., soil characteristics, topography, and climate) and fire regions based on fire frequency, size, and severity distributions. Each ecoregion is associated with establishment probabilities for all species based on the likelihood of establishment under those environmental conditions. Environmental variables may be changed at any time step to represent climate change. Within each site, LANDIS records living and dead biomass for age cohorts of all species. Species’ life history attributes include longevity, reproductive age, shade tolerance, fire tolerance relative to fire intensity, resprouting ability, and seed dispersal distances.

The probability of fire ignition in a site is spatially stochastic and increases with time since last fire based on the average fire rotation for the fire region. Fire size is stochastically modeled from a log-normal distribution described by minimum, mean, and maximum fire size. Fire severity (scale of 1 to 5) is determined from time since last fire

in relation to specified transition values. Fire-induced mortality depends on the fire tolerance for each species and age cohort, with younger cohorts preferentially experiencing mortality. At any time step, fire parameters can be altered to represent changes in fire regime or management.

Harvesting prescriptions are simulated within management units according to management area objectives, including maximizing wood production, reducing fuel loads, and enhancing wildlife quality. Harvest prescriptions can vary within and between management units and over time. Stands for harvest can be ranked according to economic, compositional, and age characteristics or randomly in accordance with management goals. After harvest, forest succession is a function of the residual species and age classes within the cell and seed dispersal from other cells.

In its current state, the biomass succession module simulates cohort growth, competition, and mortality of aboveground biomass and decomposition of litter and coarse woody debris. Biomass accumulation is dependent on existing biomass in each site and an annual increment dependent on specified maximum aboveground net primary productivity (ANPP) for each species, cohort age, and competition for space and light. Mortality associated with cohort age and growth and site disturbance is modeled and the subsequent dead foliar and woody biomass are treated as single separate pools. Decomposition proceeds according to first-order exponential decay using species- and ecoregion-specific rates for foliar litter and species-specific rates for coarse woody debris. The biomass module (Scheller and Mladenoff 2004), harvest module (Gustafson et al. 2000), and LANDIS-II are described in detail elsewhere (He and Mladenoff 1999, He et al. 1999, Scheller et al. 2007).

NuCycling Succession module

The NuCycling Succession module calculates mass, carbon, nitrogen, and phosphorus contents and fluxes for living biomass, forest floor, and soil compartments (Fig. 3). At every site, all plant cohorts are associated with values for living biomass and nutrient contents. Living biomass is divided into four compartments: leaves, wood, fine roots, and coarse roots. The forest floor is composed of leaf litter, fine root litter, and coarse woody debris, which includes dead branches, boles, and coarse roots. Annual litter cohorts are tracked separately until they reach the “near-humus” state, when the substrate becomes more homogeneous and decomposition slows (Berg 2000). This is necessary because fire influences nutrient cycling dynamics (Johnson et al. 1998), especially through combustion of forest floor material. Since fire rotation intervals may be shorter than the time from litterfall to humification (e.g., in a Jeffrey pine forest), *a priori* splitting of organic material into active, slow, and passive soil organic matter fractions (e.g., Parton et al. 1987) may overestimate soil organic matter additions. Values for mass and soil nutrients are pooled over time and species for coarse woody debris because of their relatively small importance to N and P budgets (Laiho and Prescott 2004). Nutrient concentrations of mineral rock, charcoal, and organic and mineral soils are modeled as single individual pools at each site. Charcoal is included as a separate compartment from soil organic matter because it decomposes much more slowly, supports different microbial communities, and influences process rates, including decomposition (Pietkainen et al. 2000).

Transfers of mass and nutrients between compartments depends on site conditions, with some process rates specified by the user (e.g., soil organic matter decomposition) and others calculated intrinsically (e.g., litter decomposition), depending on model sensitivity to the parameter and current knowledge. Additionally, simulated fire events transfer nutrients and mass between compartments through mortality of living biomass, combustion of aboveground live and dead biomass, and altered rates of N and P mineralization and immobilization.

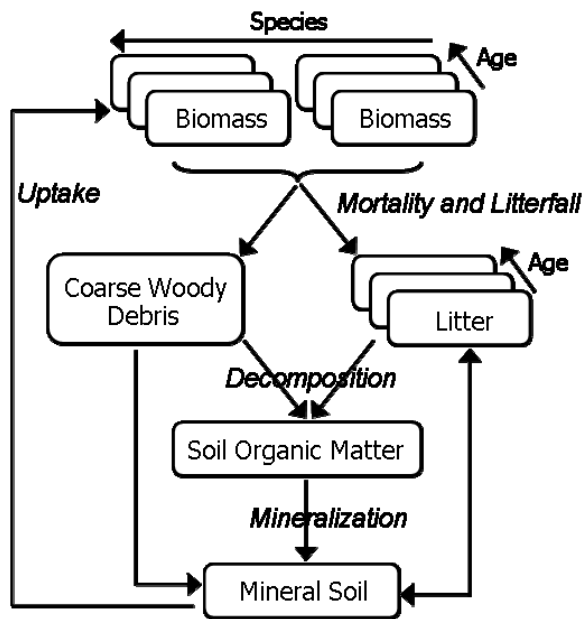


Figure 3. State compartments (boxes) and flux pathways (arrows) in the NuCycling Succession module. Biomass is tracked for each individual species and age cohort and litter for all age cohorts. All flux pathways represent movement of C, N, and P except those including mineral soil, which only include N and P.

A more detailed description of the NuCycling Succession model and its components is included in Appendix 1.

Model Calibration and Parameterization

We first divided the Lake Tahoe Basin into 11 ecoregions of relatively homogeneous potential vegetation based on the LTBMU biophysical settings (provided by Hugh Safford, Region 5 Ecologist) (Table 1, Fig. 4). For each ecoregion, fire size distribution, severity, frequency, and mortality under the historical fire regime were parameterized using LTBMU biophysical settings (Table 1). Ignition probabilities for each ecoregion were calibrated to the expected average fire severity and rotation period. Average actual evapotranspiration was derived from PRISM climate data and initial soil conditions were determined from NRCS SSURGO soil data. Although the model is very sensitive to soil organic matter decomposition rates, these values were estimated for each ecoregion because of insufficient data and were used to calibrate rates of soil organic matter accumulation.

Table 1. Ecoregions, their associated areas, and fire parameters used to model the Lake Tahoe Basin study area.

Ecoregion	Description	Area (ha)	Fire Rotation (yr)	Fire Severity
PIJE	Jeffrey pine	22615	10	Low
MCON	Mixed conifer	14324	15	Low-mixed
RFWF	Red fir-white fir	12847	35	Low-mixed
RFWP	Red fir-western white pine	11274	62	Mixed
LPcw	Lodgepole pine-cold and wet	1573	70	Mixed
LPdy	Lodgepole pine-dry and subalpine	1033	50	Low-mixed
SUAL	Subalpine	5200	400	High
ASPN	Aspen	1963	33	High
CHAP	Montane chaparral	4709	32	Mixed-high
RIPA	Riparian vegetation	4375	33	Mixed-high
SAGE	Mountain sage	931	49	High

Establishment probabilities and maximum annual net primary productivity for all tree species in each ecoregion were initialized using PnET-II for LANDIS-II (Xu et al. 2008). For the chaparral species, these variables were parameterized using published values. Other species-specific data were derived from the literature and a limited field sampling of vegetation age and nutrient concentrations from within the Tahoe Basin.

Relationships between light availability, establishment, and biomass were parameterized using the default model values. Initial communities were parameterized as a random arrangement of the current proportions for each vegetation community and height structure (used as a proxy for age structure) (U.S. Department of Interior, Geological Survey 2007).

Harvest and prescribed fire management units were defined as the seven fire districts in the Lake Tahoe Basin, effectively concentrating management activity into the lower elevation forests (U.S. Department of Agriculture et al. 2007). For all prescribed fires, fire severity was assumed to be 1 and mean fire size was 46 hectares, the mean for all planned and completed treatments in the basin from 1997-2007 (calculated from U.S. Department of Agriculture et al. 2007). We used the proportion of each fire district treated annually to calibrate ignition probability and fire rotation to 50-year return intervals (i.e. 641 ha yr^{-1}) for the Jeffrey pine and mixed conifer ecoregions within fire districts. One harvest prescription was parameterized to remove young cohorts, especially those of fir species, in accordance with the *Lake Tahoe Basin Multi-Jurisdictional Fuel Reduction and Wildfire Prevention Strategy* (U.S. Department of Agriculture et al. 2007). Other harvest prescriptions were removal of 20% and 40% of all species-age cohorts, which represent the 95% confidence boundaries for biomass removal under the strategic harvest prescription.

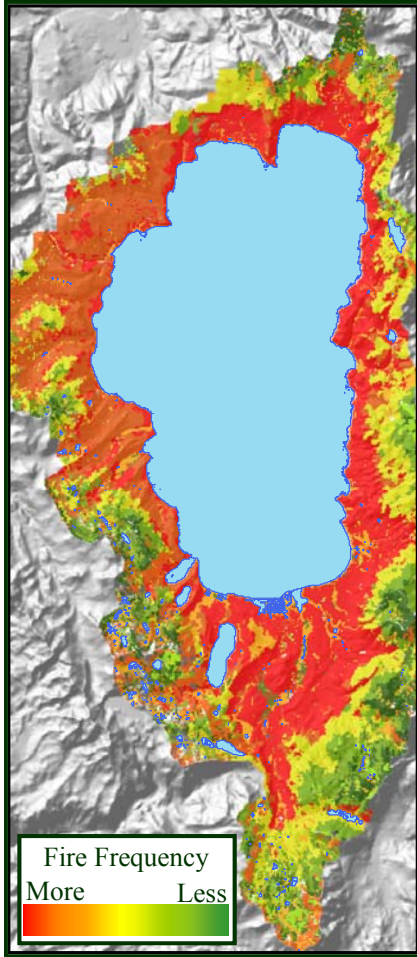


Figure 4. Ecoregions and the associated scale of relative fire frequency.

Model Evaluation

Outputs for individual model components were compared to data from several sites in the Lake Tahoe Basin and published values in the literature. Valid soil and litter samples were collected from 61 Jeffrey pine sites and 52 chaparral sites. Modeled values for soil and leaf litter total C, N, and P concentrations in the Jeffrey pine and chaparral ecoregions fell within the range of those collected in the summers of 2006 and 2007 and the means were not significantly different ($p > 0.05$) (Figs. 5-7). However, the variance for modeled concentrations is less than that for the field data, likely due to parameterization of the model using the means for all plant nutrient concentrations. Due to the annual temporal resolution and large spatial and temporal scales, we are satisfied with modeling the average condition.

Modeled decomposition rates for incense-cedar, sugar pine, and white fir litter in lower elevation Jeffrey pine and mixed conifer ecoregions are within 10% of those measured in Sequoia and Kings Canyon National Park (Stohlgren 1988) (Fig. 8).

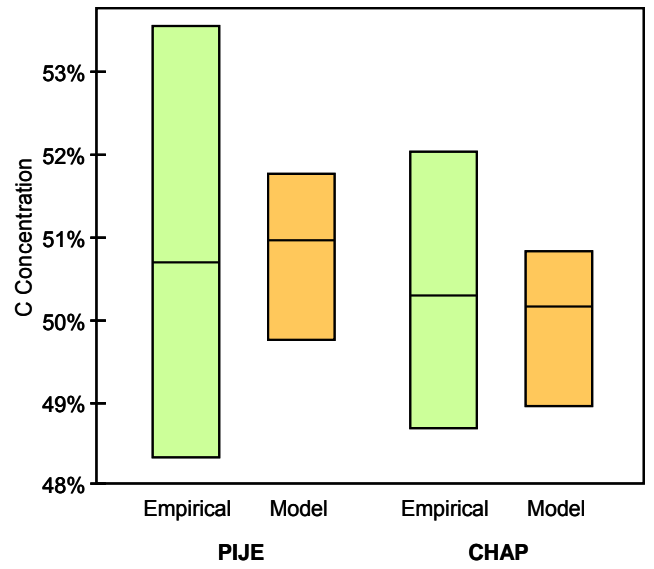


Figure 5. The range of C concentrations in soil (left) and litter (right) for the field data (green) and modeled results (orange). Horizontal lines indicate mean values.

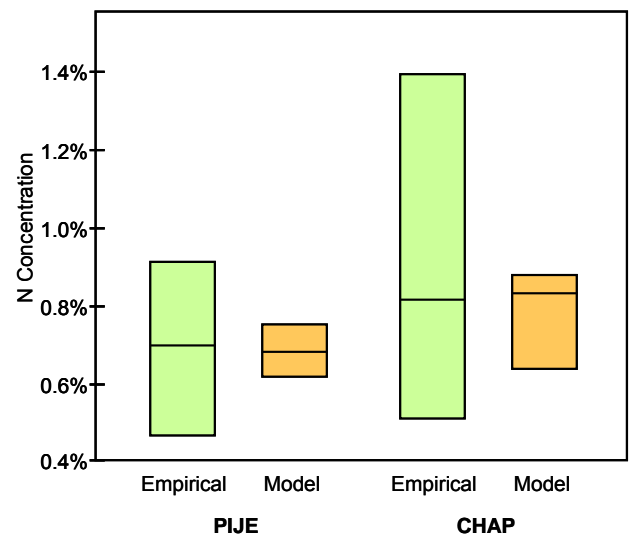
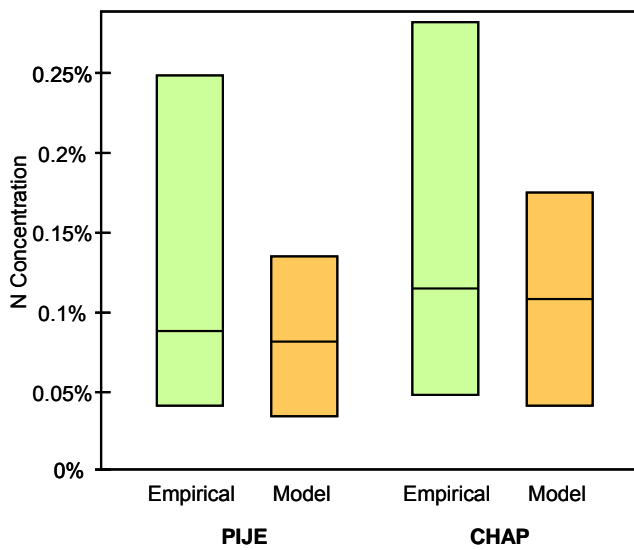


Figure 6. The range of N concentrations in soil (left) and litter (right) for the field data (green) and modeled results (orange). Horizontal lines indicate mean values.

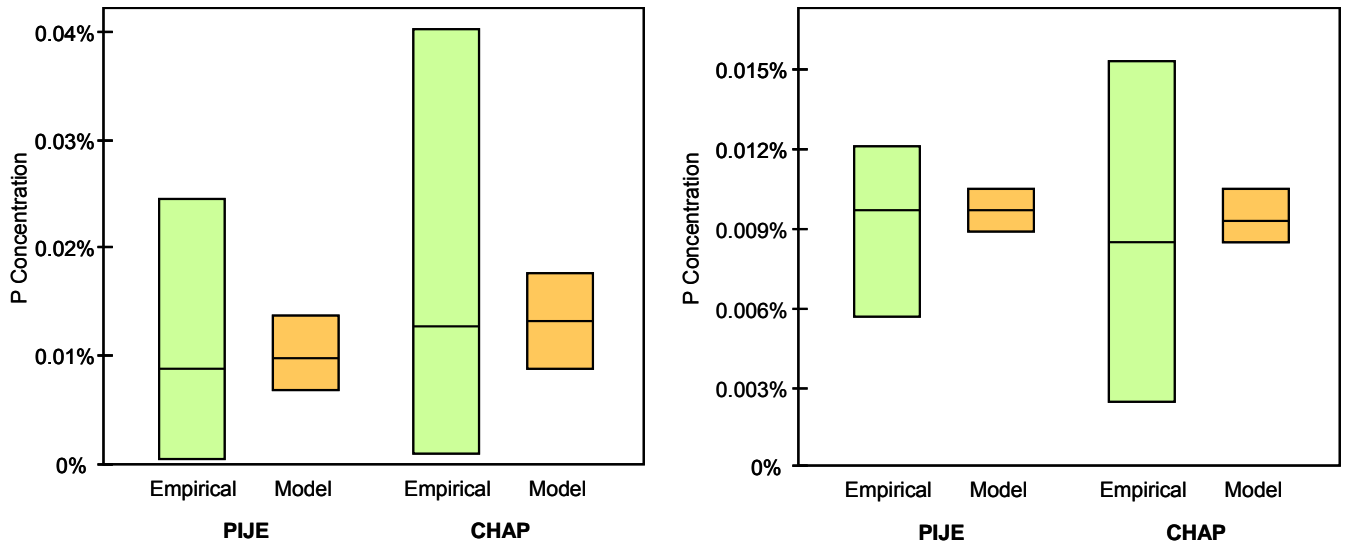


Figure 7. The range of P concentrations in soil (left) and litter (right) for the field data (green) and modeled results (orange). Horizontal lines indicate mean values.

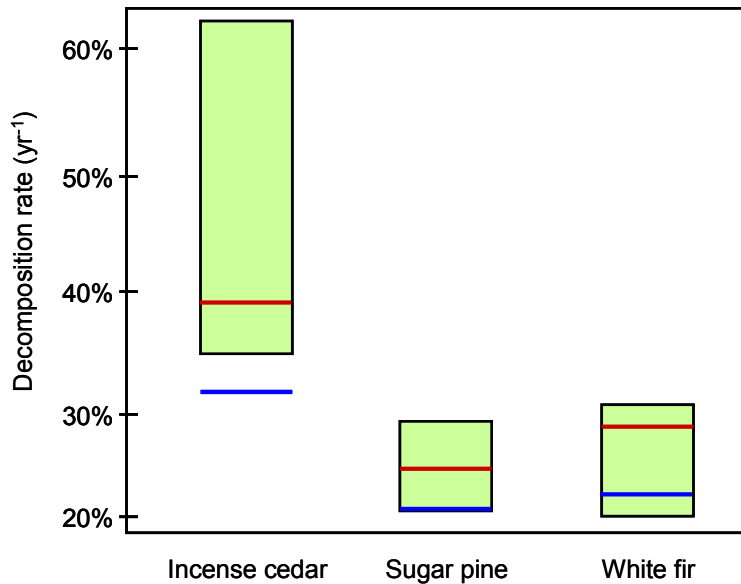


Figure 8. Evaluation of model predictions for decomposition rate for three tree species in two ecoregions. Blue lines indicate the model calculated decomposition rate in the mixed conifer ecoregion and red lines indicate it calculated in the Jeffrey pine ecoregion. The green box represents the range of values observed in Stohlgren 1988.

Model Scenarios

To address our research questions, we applied the model under multiple scenarios representing historical conditions, fire exclusion, prescribed fire, and biomass removal (i.e. fuel treatment). Scenarios representing contemporary and future conditions required an initialization, or “run-up” period of 1000 to 1500 years under the historical fire regime, followed by 120 years of fire exclusion. The fire exclusion period included a chance of catastrophic fire, such as the Angora fire. Final model outputs from the initialization simulations were used to initialize the six treatment scenarios:

- (1) Continued fire exclusion
- (2) Prescribed fire (approximately 641 hectares burned annually, the mean completed area 1997-2007, for a fire rotation of 50 years)
- (3) Prescribed fire (acres burned annually at approximately half of the historical fire frequency, but fires of smaller size, lower intensity, and in different forest types)
- (4) Prescribed fire (acres burned annually at approximating historical fire frequency, but fires of smaller size, lower intensity, and in different forest types)
- (5) Biomass removal (in accordance with the guidelines outlined in the *Lake Tahoe Basin Multi-Jurisdictional Fuel Reduction and Wildfire Prevention Strategy* (U.S. Department of Agriculture et al. 2007) at current (641 hectares burned annually) and historical disturbance frequencies)
- (6) Biomass removal (20% reduction in biomass for all cohorts) at current and historical disturbance frequencies
- (7) Biomass removal (40% reduction in biomass for all cohorts) at current and historical disturbance frequencies

Proposed annual treatment areas in the *Lake Tahoe Basin Multi-Jurisdictional Fuel Reduction and Wildfire Prevention Strategy* (U.S. Department of Agriculture et al. 2007) range between those in the half-historic frequency and historic frequency modeled treatments.

Data Analysis

For all analyses, 200 sites in each ecoregion were randomly selected and the values for all pertinent variables at those sites were extracted for 20 randomly selected model years during each fire period of interest (i.e., historical fire conditions, fire exclusion, and prescribed fire or biomass removal treatments). This process produced 4,000 data points for each variable per ecoregion in a single fire period.

To examine the effects of historical fire, fire exclusion, and current conditions on nutrient pools, we used one-way ANOVA within each ecoregion to compare between these fire periods for leachate N, litter N and P, and total N and P. If significant differences were found, the ecoregions responsible for those differences were further elucidated using Tukey's test. The interactions between ecoregion (representing differences in environmental characteristics and fire regime) and fire period were examined using two-way ANOVA and the variance associated with each was parsed. Similarly, the effects of the different treatments were compared for all nutrient pools using one-way ANOVA within each ecoregion and two-way ANOVA for ecoregion and treatment type.

To determine the relative importance of fire to nutrient cycling dynamics, we determined the numerical difference between the selected model year and the previous model year for all nutrient variables. The most parsimonious model was chosen using stepwise regression in both directions. Using the absolute difference, we partitioned the variance associated with the severity of fires that occurred in that time step or in the previous five years, the total biomass of the site, the biomass of all N-fixers at the site, fire period, and ecoregion.

Because runoff and snowmelt collectors were spatially clustered within sites and multiple collections were made, data were analyzed using repeated-measures, mixed-effects models. Mixed models account for correlation in data by partitioning the error both within- and between- subjects using random effects. For all models, both site and plot nested within site were treated as random effects. The spatial arrangement of sites led to substantial variation in precipitation, which is negative exponentially related to nutrient loads, so monthly rainfall, monthly snowfall, and accumulated snowpack were used as covariates when significant. Because litterfall varies throughout the year, Julian day standardized to October 1, the beginning of the water year, was also a covariate. We modeled $\text{NO}_2 + \text{NO}_3\text{-N}$, $\text{NH}_4\text{-N}$, and $\text{OPO}_4\text{-P}$ concentrations and quantities in surface runoff and snowmelt in relation to treatment and time since treatment. Because vegetation composition varied between sites, we were unable to include it in the models. Forest floor and understory nutrient data before and after treatment were available for the Gondola and Truckee sites, so separate models including those variables were made for each nutrient concentration and quantity. A significance level of $\alpha < 0.10$ was used to determine the best models.

Results and Discussion

To what extent do modeled nutrient pools differ under historical fire, fire exclusion, and current conditions?

Leachate N was positively associated with fire frequency and severity, with the historical fire regime producing the most leachate N, prescribed fire an intermediate amount, and fire exclusion the lowest amount in all ecoregions (Fig. 9). Ecoregion explained 1.81% of the variance, fire period explained 0.44%, and the interaction between them (indicating the magnitude of the difference in fire frequency and severity between fire periods for each ecoregion) explained 0.77%. Because leaching events are sporadic and generally produce low values except under extreme conditions (e.g., a fire event or huge pulse of N-fixing species), the variance explained by these large-scale predictor variables is low.

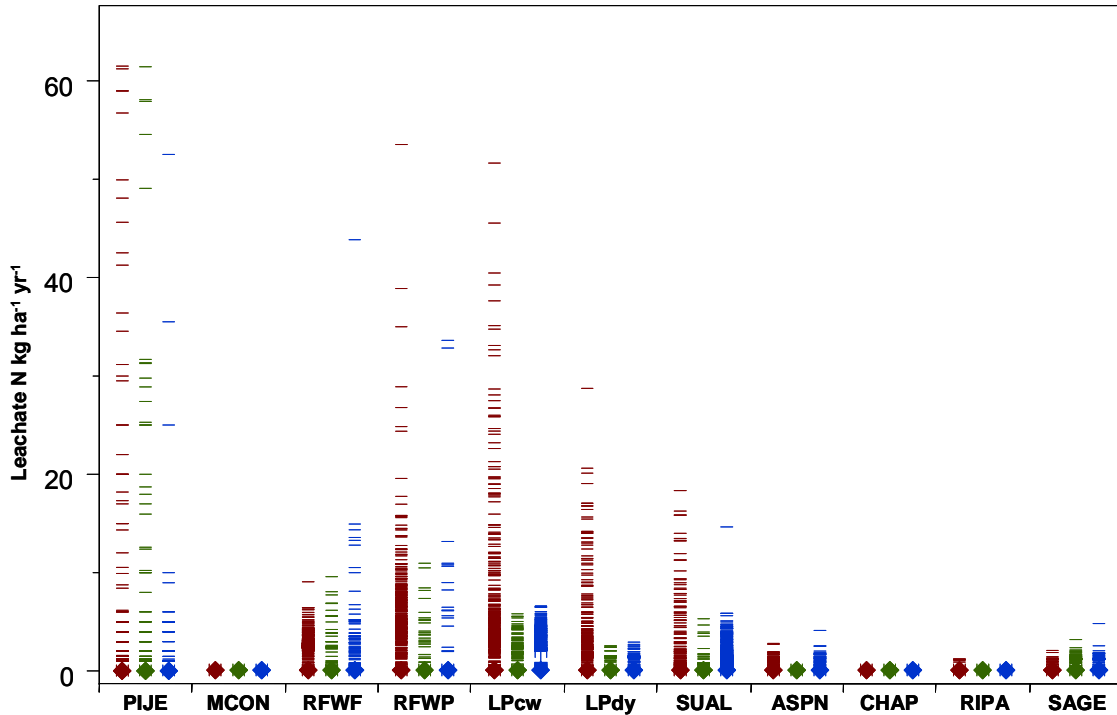


Figure 9. Box plots for leachate N indicating the median (diamond), quartiles (boxes), and outliers (horizontal bars) under the historical fire regime (red), fire exclusion (green), and current prescribed fire (blue) for all ecoregions.

The Jeffrey pine ecoregion had the highest mean leachate N under historical fire and fire exclusion ($1.17 \pm 0.968 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ and $0.994 \pm 0.847 \text{ kg N ha}^{-1} \text{ yr}^{-1}$; mean \pm SE), while the lodgepole pine-cold and wet ecoregion had the highest under prescribed fire ($0.77 \pm 0.42 \text{ kg N ha}^{-1} \text{ yr}^{-1}$). Tukey's test indicated that the Jeffrey pine, red fir-white fir, and lodgepole pine-dry and subalpine ecoregions had the highest leachate N that was not significantly different under the historical fire regime. Under fire exclusion, Tukey's test indicated that leachate N fluxes for the Jeffrey pine and subalpine ecoregions were not significantly different. For current prescribed fire, the Jeffrey pine, red fir-white fir, and lodgepole pine-cold and wet ecoregions did not significantly differ with regard to leachate N.

Although the hectare-based differences in leachate N under fire exclusion compared to those under historical fire were small, the aggregated difference may have a relatively large effect on lake water quality. At the scale of the entire basin, fire exclusion reduced leachate N by $15,720 \pm 3458 \text{ kg N yr}^{-1}$ and prescribed fire reduced it by $18,971 \pm 4800 \text{ kg N yr}^{-1}$ compared to the historical fire regime, due primarily to the decrease in leachate N from the Jeffrey pine ecoregion (Fig. 10).

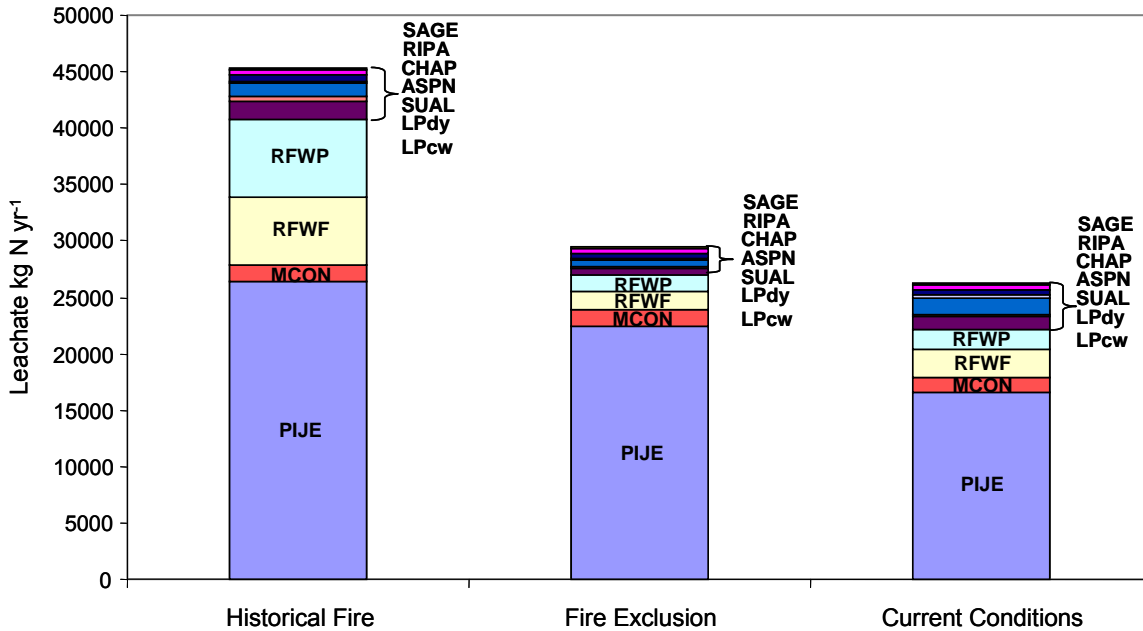


Figure 10. Mean total annual leachate N (kg N yr⁻¹) for the Lake Tahoe Basin illustrating the contribution of each ecoregion during each fire period.

Contrary to leachate N, litter N and P were highest under fire exclusion, lowest under historical fire, and intermediate under prescribed fire (Figures 11 and 12). Fire directly reduces litter quantity, and thus its effect is more pronounced in ecoregions with more frequent fire (e.g., Jeffrey pine, mixed conifer, and chaparral ecoregions). Ecoregion explained 31.46% of variance in litter N, fire period explained 2.80%, and the interaction between them explained 7.94% for litter N; the percentages of variance explained for litter P were within three-hundredths of those for litter N. The high explanatory power of ecoregion is likely a function of the highly significant difference between the group of ecoregions with high litter N and P contents (Jeffrey pine, mixed conifer, and chaparral) and the other ecoregions.

The chaparral ecoregion had the highest litter N and P under historical fire (338.93 ± 12.945 kg N ha⁻¹ and 19.57 ± 0.753 kg P ha⁻¹), fire exclusion (1465.22 ± 18.336 kg N ha⁻¹ and 86.07 ± 1.053 kg P ha⁻¹), and prescribed fire (1008.76 ± 18.039 kg N ha⁻¹ and 66.61 ± 1.037 kg P ha⁻¹). Jeffrey pine litter N was only significantly lower than that in the chaparral ecoregion under prescribed fire and Jeffrey pine litter P was significantly lower than chaparral litter P under fire exclusion and prescribed fire. When the spatial extent of ecoregions is considered, the Jeffrey pine ecoregion is a much larger aggregate source of litter N and P than the chaparral ecoregion. Mixed conifer also became more important under fire exclusion and the current prescribed fire conditions (Fig. 13). These ecoregions are more likely to be the source of litter N and P that may leach into runoff, especially considering their closer proximity to Lake Tahoe.

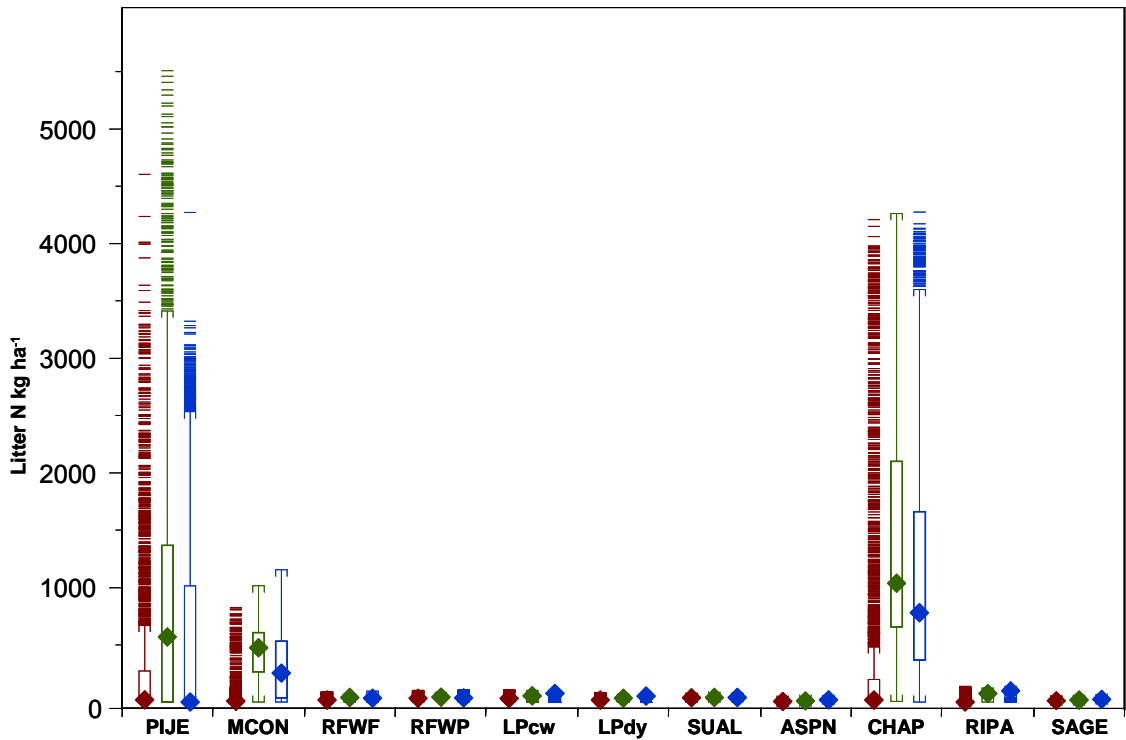


Figure 11. Box plots for litter N indicating the median (diamond), quartiles (boxes), and outliers (horizontal bars) under the historical fire regime (red), fire exclusion (green), and current prescribed fire (blue) for all ecoregions.

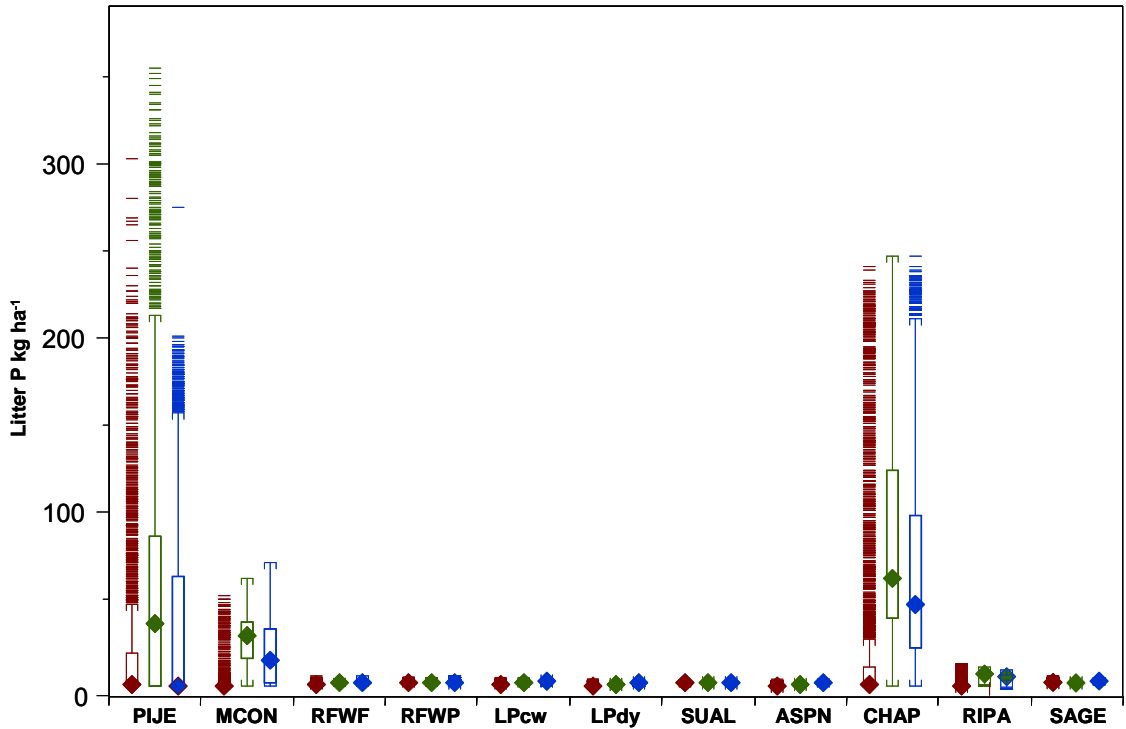


Figure 12. Box plots for litter P indicating the median (diamond), quartiles (boxes), and outliers (horizontal bars) under the historical fire regime (red), fire exclusion (green), and current prescribed fire (blue) for all ecoregions.

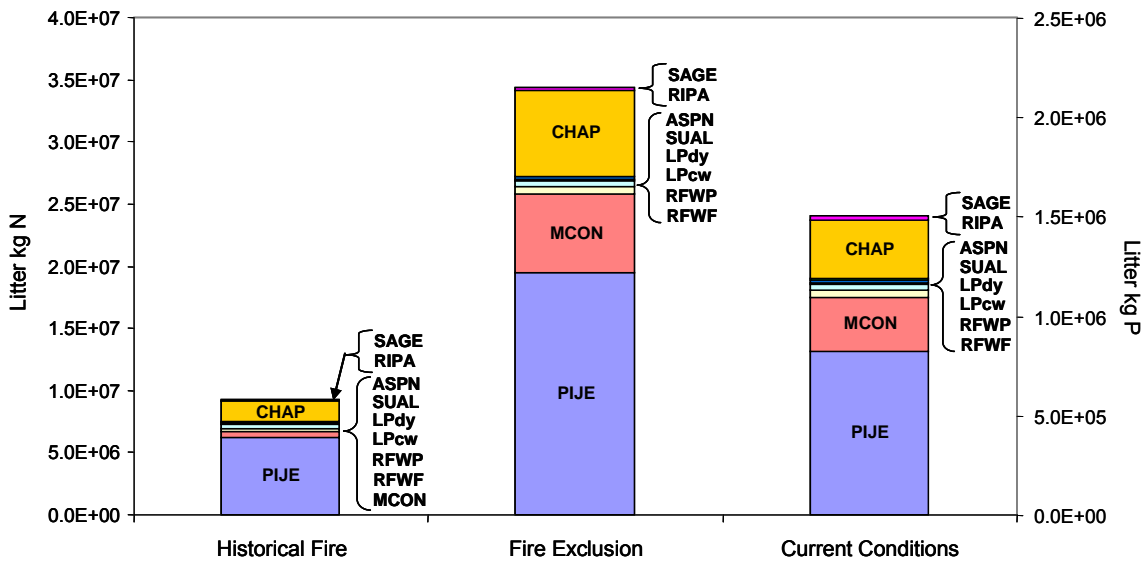


Figure 13. Mean total litter N (kg N) and total litter P (kg P) for the Lake Tahoe Basin illustrating the contribution of each ecoregion during each fire period.

Total N exhibited variable patterns with changes in fire period (Fig. 14). The dominance of N-fixing species in the chaparral ecoregion resulted in significantly higher total N than in any other ecoregion under historical fire ($16,247 \pm 292 \text{ kg N ha}^{-1}$), fire exclusion ($13,933 \pm 309 \text{ kg N ha}^{-1}$), and current prescribed fire conditions ($14,041 \pm 287 \text{ kg N ha}^{-1}$). N-fixing species have higher N concentrations in their tissues and directly contribute N to the soil through exudates and decomposition of fine root biomass that is rich in N. Despite the near elimination of combustion losses associated with fire exclusion, chaparral experienced a decrease in total N because the biomass of N-fixing species decreased from $31,147 \pm 401 \text{ kg N ha}^{-1}$ to $6544 \pm 267 \text{ kg N ha}^{-1}$. In all other ecoregions, total N was not significantly different between historical fire and fire exclusion scenarios. Prescribed fire only led to a significant increase in total N compared to fire exclusion in the mixed conifer ecoregion, where low severity fires resulted in higher total biomass ($91,150 \pm 841 \text{ kg N ha}^{-1}$ versus $61,193 \pm 1002 \text{ kg N ha}^{-1}$) and higher biomass of N-fixing species ($9085 \pm 267 \text{ kg N ha}^{-1}$ versus $6109 \pm 100 \text{ kg N ha}^{-1}$).

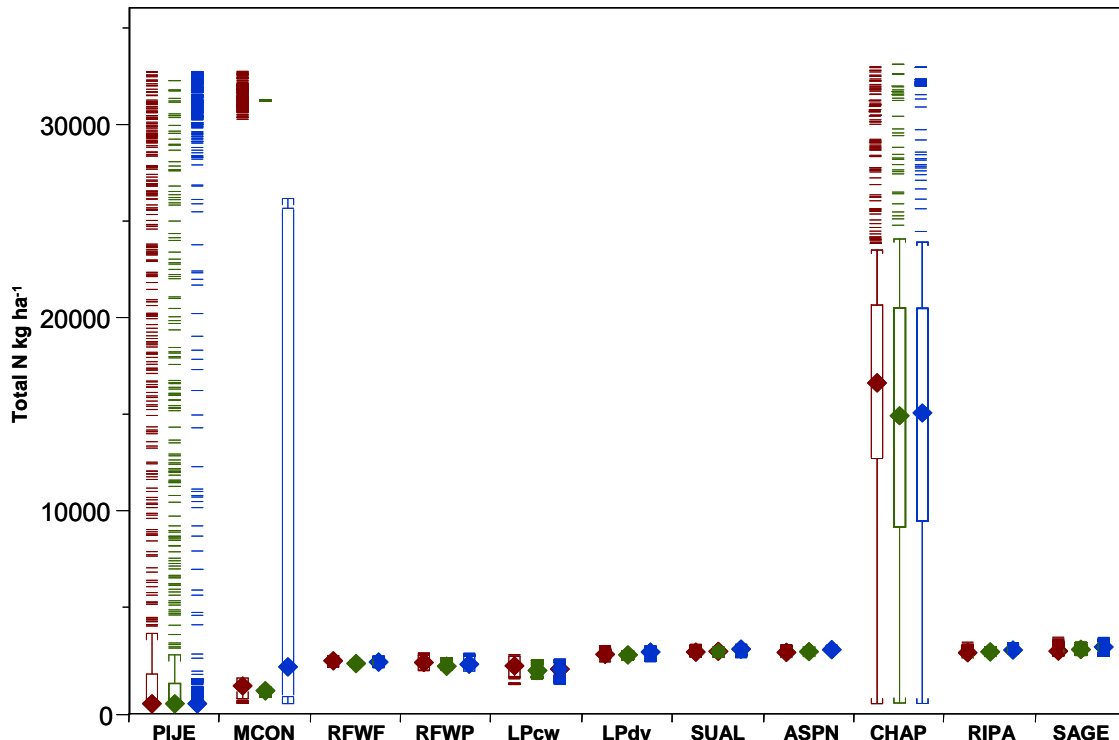


Figure 14. Box plots for total N indicating the median (diamond), quartiles (boxes), and outliers (horizontal bars) under the historical fire regime (red), fire exclusion (green), and current prescribed fire (blue) for all ecoregions.

Ecoregion explained 46.90% of variance in total N, fire period explained 1.47%, and their interaction explained 10.06%. The high value for ecoregion is likely the result of the large difference between chaparral and the other ecoregions. Using the total N for each ecoregion, the chaparral ecoregion still contained the highest total N under the historical fire regime and fire exclusion, but mixed conifer included the most under current prescribed fire (Fig. 15). Although prescribed fire reduced the amount of litter relative to fire exclusion (Fig. 13), the much larger increase in biomass in the mixed conifer and Jeffrey pine ecoregions resulted in a net increase in total N. Considering that modeled component C:N ratios remain within a relatively small range, this implies an increase in net C storage, which has been suggested as one way to mitigate climate change.

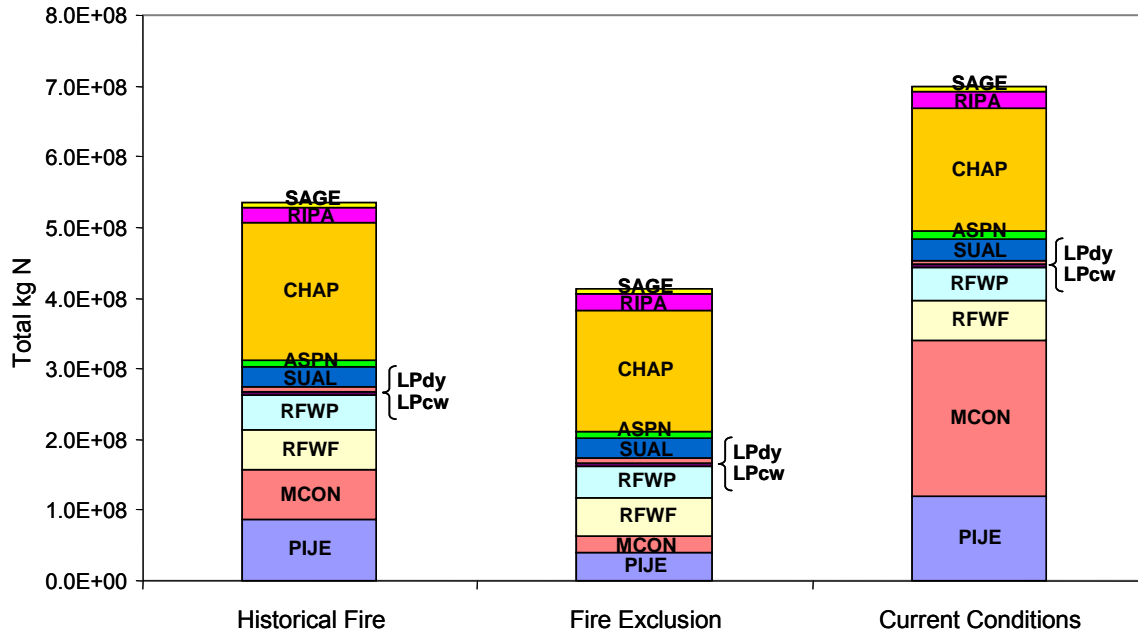


Figure 15. Mean total N (kg N) for the Lake Tahoe Basin illustrating the contribution of each ecoregion during each fire period.

For all ecoregions, total P was lowest under historical fire, intermediate under fire exclusion, and highest under current prescribed fire (Fig. 16). Since fire is the only means to remove P from the model, total P is more sensitive to fire period than total N, with fire period explaining 13.85% of the variance. Because the model is chronological and N deposition occurs continuously, total P increases directly with the rate of N deposition (approximately $1 \text{ kg ha}^{-1} \text{ yr}^{-1}$), which explains 67.40% of the variance. Within each fire period, there were no significant differences between ecoregions. Since the hectare-based values were not different, aggregated total P for each ecoregion was proportional to its area (Fig. 17).

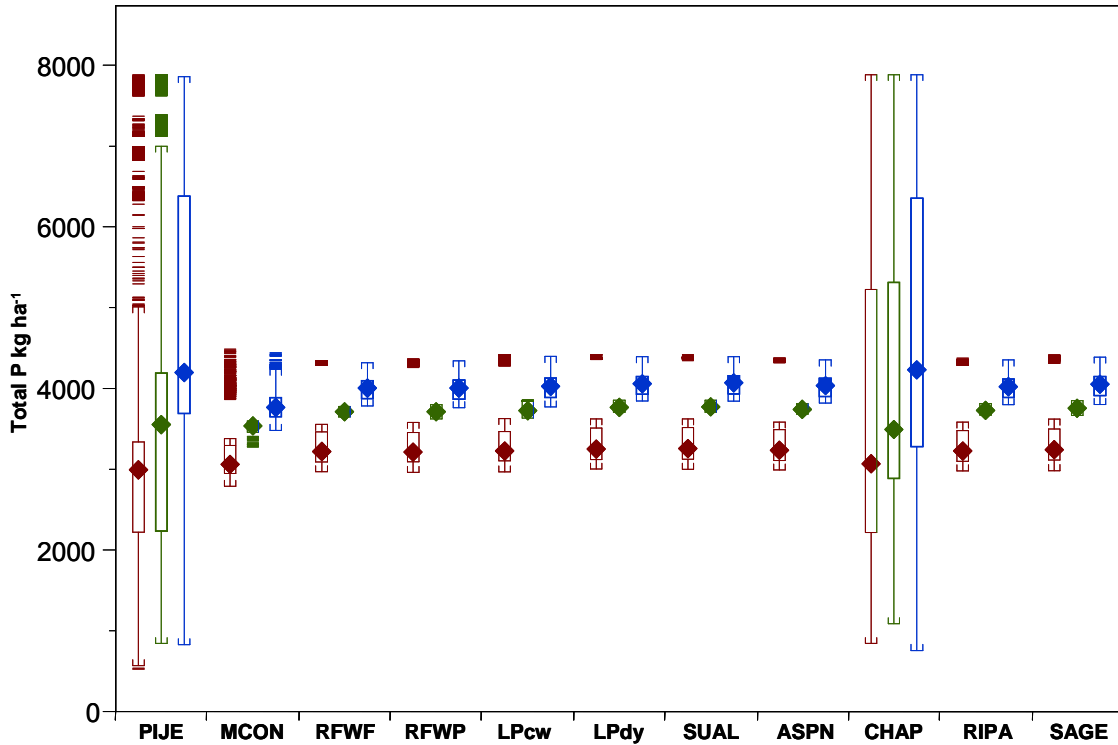


Figure 16. Box plots for total P indicating the median (diamond), quartiles (boxes), and outliers (horizontal bars) under the historical fire regime (red), fire exclusion (green), and current prescribed fire (blue) for all ecoregions.

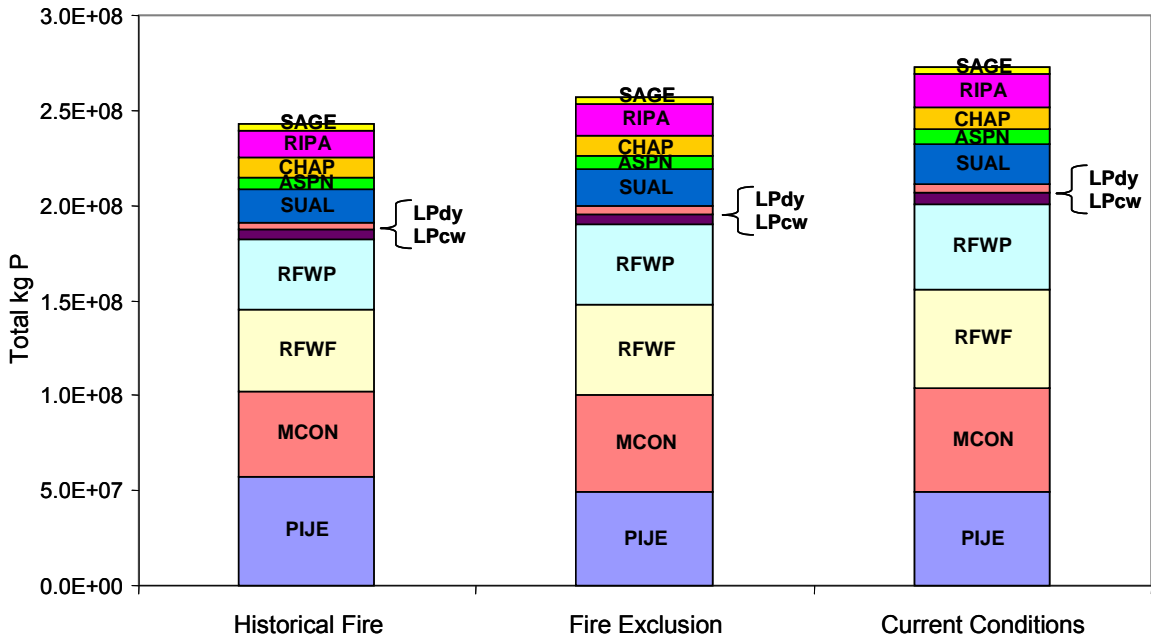


Figure 17. Mean total P (kg P) for the Lake Tahoe Basin illustrating the contribution of each ecoregion during each fire period.

How do alternative management scenarios compare with regard to their long-term effects on nutrient pools?

All management treatments occurred primarily in the Jeffrey pine and mixed conifer ecoregions, and the magnitudes of treatment effects were similar in both ecoregions; we therefore primarily present results for Jeffrey pine.

Treatment did not significantly affect leachate N, which was similar for all treatments and the historic fire regime (Fig. 18). Prescribed fire at the historic frequency had the highest leachate N at $1.23 \pm 0.18 \text{ kg N ha}^{-1} \text{ yr}^{-1}$, and the current harvesting regime at the historic frequency had the lowest at $1.11 \pm 0.14 \text{ kg N ha}^{-1} \text{ yr}^{-1}$. Although not significant, prescribed fire treatments had slightly more leachate N than mechanical treatments. In the mixed conifer ecoregion, prescribed fire at the historic frequency had the highest leachate N ($0.37 \pm 0.08 \text{ kg N ha}^{-1} \text{ yr}^{-1}$), which was significantly higher than that of all other ecoregions except prescribed fire at half the historical frequency. Leachate N for these two treatments was significantly higher than that under the historical fire regime, but all other treatments were not significantly different. Prescribed fire at higher frequencies than the current treatment plan does increase leachate N significantly in the mixed conifer region, and the total increase at the ecoregion level would be $3843 \pm 1138 \text{ kg N yr}^{-1}$.

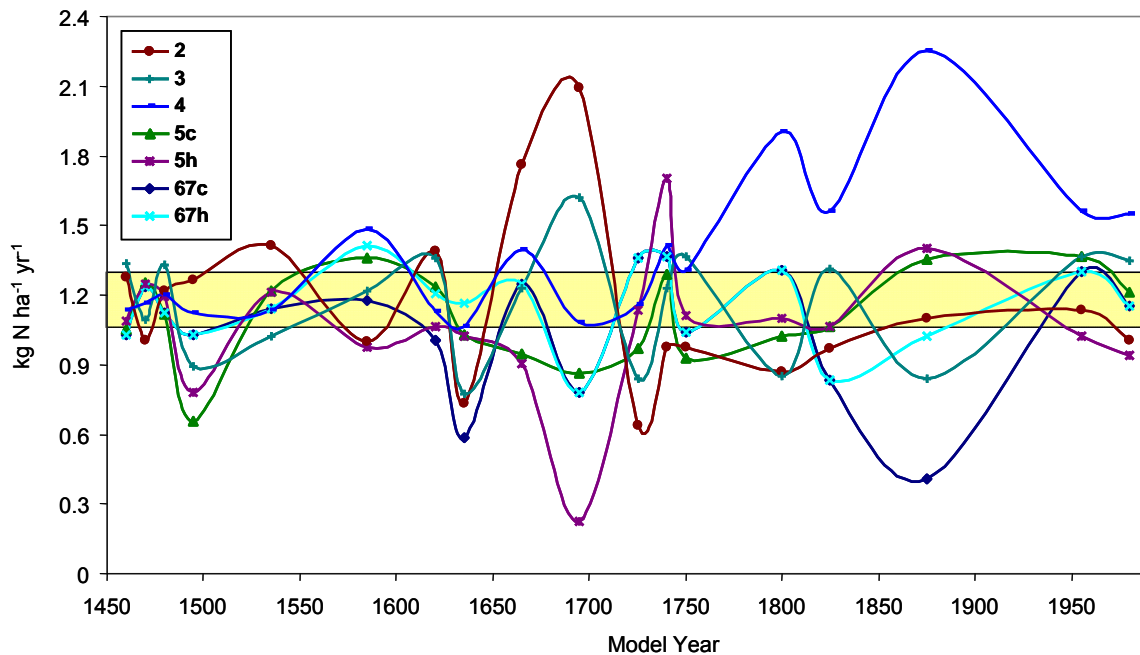


Figure 18. Leachate N dynamics in the Jeffrey pine ecoregion under the various management scenarios. The legend key corresponds to the numbering in the management scenarios section and h and c refer to high and current frequencies. The yellow region represents the 95% confidence interval for the mean under the historic fire frequency.

Litter N was significantly lower under prescribed fire at the historic and half the historic frequencies ($220.4 \pm 17.8 \text{ kg N ha}^{-1}$ and $274.1 \pm 19.8 \text{ kg N ha}^{-1}$ respectively) than under the other treatments and the historic fire regime (Fig. 19). All other treatments, including the current prescribed fire frequency, were not significantly different and had higher amounts of litter N than that during the historic fire regime. The highest amount

was associated with the current mechanical treatment strategy with a fire rotation of 50 years ($593.5 \pm 107.8 \text{ kg N ha}^{-1}$). Litter is removed by prescribed fire treatments and augmented by mechanical treatments, and 43.02% of the variability in litter N was explained by treatment accordingly. The mixed conifer ecoregion exhibited the same pattern, with the lowest litter N occurring under prescribed fire at the historic frequency ($410.7 \pm 22.1 \text{ kg N ha}^{-1}$) and the highest under the current mechanical treatment frequency ($684.5 \pm 39.3 \text{ kg N ha}^{-1}$). Aggregated to each ecoregion, prescribed fire treatments at the historic frequency result in a net decrease of $1,459,524 \pm 392,547 \text{ kg N}$ in the Jeffrey pine ecoregion and $1,425,053 \pm 310,560 \text{ kg N}$ in the mixed conifer ecoregion.

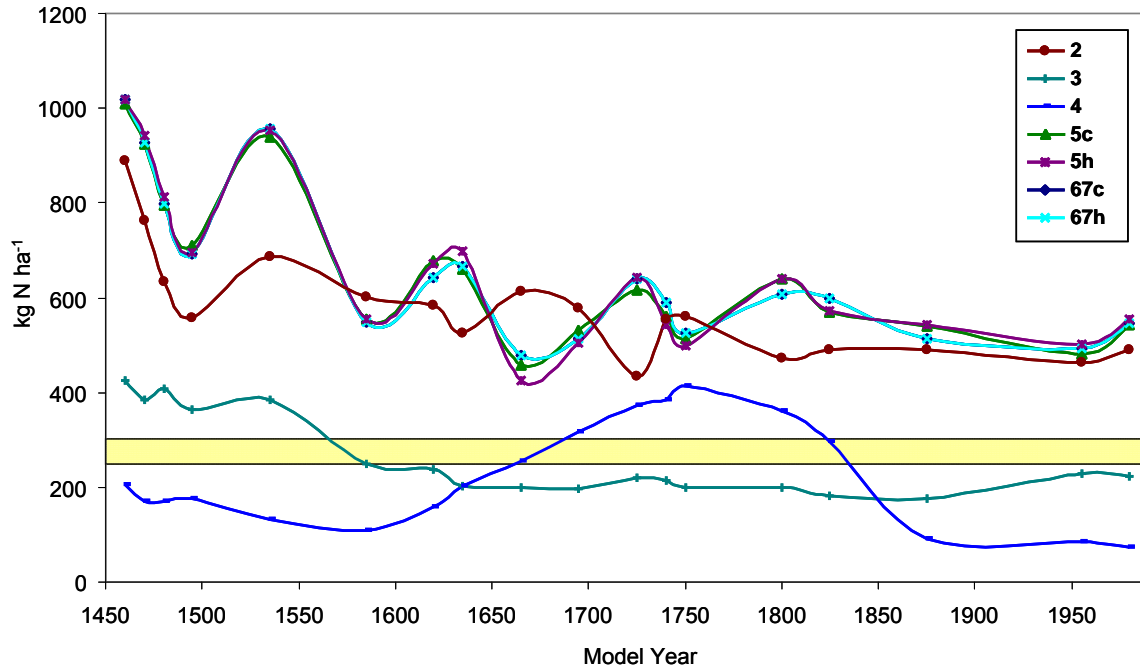


Figure 19. Litter N dynamics in the Jeffrey pine ecoregion under the various management scenarios. The legend key corresponds to the numbering in the management scenarios section and h and c refer to high and current frequencies. The yellow region represents the 95% confidence interval for the mean under the historic fire frequency.

As expected, litter P behaved similarly to litter N and treatment explained 43.02% of the variability. Litter P under prescribed fire at the historic frequency ($14.7 \pm 0.6 \text{ kg P ha}^{-1}$) was similar to that under prescribed fire at half the historic frequency, and significantly lower than that under all other treatments and the historic fire regime (Fig. 20). The highest litter P occurred under the current mechanical treatment strategy ($37.0 \pm 1.1 \text{ kg P ha}^{-1}$) and was similar to the other treatments and significantly higher than that under the historical fire regime. Litter P in the mixed conifer followed the same pattern, with $23.5 \pm 2.1 \text{ kg P ha}^{-1}$ using prescribed fire at the historic frequency and $46.2 \pm 2.7 \text{ kg P ha}^{-1}$ using the current mechanical treatment strategy. Under the best treatment, litter P decreased by $101,135 \pm 13,569 \text{ kg P}$ in the Jeffrey pine ecoregion and $78,782 \pm 30,080 \text{ kg P}$ in the mixed conifer ecoregion.

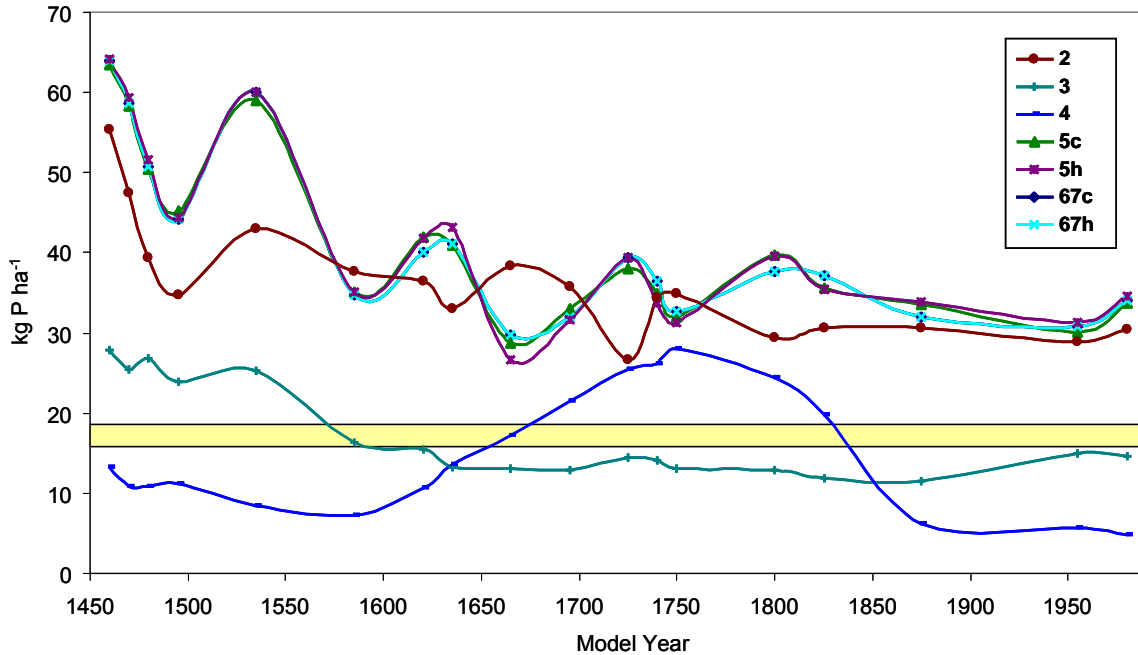


Figure 20. Litter P dynamics in the Jeffrey pine ecoregion under the various management scenarios. The legend key corresponds to the numbering in the management scenarios section and h and c refer to high and current frequencies. The yellow region represents the 95% confidence interval for the mean under the historic fire frequency.

Biomass treatments had significantly lower total N and P relative to prescribed fire treatments due to their greater reductions in living biomass (Fig. 21). 16.3% of variability in total N and 12.5% of variability in total P were explained by treatment. Biomass treatments and prescribed fire at the historic frequency maintained historic levels of total N and P due to the removal of large amounts of biomass, but prescribed fire treatments did not due to their lower severity, and thus lower amount of combustion. The current prescribed fire regime led to the largest increase in total N and P ($11,843 \pm 1,049$ kg N ha⁻¹ and $4,871 \pm 785$ kg P ha⁻¹). Mixed conifer followed a similar pattern.

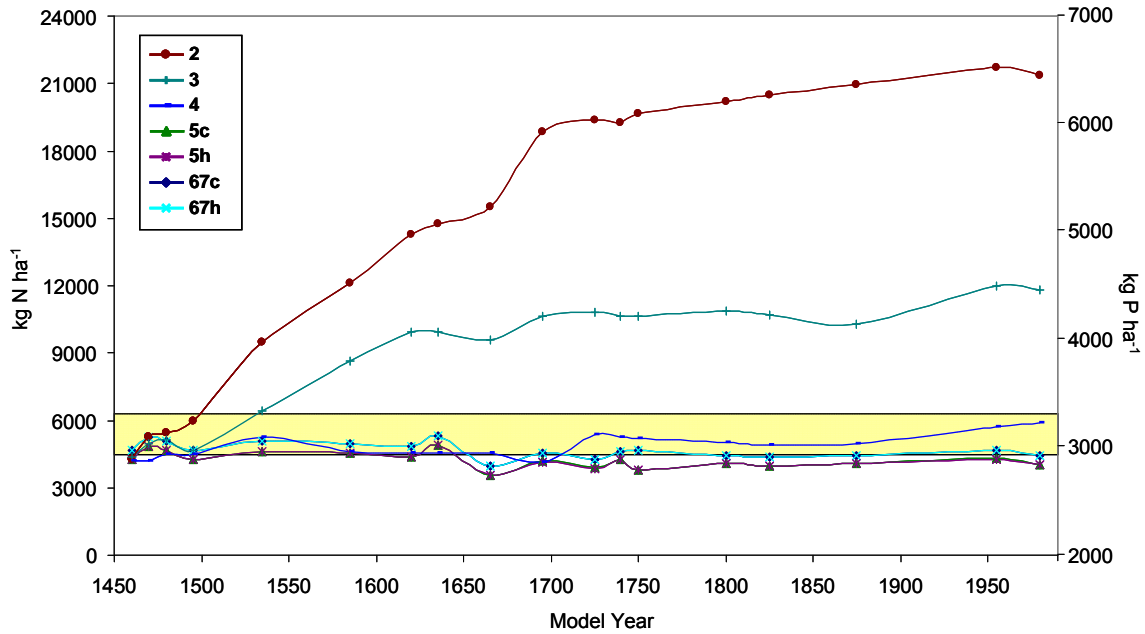


Figure 21. Total N and P dynamics in the Jeffrey pine ecoregion under the various management scenarios. The legend key corresponds to the numbering in the management scenarios section and h and c refer to high and current frequencies. The yellow region represents the 95% confidence interval for the mean under the historic fire frequency.

In comparison to microbially-mediated decomposition, how important is fire to nutrient cycling dynamics?

Model results suggest that the amount of leachate N is directly proportional to the quantity of N mineralized by fire events. The occurrence of a fire within the model year explained 47.04% of the variance in leachate N, its interaction with total biomass explained 12.33%, and total biomass itself explained 6.95%. The amount of N mineralized is dependent on the amount of combustion from the living biomass and dead biomass, consisting of litter and coarse woody debris. The amount of dead biomass explained an additional 14.17% of variability and its interaction with a fire occurrence within the model year explained an additional 15.28%. The interaction terms between fire occurrence and biomass likely represent the amount of combusted material.

The model for litter N included total biomass (which explained 52.18% of the variability), ecoregion (25.34%), and the number of fires within the previous 5 years (4.07%). Similarly for litter P, total biomass explained 51.38% of variability, ecoregion explained 24.31%, and the number of fires within the previous 5 years explained 5.94%. Because litter inputs depend on the amount of aboveground biomass and the removal of litter is inconsistent, litter N and P contents are not strongly influenced by fire occurrence over the long time scales examined in this model. However, the magnitude of the change in litter N and P after a fire event is approximately 45% greater than that during a non-fire year. Since fire occurrence also influences total biomass, the explanatory power of fire may include part of that in total biomass.

Total N can only increase due to deposition or N fixation and decrease through combustion or leaching. The interaction between ecoregion and fire period accounted for 58.43% of variability, biomass of N-fixing species accounted for 13.37%, and the number

of fires in the previous five years accounted for 5.37%. The interaction between ecoregion and fire period likely explains the variation in the change in fire frequency between ecoregions. In the model, deposition and combustion are the only means by which total P can increase or decrease. Fire period accounted for 15.86% of the variability, the interaction of fire in the model year and total biomass for 17.42%, fire in the model year for 2.69%, and total biomass for 2.87%.

As hypothesized, decomposition rates were lower in ecoregions with greater fire frequency. For all species, a logarithmic function of the form $y = \alpha \cdot \ln(x) + \beta$ with decomposition rate as the dependent variable and fire rotation as the independent variable provided $R^2 = 0.5589$. In the model, decomposition is directly related to AET (Eq. 4, Appendix 1) and in the Lake Tahoe Basin, AET increases as the expected fire frequency decreases.

What are realistic ranges of potential N and P loading in surface runoff and snowmelt?

Concentrations of $\text{NO}_2 + \text{NO}_3\text{-N}$ in surface runoff ranged from 0 mg L^{-1} to 136.79 mg L^{-1} (equivalent to 1.37%) and quantities from 0 mg to 26.75 mg, with concentrations varying significantly by site and treatment (Fig. 22). At the Gondola and Truckee sites, fire increased $\text{NO}_2 + \text{NO}_3\text{-N}$ concentrations and quantities, while at the North Shore site fire led to a significant decrease in $\text{NO}_2 + \text{NO}_3\text{-N}$ concentration and an insignificant increase in quantity. Wildfire (Gondola) increased concentration by $0.49 \pm 0.28 \text{ mg L}^{-1}$ (mean \pm standard error) and quantity by $0.006 \pm 0.007 \text{ mg}$, while prescribed fire (Truckee and North Shore) increased concentration by $1.16 \pm 0.52 \text{ mg L}^{-1}$ and quantity by $0.26 \pm 0.12 \text{ mg}$, likely due to the magnitude of the increase at Truckee.

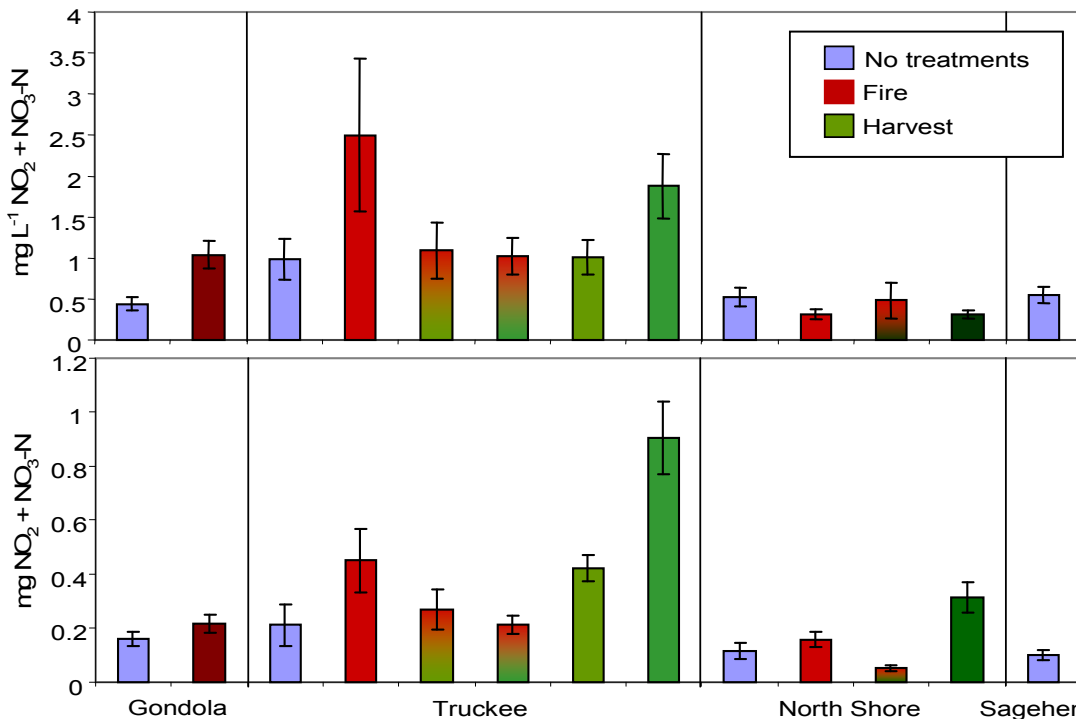


Figure 22. Mean±standard errors for concentrations (top panel) and quantities (bottom panel) of $\text{NO}_2 + \text{NO}_3\text{-N}$ in surface runoff by site and treatment.

Harvesting had mixed effects; whole tree harvest increased the concentration by $1.84 \pm 0.59 \text{ mg L}^{-1}$ and quantity by $1.0 \pm 0.14 \text{ mg}$, while cut-to-length harvesting increased the concentration by $2.23 \pm 0.59 \text{ mg L}^{-1}$ and quantity by $1.18 \pm 0.14 \text{ mg}$. The difference between harvesting techniques may be due to their effects on the forest floor. Whereas cut-to-length harvesting significantly increased forest floor N by $120.46 \pm 81.27 \text{ kg ha}^{-1}$, whole-tree harvesting insignificantly decreased it by $35.42 \pm 88.25 \text{ kg ha}^{-1}$. The combination of fire and harvest did not significantly change or significantly decreased the concentration and quantity, likely due to substantial reductions in the forest floor and a cooler burning temperature due to reduced fuels.

Both time since fire and time since harvest were negatively related to the concentration and quantity of $\text{NO}_2 + \text{NO}_3\text{-N}$ (Fig. 23). Because harvesting occurred prior to prescribed fire for all treatments that included both components, the patterns are similar. Concentration decreased by $0.0006 \pm 0.0003 \text{ mg L}^{-1}$ for every day after fire and by $0.0016 \pm 0.0003 \text{ mg L}^{-1}$ for every day after harvest, and quantity decreased similarly. While treatment immediately increases the concentration, the effect decreases gradually over time, resulting in similar levels to the initial concentration within 2-3 years.

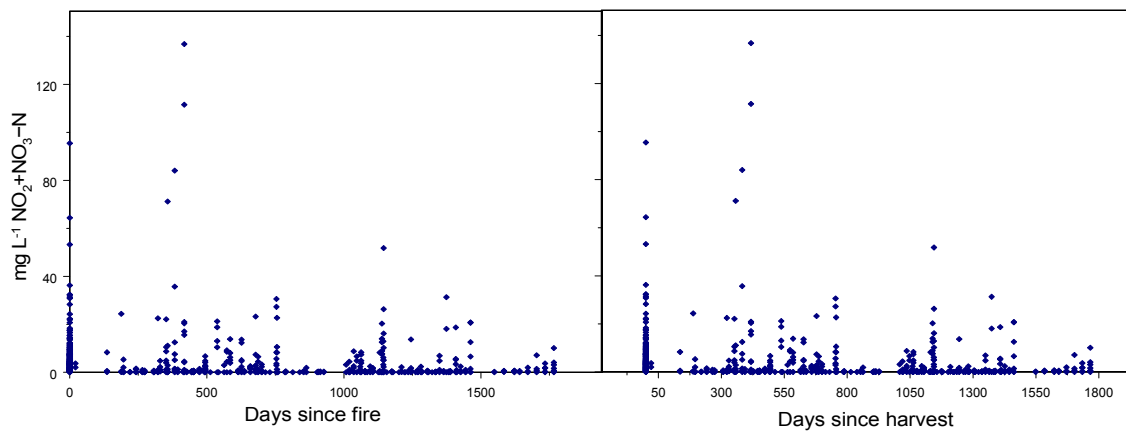


Figure 23. Scatter plots of days since treatment and concentration of $\text{NO}_2 + \text{NO}_3\text{-N}$ in surface runoff.

Because surface runoff is hypothesized to leach primarily from the forest floor, we would expect increased forest floor mass and nutrients to be positively related to $\text{NO}_2 + \text{NO}_3\text{-N}$ concentration and quantity in surface runoff. However, the models indicate that as forest floor N increased, the concentration insignificantly decreased by $0.0007 \pm 0.0006 \text{ mg L}^{-1}$ and the quantity by $0.0005 \pm 0.0006 \text{ mg L}^{-1}$. Likewise, the biomass of the understory was also insignificantly and negatively related with a similar magnitude. This pattern occurred because forest floor increased with time since fire and time since harvest, confounding the expected relationship.

Concentrations and quantities of $\text{NH}_4\text{-N}$ varied significantly between sites and by treatment (Fig. 24). Concentrations varied from 0 to 963.73 mg L^{-1} and quantities from 0 to 136.5 mg, with the highest values occurring immediately after fire. Like $\text{NO}_2 + \text{NO}_3\text{-N}$, fire increased $\text{NH}_4\text{-N}$ concentrations at the Gondola and Truckee sites, but decreased the concentration at the North Shore site. When the sample volume was taken into account, the quantity of $\text{NH}_4\text{-N}$ increased significantly at the Gondola site, insignificantly decreased at Truckee, and decreased significantly at North Shore. Wildfire significantly

increased the concentration of $\text{NH}_4\text{-N}$ by $1.53 \pm 1.00 \text{ mg L}^{-1}$ and insignificantly decreased the quantity taking the repeated measures into account. Prescribed fire did not significantly affect concentration and decreased the amount by $0.26 \pm 0.15 \text{ mg}$.

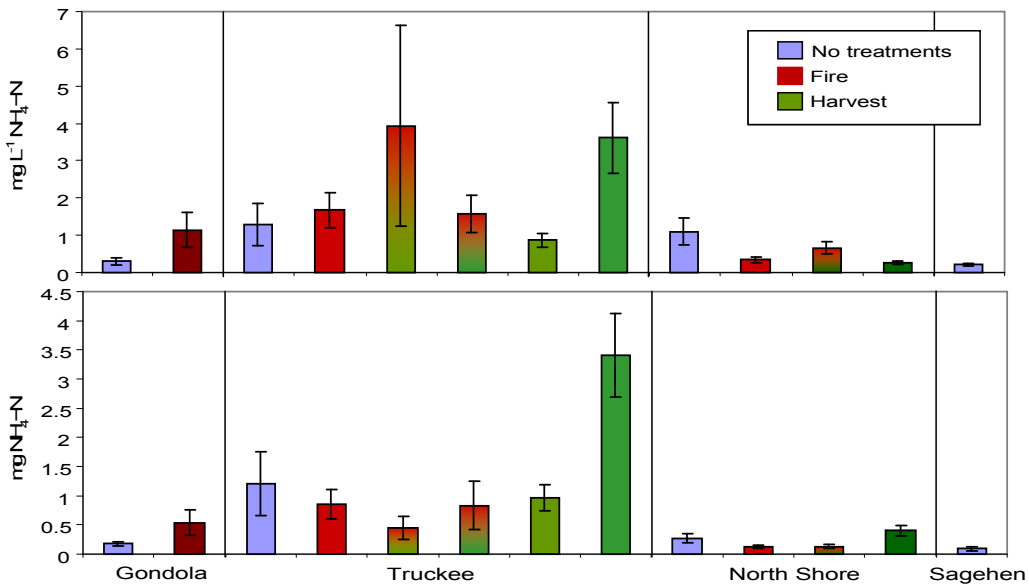


Figure 24. Mean±standard errors for concentrations (top panel) and quantities (bottom panel) of $\text{NH}_4\text{-N}$ in surface runoff by site and treatment.

Whole-tree harvesting significantly increased $\text{NH}_4\text{-N}$ concentration by $6.33 \pm 1.89 \text{ mg L}^{-1}$ and cut-to-length harvesting led to a significant $3.65 \pm 1.94 \text{ mg L}^{-1}$ increase. Whole-tree harvesting trivially decreased forest floor mass, while cut-to-length harvesting significantly increased forest floor N by $81.27 \pm 35 \text{ kg ha}^{-1}$, contrary to the expected relationship. Time since fire significantly decreased concentration by $0.0012 \pm 0.0009 \text{ mg L}^{-1} \text{ day}^{-1}$ and $0.0005 \pm 0.0003 \text{ mg day}^{-1}$; time since harvest had larger effects on concentration ($0.0052 \pm 0.001 \text{ mg L}^{-1} \text{ day}^{-1}$) and quantity ($0.0035 \pm 0.0003 \text{ mg day}^{-1}$) (Fig. 25). There appears to be a threshold at approximately 3 years after harvest for the quantity of $\text{NH}_4\text{-N}$, but there were insufficient data to interpret it. Forest floor and understory masses had no significant effects on concentration or quantity.

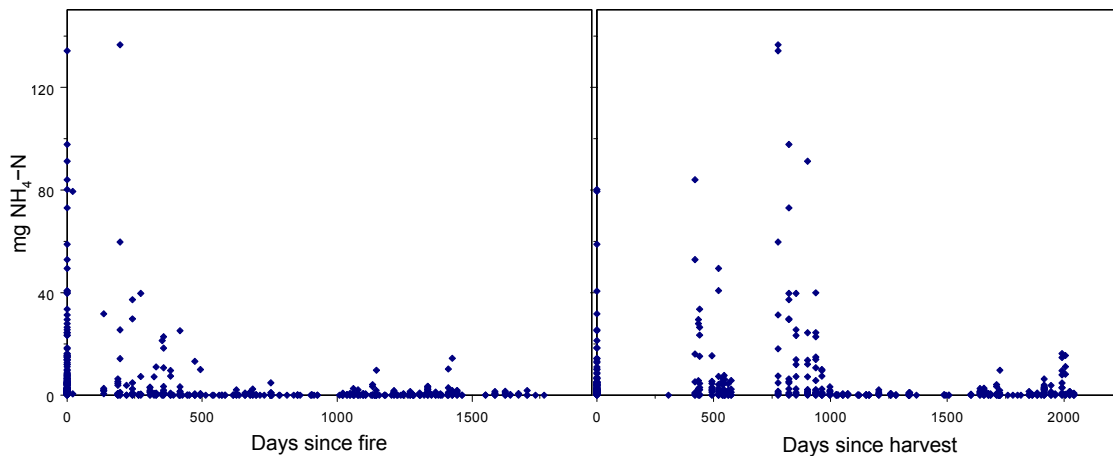


Figure 25. Scatter plots of days since treatment and the amount of $\text{NH}_4\text{-N}$ in surface runoff.

Concentrations and quantities of $\text{OPO}_4\text{-P}$ responded similarly to $\text{NH}_4\text{-N}$ with respect to treatment (Fig. 26), with a maximum concentration of 175.54 mg L^{-1} and maximum quantity of 35.31 mg . Wildfire significantly increased and prescribed fire significantly decreased both the concentration and quantity ($0.33 \pm 0.19 \text{ mg L}^{-1}$ and $0.009 \pm 0.004 \text{ mg}$ for wildfire, and $-0.51 \pm 0.33 \text{ mg L}^{-1}$ and $-0.31 \pm 0.11 \text{ mg}$ for prescribed fire). Whole-tree harvesting significantly decreased $\text{OPO}_4\text{-P}$ concentration by $0.61 \pm 0.36 \text{ mg L}^{-1}$ and quantity by $0.41 \pm 0.11 \text{ mg}$, while cut-to-length harvesting had no significant effect. Time since fire and time since harvest both significantly decreased nutrient concentration and quantity, with the same pattern observed in $\text{NH}_4\text{-N}$. Forest floor and understory masses did not have a significant relationship with either concentration or quantity.

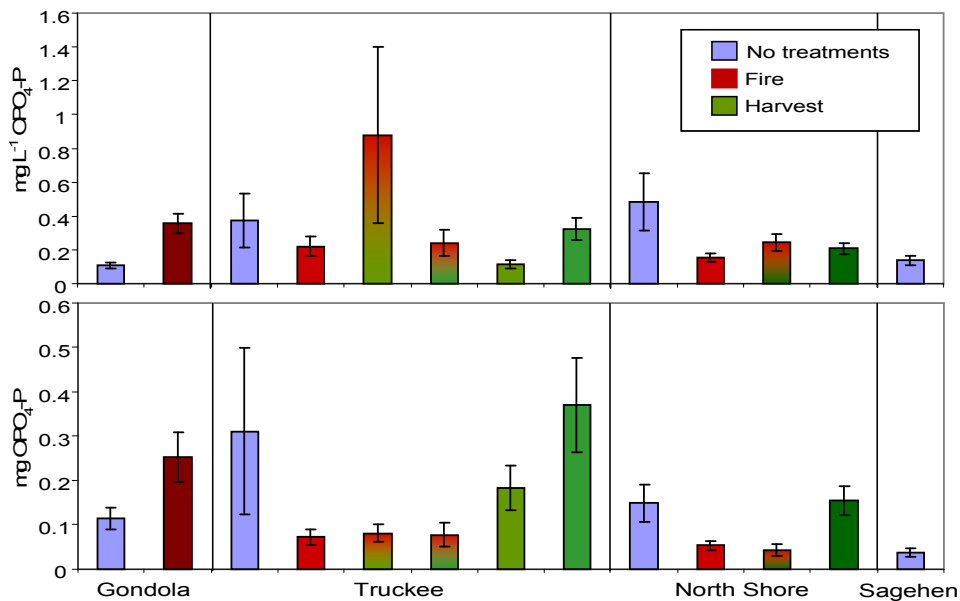


Figure 26. Mean±standard errors for concentrations (top panel) and quantities (bottom panel) of $\text{OPO}_4\text{-P}$ in surface runoff by site and treatment.

Nutrients in snowmelt were not significantly affected by fire or harvest treatments, but snowmelt collectors were not installed until over a year after fire and over two years after harvest at all sites (concentrations and quantities of $\text{NO}_2+\text{NO}_3\text{-N}$ are shown in Fig. 27). $\text{NO}_2+\text{NO}_3\text{-N}$ concentrations varied from 0 to 5.12 mg L^{-1} and quantities from 0 to 1.18 mg per event, $\text{NH}_4\text{-N}$ concentrations varied from 0 to 24.35 mg L^{-1} and quantities from 0 to 4.57 mg , and $\text{OPO}_4\text{-P}$ concentrations varied from 0 to 5.49 mg L^{-1} and quantities from 0 to 1.18 mg . Nutrient concentrations were negatively related to time since treatments ($-0.025 \pm 0.012 \text{ mg L}^{-1} \text{ yr}^{-1}$ for $\text{NO}_2+\text{NO}_3\text{-N}$, $-0.06 \pm 0.04 \text{ mg L}^{-1} \text{ yr}^{-1}$ for $\text{NH}_4\text{-N}$, and $-0.012 \pm 0.008 \text{ mg L}^{-1} \text{ yr}^{-1}$ for $\text{OPO}_4\text{-P}$) and nutrient quantities were positively related to time since treatments for $\text{NH}_4\text{-N}$ ($0.045 \pm 0.015 \text{ mg yr}^{-1}$) and $\text{OPO}_4\text{-P}$ ($0.009 \pm 0.003 \text{ mg yr}^{-1}$) (the relationships for the concentration of $\text{OPO}_4\text{-P}$ are shown in Fig. 28). The relatively strong effects of time since treatment indicate that the treatments themselves were likely important, but the temporal mismatch between the treatments and

installation of collectors possibly concealed the effect. Forest floor measurements were not available for snowmelt collectors.

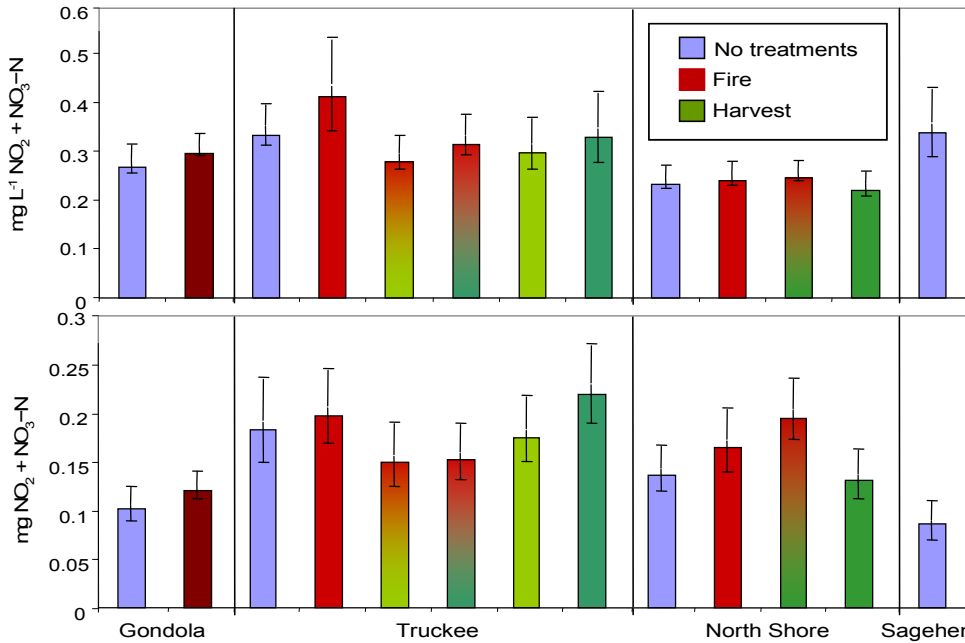


Figure 27. Mean±standard errors for concentrations (top panel) and quantities (bottom panel) of $\text{NO}_2 + \text{NO}_3\text{-N}$ in snowmelt by site and treatment. No differences are significant.

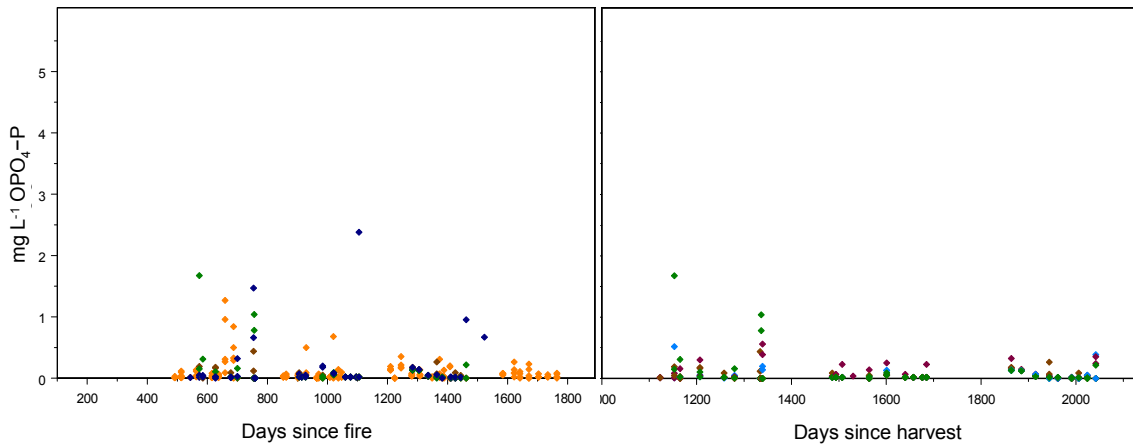


Figure 28. Scatter plots of days since treatment and the concentration of $\text{OPO}_4\text{-P}$ in snowmelt by treatment. The seasonal effect within each year's data is a covariate in the analysis.

Significance and Conclusions

(1) To what extent do modeled nutrient pools differ under historical fire, fire exclusion, and current conditions?

Fire exclusion increased litter and total nutrients above their levels under historical fire in all ecoregions, with the effects more pronounced where fires were historically more frequent (e.g., the Jeffrey pine ecoregion). Conversely, fire exclusion decreased the amount of leachate N in most ecoregions because leaching events are strongly associated with large pulses in available N, which most commonly occur after fires.

(2) How do alternative management scenarios compare with regard to their long-term effects on nutrient pools?

Lower elevation forests, including the Jeffrey pine, mixed conifer, and chaparral ecoregions, generally had higher leachate N and litter N and P under all scenarios. For leachate N, the Jeffrey pine and chaparral ecoregions may have historically been a significant source of nutrients to Lake Tahoe. Because leachate N depends on the sporadic large pulses of mineral N that are primarily produced by fire events, prescribed fire treatments were generally less successful than mechanical treatments at reducing leachate N. However, this was only significant in the mixed conifer ecoregion.

Although prescribed fire at the current 50-year fire rotation (641 ha yr^{-1}) reduced litter N and P relative to fire exclusion, it was unable to reduce them to historical levels, even after 500 years. However, prescribed fire at double this frequency or more, as proposed in the plan by the U.S. Department of Agriculture et al. (2007), led to reductions below historic levels because treatments were prioritized to stands with the most leaf litter. Mechanical treatments led to increased litter N and P that were significantly higher than those historically and similar to those under fire exclusion. Mechanical treatments add mass to the forest floor, but also reduce aboveground biomass, and thus litter production.

Total N and P depend heavily on total biomass at the site, which can be removed through combustion or mechanical fuel treatments. Treatments that removed more aboveground material were more successful at reducing total N and P than those that did not, but the method of this removal influences C storage. If biomass is combusted, total C sequestration decreases and CO_2 and NO_x are released, which may have implications for air quality and climate change.

(3) In comparison to microbially-mediated decomposition, how important is fire to nutrient cycling dynamics?

The modeling analysis supports the hypothesis by Johnson et al. (1998) that N cycling dynamics are dominated by fire events in at least some semi-arid regions, such as the Lake Tahoe Basin. The amount of leachate N was directly proportional to the quantity of N mineralized by fire events. Variance partitioning of model outputs showed that the ecoregion-specific effects of fire period explained most of the simulated variation in total N. However, the results of our simulation analyses should be considered within the context of model assumptions and uncertainties. This model did not include surface or groundwater hydrology, and thus estimates are of potential nutrient sources (i.e., modeled leachate N and litter N and P) to Lake Tahoe instead of potential nutrient fluxes. To model potential nutrient fluxes would require linkage to a landscape-scale hydrological model and an understanding of the functional role of riparian areas as potential sinks and filters for nutrients. Additionally, the model does not include other forest processes, such as bark beetle spread and associated tree mortality, which may greatly influence both forest and nutrient cycling dynamics in the Lake Tahoe Basin. LANDIS-II does include a biological disturbance agent module that is useful for this purpose (Sturtevant et al. 2004). Finally, the model assumed a constant climate, and results may differ under realistic scenarios of future climate change.

(4) What are realistic ranges of N and P loading in surface runoff and snowmelt?

Nutrient concentrations and quantities in surface runoff did not respond predictably to forest floor and understory mass. Considering the forest floor is likely the source of nutrients in surface runoff, the lack of relationship was surprising. However, the forest floor and understory datasets had limited temporal and spatial resolution, with a maximum of 2 to 3 measurements for each plot at only two sites. However, the amount of fresh litter, which likely has higher nutrient concentrations than older litter, may be a more important measure. The species composition of the forest floor may also be quite important, especially considering the variation in decomposition rates between species.

In general, wildfire increased nutrient concentrations and quantities in surface runoff, with the effect decreasing over time. The effects of prescribed fire were variable between sites for nutrients, but also showed a significant negative effect of time since fire. Whole tree harvesting had greater effects than cut-to-length harvesting, although the magnitude and direction of the effects were variable. The combination of prescribed fire and harvesting treatments appeared to mitigate the individual effects of both treatments, leading to only slight changes relative to the control sites, especially for nutrient quantities. Unlike surface runoff nutrients, snowmelt nutrients were not significantly related to treatments or time since treatment. Because vegetation varied primarily with site, we were unable to determine the importance of ecoregion or forest composition on nutrients in surface runoff or snowmelt.

Management Recommendations

Our model and simulation results provide another means by which to evaluate management strategies in the Lake Tahoe Basin. The contradictory effects of prescribed fire on the amount of leachate N and litter N and P highlight the conflict between two primary goals in the basin: to improve water quality and to reduce fire risk. Because the proportion of N leachate and N and P in surface runoff that actually enters Lake Tahoe is currently unknown, model results should not be used to prioritize between treatments for these sources. Nutrients in surface runoff varied with treatments, but the relationships varied between sites and were not sufficiently predictable for extrapolation to other sites or evaluation of management actions.

Fire regulation of leachate and litter nutrients – Model results suggest that fire events are strongly tied to greater amounts of leachate N. **Since simulated leachate N was highest under the historical fire regime, the past clarity of Lake Tahoe suggests it was historically able to cope with that influx of N, which was greater than that currently created by prescribed fires.** Considering the other nutrient inputs into the lake at present, management should exercise caution with the amount and placement of prescribed fires. Litter N and P are most strongly influenced by total biomass, which in turn exerts a strong influence on litter production. This suggests that any management strategy that reduces biomass will reduce litter, and thus may potentially reduce N and P in surface runoff. However, the empirical relationship between forest floor mass and nutrients in surface runoff was unclear.

Fuel treatment location – **Because the Jeffrey pine, mixed conifer, and chaparral ecoregions have the greatest leachate N and litter N and P levels at both the hectare-**

and ecoregion scale, fuel treatments in these forest types will be most likely to reduce nutrient inputs to Lake Tahoe. The current management plan places the majority of treatments in the Jeffrey pine and mixed conifer ecoregions, where the reduction of fuel loads and fire risk is greater (U.S. Department of Agriculture et al. 2007). **Considering the model indicates the chaparral ecoregion had a greater storage of soil organic matter, it may be prudent to avoid disturbing chaparral sites with treatment.**

Fuel treatment methods – Relative to fire exclusion and biomass removal, the use of prescribed fire has the possibility of increasing leachate N in the Jeffrey pine and mixed conifer ecoregions. However, modeled increases were small and only significant in the mixed conifer ecoregion. Prescribed fire at higher frequencies than the current plan did significantly decrease litter N and P, and thus the reduction in surface runoff nutrients is likely to outweigh the increase in leachate N. **Mechanical biomass removal treatments may be more prudent in riparian areas and near the lakeshore, where leachate has a higher probability of entering Lake Tahoe, but model results primarily recommend prescribed fire if the management goal is to reduce litter N and P, and hence to reduce availability of these nutrients for surface runoff.** Conversely, the field data suggest that mechanical harvesting may not increase nutrients as much as prescribed fire at some sites. Further information about the relative abilities of these nutrient forms to enter Lake Tahoe may help determine which treatment strategy is most favorable.

Fuel treatment frequency – **Although treatments at the current 50-year fire rotation (approximately 641 hectares annually) have the potential to reduce litter N and P below their levels under fire exclusion, higher frequencies are needed to return to the historic range of variability for N and P cycling.** Fuel treatments at half the historic fire frequency did successfully reduce litter N and P and did not significantly increase leachate N. Approximately 2,089 hectares would need to be treated annually to approach that fire frequency, which is within the range scheduled in the *Lake Tahoe Basin Multi-Jurisdictional Fuel Reduction and Wildfire Prevention Strategy* (U.S. Department of Agriculture et al. 2007), but more than double the amount normally completed.

Research Products

Current Products

Ganschow, S.L., P.J. Weisberg, D.W. Johnson, and W.W. Miller. 2006. Effects of historical and alternative fire regimes on nutrient cycling in the Lake Tahoe Basin. Tahoe Research Symposium, Incline Village CA, October 18 – 20 2006. Poster presentation.

Ganschow, S.L., P.J. Weisberg, D.W. Johnson, and W.W. Miller. 2007. Modeling the effects of historical and current fire regimes on nitrogen cycling in the Lake Tahoe Basin. Annual Meeting of the International Association for Landscape Ecology (US Chapter), Tucson AZ, April 9 – 13 2007. Oral presentation.

Ganschow, S.L., P.J. Weisberg, D.W. Johnson, and W.W. Miller. 2007. Effects of changing disturbance regimes on watershed-scale nutrient cycling: An integrated

modeling approach. Ecological Society of America/Society for Ecological Restoration joint annual meeting, San Jose, CA, 8/5 – 8/10/2007. Oral presentation.

Ganschow, S.L., P.J. Weisberg, R.M. Scheller, D.W. Johnson, and W.W. Miller. 2007. Modeling carbon and nitrogen cycling in the Lake Tahoe Basin. LANDIS-II Annual Workshop, Woodruff, WI, October 15-17, 2007. Oral presentation.

Miller, W.W., D.W. Johnson, R.F. Walker, S.L. Ganschow, and P.J. Weisberg. 2007. Restoring forest health: the effects of biomass management on potential nutrient delivery to Lake Tahoe. Ecological Society of America/Society for Ecological Restoration joint annual meeting, San Jose, CA, 8/5 – 8/10/2007.

Miller, W.W., Johnson, D.W., Ganschow, S.L., Walker, R.F., Weisberg, P.J., Loupe, T.M. 2009. Effects of biomass management on potential nutrient delivery to Lake Tahoe. *Restoration Ecology*, accepted.

The NuCycling-Succession model is itself a useful product. The LANDIS-II model has been applied to numerous forest management questions throughout much of the United States (<http://www.landis-ii.org/>) and is likely the most widely used model for simulating forest disturbance and succession over landscape scales. With the assistance of the LANDIS developers at the University of Wisconsin-Madison, we are the first to develop a nutrient cycling extension for this model. Our model has been coded as an extension of LANDIS-II (<http://www.landis-ii.org/exts/nutrient-cycling-succession>) and will eventually be made accessible to the broader LANDIS user community. Since our model is currently parameterized for the Lake Tahoe Basin and its historical and current fire regimes, there is an opportunity for the model to be applied to a diversity of locally and regionally relevant management questions.

Pending Products

As part of Sarah Ganschow's M.S. Thesis work, two articles are being prepared for submission to peer-reviewed journals. A first paper will describe the development of the simulation model, including model evaluation. A second paper will focus on our model applications to describe the effects of fire exclusion and fire management on landscape-level nutrient cycling in the Lake Tahoe Basin.

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Appendix 1. Detailed description of the NuCycling Succession Model

Biomass Dynamics

Excluding disturbance, simulated annual primary productivity and mortality determine cohort biomass. Because minimal productivity and mortality data are available at the large scales represented in this model, two main simplifying assumptions were made. We assumed productivity and mortality would equalize after many decades, leading to an equilibrium biomass condition, and that density information is implicitly included in the model. Within each vegetation component, the concentrations of carbon, nitrogen, and phosphorus differ for each species, but are assumed to remain spatially and temporally constant (Table A1).

Table A1. Model parameters for nutrient concentrations by vegetation component and species.

Species Code	Leaf Lignin	Leaf C	Leaf N	Leaf P	Litter C	Litter N	Litter P	Wood C	Wood N	Wood P	Fine Root C	Fine Root N	Fine Root P
PiJe	0.28	0.5	0.015	0.001	0.5	0.0068	0.0008	0.5	0.0007	0.00001	0.5	0.008	0.0008
PiLa	0.18	0.5	0.015	0.001	0.5	0.0071	0.0009	0.5	0.0007	0.00001	0.5	0.0085	0.0009
CaDe	0.1	0.5	0.015	0.001	0.5	0.0063	0.0007	0.5	0.0007	0.00001	0.5	0.007	0.0007
AbCo	0.17	0.5	0.016	0.001	0.5	0.0077	0.0008	0.5	0.0007	0.00001	0.5	0.0085	0.0008
AbMa	0.17	0.5	0.016	0.001	0.5	0.008	0.0008	0.5	0.001	0.00001	0.5	0.009	0.0008
PiMo	0.26	0.5	0.015	0.001	0.5	0.0051	0.0007	0.5	0.0007	0.00001	0.5	0.006	0.0008
PiCo	0.3	0.5	0.014	0.001	0.5	0.0054	0.0006	0.5	0.0007	0.00001	0.5	0.0072	0.0006
TsMe	0.24	0.5	0.015	0.001	0.5	0.005	0.0008	0.5	0.0007	0.00001	0.5	0.006	0.0008
PiAl	0.27	0.5	0.011	0.001	0.5	0.0049	0.0008	0.5	0.0007	0.00001	0.5	0.006	0.0008
PoTr	0.18	0.48	0.022	0.001	0.48	0.0062	0.0008	0.5	0.0007	0.00001	0.5	0.0077	0.0008
ArTr	0.15	0.5	0.013	0.001	0.5	0.0051	0.0009	0.5	0.0007	0.00001	0.5	0.0063	0.0009
NRip	0.18	0.48	0.021	0.001	0.48	0.0063	0.0009	0.5	0.0007	0.00001	0.5	0.008	0.0008
Alln	0.16	0.48	0.018	0.001	0.48	0.0095	0.0008	0.5	0.0007	0.00001	0.5	0.018	0.0008
NoR1	0.25	0.5	0.012	0.001	0.5	0.0075	0.0008	0.5	0.0007	0.00001	0.5	0.0085	0.0008
NoR2	0.25	0.5	0.015	0.001	0.5	0.007	0.0008	0.5	0.0007	0.00001	0.5	0.008	0.0008
NoSe	0.25	0.5	0.015	0.001	0.5	0.007	0.0008	0.5	0.0007	0.00001	0.5	0.0082	0.0008
FiRe	0.25	0.5	0.017	0.001	0.5	0.011	0.0008	0.5	0.0007	0.00001	0.5	0.017	0.0008
FiSe	0.25	0.5	0.017	0.001	0.5	0.008	0.0008	0.5	0.0007	0.00001	0.5	0.016	0.0008

Net Primary Productivity

Simulated aboveground net primary productivity (ANPP) is dependent on the maximum ANPP for the species and the ratio of current biomass to potential biomass, representing available ‘growing space’. Under ideal conditions, simulated ANPP increases logarithmically and asymptotically toward the potential maximum biomass for the cohort (Scheller and Mladenoff 2004). Competition is implicitly modeled as a reduction of potential maximum biomass, and thus a decrease in growth, if a stand contains more than one cohort. Because nitrogen (N) is often considered the most limiting nutrient in temperate forests where deposition rates are low (Vitousek and Howarth 1991), we included a soil N multiplier (Pastor and Post 1985) based on the fertilizer trials of Mitchell and Chandler (1939) and parameterization by Aber et al. (1979). A Mitscherlich equation is used to describe the relationship between expected foliar N concentration and relative soil N availability:

$$\text{ExpFol}_{\%N} = a[1.0 - 10.0^{-c(b + RN)}] \quad (\text{Eq. 1})$$

where a, b, and c are given a set of values based on the species tolerance for low N availability (Table A2). RN is relative N availability on the Mitchell and Chandler scale, calculated as:

$$RN = -170 + 4.0(\text{Min}_N) \quad (\text{Eq. 2})$$

in which Min_N is the modeled available N in kilograms per hectare per year. A linear equation was used to convert foliar N concentration into relative growth rates (Aber et al. 1979):

$$\text{RGR}_N = d + e(\text{ExpFol}_{\%N}) \quad (\text{Eq. 3})$$

The RGR_N is bounded between 0 and 1 and used as a multiplier for potential ANPP. Values for variables d and e are provided in Table A2. Species N tolerance was classified according to the USDA PLANTS Database (2007), with tolerance levels 1 through 3 corresponding to intolerant, intermediate, and tolerant species, and tolerance levels 4 through 6 corresponding to N-fixing species (Table A3). If a species fixes N, we assume it is not N limited and the soil N multiplier was set to 1.

Table A2. Coefficients for expected foliar N (Eq. 1) and relative growth factor (Eq. 2) by tolerance class (from Pastor and Post 1985).

N Tolerance Class	a	b	c	d	e
Intolerant	2.99	207.43	0.00175	-1.7	1.0
Intermediate	2.94	117.52	0.00234	-0.5	0.5
Tolerant	2.79	219.77	0.00179	-0.3	0.6

Table A3. Species-specific parameters for ecological parameters, including nitrogen and fire tolerance.

Species Code	Lifespan	Sexual Maturity	Shade Tol.	N Tol.	Fire Tol.	Seed Dispersal Dist.		Vegetative Reprod. Prob.	Sprout Age		Post-Fire Regen
						Effect.	Max.		Min.	Max.	
PiJe	500	9	3	3	5	20	500	0	0	0	none
PiLa	500	11	3	3	4	30	500	0	0	0	none
CaDe	500	11	3	2	4	40	500	0	0	0	none
AbCo	400	20	5	2	3	60	500	0	0	0	none
AbMa	600	22	4	3	3	60	800	0	0	0	none
PiCo	600	4	3	2	2	60	1000	0	0	0	none
PiMo	400	7	3	3	2	160	800	0	0	0	none
TsMe	800	20	5	2	1	115	575	0.001	15	600	none
PiAl	800	20	3	3	1	4400	22000	0	0	0	none
PoTr	150	20	1	2	1	1000	5000	0.9	10	100	resprout
ArTr	80	2	1	3	1	50	10000	0	0	0	none
NRip	100	7	2	2	2	1000	5000	0.7	4	70	resprout
Alln	80	5	1	4	1	1000	5000	0.8	3	50	resprout
NoR1	60	4	2	2	3	50	10000	0.4	2	40	resprout
NoR2	60	4	2	2	3	50	10000	0.4	2	40	resprout
NoSe	60	3	2	3	2	50	10000	0	0	0	none
FiRe	60	4	2	4	3	50	10000	0.3	2	40	resprout
FiSe	60	3	2	4	2	50	10000	0	0	0	none

ANPP is divided into leaf and wood components using dimensionless biomass quotients from Niklas and Enquist (2002). For deciduous species, 39% of ANPP is allotted to leaves and the remaining 61% is allotted to wood, whereas evergreen species allot 57% of growth to leaves and 43% to wood. Similarly, belowground net primary

productivity is simulated using the average dimensionless production quotients from White et al. (2000). NPP for fine roots is calculated as 120% of foliar NPP for deciduous species and 140% for evergreen species, while NPP for coarse roots is 22% of wood ANPP for deciduous species and 29% for evergreen species.

Mortality

In LANDIS-II, total cohort mortality occurs due to disturbance or age and partial mortality due to growth and age (Scheller and Mladenoff 2004). Growth-related mortality includes self-thinning and other development processes and is simulated as a function of current biomass relative to site biomass. Age-related mortality is caused by the aging of the cohort and is modeled as a function of cohort age in relation to maximum age. Because eventual biomass equilibrium is assumed, partial cohort mortality does not exceed ANPP.

Aboveground mortality is split proportionally between leaf and wood compartments. Like belowground productivity, belowground mortality is simulated using dimensionless quotients, with fine root mortality in equal proportion to leaf mortality and coarse root mortality 22% of wood mortality for deciduous species and 29% for evergreen species (White et al. 2000).

Turnover

Because we assume constant nutrient concentrations and do not explicitly model tree vigor, leaf turnover is approximated as the cohort's leaf biomass divided by the species' leaf longevity. The N and P translocated prior to leaf turnover are used for new growth. Fine root turnover is assumed proportional to leaf turnover (White et al. 2000).

N Fixation

We defined three levels of N fixation (N tolerances 4 through 6) based on the amount of N fixed in excess of the plant's requirement: no excess N fixed, low amounts fixed (up to $10 \text{ kg N ha}^{-1} \text{ yr}^{-1}$), and high amounts fixed (up to $80 \text{ kg N ha}^{-1} \text{ yr}^{-1}$). For low and high amounts of excess N fixed, the annual amount fixed is scaled from zero to the maximum amount fixed according to the cohort's biomass relative to its maximum biomass in that ecoregion.

Forest Floor Dynamics

The mass and nutrient contents of input materials from turnover, mortality, and disturbance, and the rates of decomposition and mineralization determine the mass and nutrient dynamics of the forest floor. Because the model operates on an annual or longer time step, we assume all turnover and mortality takes place before decomposition and that the mineralized nutrients are available for growth the following year. We assume that the process of decomposition can be treated as exponential decay in which the forest floor pools have different decay rates (e.g., Pastor and Post 1985, Parton et al. 1987, White et al. 2000).

Leaf and Fine Root Litter Decomposition

Foliar and fine root litter decomposition follows the three-phase model outlined in Berg and Staaf (1981) and Berg (2000) (Figure A1). In the first two phases, annual

cohorts are comprised of the sum of all litter cohorts for that year, with weighted averages used to determine the associated nutrient proportions, decomposition rates, and limit values. During the first phase, decomposition is limited by lack of nutrients, so N is immobilized from the available mineral pool by the microbial community until a critical C:N ratio of 40 is reached (Prescott et al. 2000). The decomposition rate is a function of AET and initial litter quality (Fan et al. 1998). Phase 2 decomposition continues at the same rate as in phase 1, but results in less decomposed material due to less available material, and is limited by the recalcitrance of the remaining organic material, primarily consisting of lignin (Berg and Staaf 1981 and Berg 2000). Net N mineralization begins during this phase in conjunction with the beginning of lignin decomposition (Moore et al. 2006). The transition to phase 3 is controlled by a limit value to decomposition (Berg et al. 1996), at which point decomposition has slowed and the litter has become more homogeneous, so it is transferred to the soil organic matter.

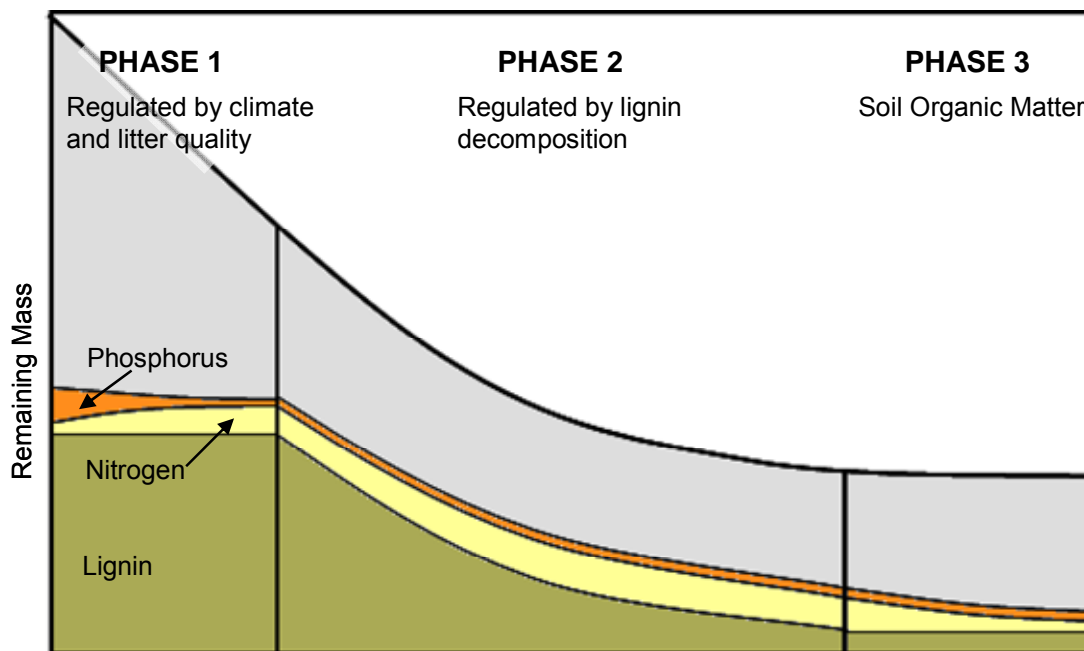


Figure A1. Three-part model of decomposition showing relative fluxes of lignin, nitrogen, and phosphorus during each phase. Proportions are not accurate. Modified from Berg 2000.

The decomposition rate (k) for phases 1 and 2 is calculated as the weighted average of all cohorts' litter or dead fine roots contributions that year. Although non-additive patterns of mass loss are common in mixed-species litter (Gartner and Cardon 2004), the direction and magnitude of these effects are difficult to predict and may be influenced disproportionately by a single or few species (Wardle et al. 1997), so these effects were not included.

For foliar litter, the decomposition rate for each cohort's litter is a function of the species' initial lignin and N concentrations and site actual evapotranspiration (AET) according to equations 7, 10, and 11 in Fan et al. (1998):

$$k = 8.35(\text{Fol}_{\%Lj}:\text{Fol}_{\%Nj})^{-0.784} \times \text{CFI} \quad (\text{Eq. 4})$$

The Climate Factor Index (CFI), which scales decomposition in relation to standard potential evapotranspiration (PET; 551 mm yr⁻¹) and a standard temperature of 10°C, is defined as:

$$\text{CFI} = K_{\text{Regional}} / K_{551} \quad (\text{Eq. 5})$$

CFI is less than 1.0 if conditions are cooler and drier than standard conditions, and greater than 1.0 if conditions are warmer and moister. K_{Regional} is a function of site AET and litter initial lignin concentration as estimated by Meentemeyer (1984):

$$K_{\text{Regional}} = \{(-3.44618 + 0.10015\text{AET}) - (0.01341 + 0.00147\text{AET}) \times \text{Fol}_{\%L_j}\} / 100 \quad (\text{Eq. 6})$$

K_{551} is calculated using Eq. 6 with a site AET of 551 mm yr⁻¹.

Analyses of root decomposition rates in conifers and with combined life forms indicate that root decomposition is relatively insensitive to AET (Berg et al. 1998, Silver and Miya 2001). Therefore, fine root decomposition rates were instead calculated from fine root litter initial C and N concentrations (revised Fig. 3b, Silver and Miya 2001):

$$k = e^{3.92 - \{1.12 \times \ln(\text{FR}_{\%C} / \text{FR}_{\%N})\}} \quad (\text{Eq. 7})$$

where $\text{FR}_{\%C}$ is the C concentration and $\text{FR}_{\%N}$ is the N concentration of the fine roots.

Although these decomposition rates remain constant for the first two phases, net N immobilization generally occurs during phase 1 and net N mineralization begins in phase 2. The net change in N during phase 1 is calculated according to Noij et al. (1993):

$$N_{\text{min}} = \text{Lit}_C \times (k / \text{Lit}_C : \text{Lit}_N) - \text{Mic}_{\text{CUE}} \times \text{Lit}_C \times (k / \text{Mic}_{\text{C:N}}) \quad (\text{Eq. 8})$$

where Lit_C and Lit_N are the amount of C and N in the litter, Mic_{CUE} is the carbon use efficiency of the decomposer microbes, and $\text{Mic}_{\text{C:N}}$ is the microbial C:N ratio. Microbial carbon use efficiency is set to a default value of 0.5 and microbial C:N varies between 10 for angiosperm litter and 20 for conifer litter. The sign of N_{min} determines whether N is mineralized to the mineral soil compartment from the litter (+) or immobilized from the mineral soil compartment into the litter (-). A critical C:P ratio is used to determine if net P mineralization occurs in phase 1. If the C:P ratio is greater than 900, P is conserved; otherwise, P is mineralized proportionally to mass (Prescott et al. 2000). For each annual litter cohort, the transition from phase 1 to phase 2 occurs when the C:N ratio decreases to less than 40 (Prescott et al. 2000). During the second phase of decomposition, N and P mineralize proportionally to mass loss (Berg and Staaf 1981, Moore et al. 2006).

The transition between phases 2 and 3 occurs when the amount of mass loss for the annual litter cohort exceeds the limit to mass loss (simplified from Berg et al. 1996):

$$L_m = 0.89497 + 10 \times \text{Fol}_{\%L} \quad (\text{Eq. 9})$$

Verburg and Johnson (2001) found that an estimated 93% of initial litter mass was decomposed prior to entering the soil organic matter and our calculated limits to mass loss ranged from 85 to 98%, with a mean of 95%.

Coarse Woody Debris Decomposition

Decomposition of coarse woody debris (CWD) is modeled as a single exponential decay function where the decomposition rate is the weighted mean of the species-specific decomposition rates. CWD decomposition rates have not been shown to change consistently with temperature (Harmon et al. 2000) and are therefore not ecoregion-specific. N and P are mineralized at the same rate as mass loss because this accurately represents nutrient loss through decomposition at annual or greater time scales (Laiho and

Prescott 1999) and CWD decomposition generally contributes less than 5% of available mineral N and 10% of available mineral P (Laiho and Prescott 2004). Decomposition rates are so low that fire will likely combust logs before they completely decompose (e.g., Boulanger and Sirois 2006).

Soil Dynamics

The mineral soil pool consists of N, comprised of NO_3^- and NH_4^+ , and various ortho-phosphates, including PO_4^{3-} , that are available for plant uptake. Although there is some evidence that some plants can take up organic nitrogen, it is difficult to predict which species will do so (Lipson and Nasholm 2001, Neff et al. 2003) and we did not include this pathway in the model. We modeled soil organic matter (SOM) as a single pool consisting of the material remaining after the final transition during decomposition of leaf litter and dead fine roots. SOM decomposition is modeled as a single exponential decay function with an ecoregion-specific decomposition rate integrating all site conditions. Because the effects of temperature on decomposition are uncertain (Davidson and Janssens 2006 and Fierer et al. 2005) and the model uses an annual time step and does not explicitly include weather, we did not specifically include temperature-dependent decomposition. Since the first transition during leaf litter and fine roots decomposition is dependent on meeting the critical C:N ratio and P is released in accordance with a critical C:P ratio prior to the final transition, all inputs to SOM have similar C:N:P ratios.

Fire Dynamics

Because fire is hypothesized to be the most important control of N cycling in semi-arid regions (Johnson et al. 1998), we modeled atmospheric loss, mineralization, and transfer of nutrients between living biomass, the forest floor, soil, and charcoal. For each of the five possible fire severities, different proportions of leaf and wood biomass, litter, and coarse woody debris are combusted and an equivalent proportion of fine and coarse roots are transferred to their respective dead pools. We assume that 80% of existing charcoal is consumed by the fire (Czimczik et al. 2005), meaning that charcoal functions as a delay between initial combustion of the organic material and release of a small portion of the nutrients to the mineral soil. As a result of combustion, we simulated a 1% transfer of N from the combusted material to the mineral soil and a 42% transfer of P (Raison et al. 1985). Due to its low gasification temperature, atmospheric losses of N are considerably higher than those of P and are commensurate with organic combustion (Raison et al. 1985). We model an 8% conversion of combusted organic material to charcoal, which is the mean value from the review by Preston and Schmidt (2006). Because the occurrence and amount of soil organic matter combustion is difficult to predict (Johnson and Curtis 2001), we assumed no combustion of soil organic matter.

Appendix 2. References to Detailed Model Description

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