

Uncertainty in carbon allocation strategy and ecophysiological parameterization influences on carbon and streamflow estimates for two western US forested watersheds



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ARTICLE INFO

Article history:

Received 18 May 2016

Received in revised form

22 September 2016

Accepted 24 September 2016

Available online 1 October 2016

Keywords:

Carbon allocation

Ecohydrology

Process based modeling

Ecophysiology

Parameter Sensitivity

ABSTRACT

Increasingly sophisticated process-based ecosystem models account for the ability of plants to vary the proportion of net photosynthate that is allocated to individual organs – such as leaves, stems and roots. Because the governing mechanisms are still not well understood, models differ in the strategies used to represent carbon allocation processes. Allocation schemes may have important implications for ecosystem structure and biogeochemical cycling, thus there is a need to better understand how different carbon allocation strategies influence estimates of variables that are of interest to model users. At the same time, uncertainty in other ecophysiological parameters that are commonly used in carbon cycling models may influence these estimates and interact with different carbon allocation strategies. We use a coupled ecohydrologic model to understand how uncertainty in three relatively simple allocation strategies affects carbon (C) and streamflow estimates in two case study forested mountain watersheds in the western United States: a relatively wet site located in the western Oregon Cascades, and a drier site in California's Sierra Nevada. Ecophysiological parameters controlling productivity rates, morphology, and nutrient requirements for growth are varied as well. The influence of specific ecophysiological parameters and allocation strategies on C sequestration and streamflow estimates differed between sites. At the wetter site, uncertainty in C cycling processes resulted in a three-fold difference in potential sequestered carbon, but had a negligible effect on annual and low monthly streamflow estimates. Conversely, at the drier site, C pool estimates showed limited sensitivity to ecophysiological parameter uncertainty, but considerable difference in annual and low monthly streamflow estimates across ecophysiological assumptions. At both sites, stemwood C pool estimates exceeded literature-derived field values when branch mortality—a surrogate for density thinning—was not included in addition to background mortality. Despite using site- and species-specific information, we are unable to invalidate any of the allocation strategies considered. Our results suggest that uncertainty in parameterization of ecophysiological parameters and assumptions about carbon allocation can strongly influence model estimates of both streamflow and forest carbon sequestration potential, but that influence is likely to vary with site bioclimatic characteristics.

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1. Introduction

Carbon allocation is a fundamental part of forest ecosystem carbon cycling. An increase in the concentration of atmospheric CO₂ has stimulated interest in better understanding the forest ecosystem carbon cycle, forested landscape responses to changes

in atmospheric drivers, and the role that forests play in global fluxes. Forest carbon cycling is particularly relevant in the design of low-cost mitigation strategies that utilize the potential of forests to act as carbon (C) sinks (IPCC, 2007; Pan et al., 2011). Biogeochemical ecosystem models are tools that are frequently used to understand and predict carbon cycling processes through physical representations of photosynthesis and allocation processes, e.g. BGC (Coughlan and Running, 1997), TEM (Raich et al., 1991), and 3-PG (Landsberg and Waring, 1997). These physically based models use meteorological moisture and energy inputs to calculate the exchange of water and carbon between vegetation and the atmosphere (i.e., evaporation, transpiration, photosynthesis, and

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respiration). Process-based and dynamic global vegetation models (DGVMs) demonstrate considerable uncertainty in their projections of the future terrestrial carbon balance (Ahlström et al., 2012; Friedlingstein et al., 2014). DGVMs in general agree that North America's mid-latitude forests will continue to act as carbon sinks (Ahlström et al., 2012), and forests in the Pacific Northwest and northern California in particular have the theoretical potential to store 46% more C than they are currently estimated to hold (Hudiburg et al., 2009).

Previous efforts have used observations to improve ecosystem models' representation of the C cycle (De Kauwe et al., 2014; Law et al., 2006; Siqueira et al., 2006) and have demonstrated considerable uncertainty in model estimates of net ecosystem exchange, evapotranspiration, and allocation (Mitchell et al., 2009; Wang et al., 2009). Discrepancies between observations and model estimates may be due to errors in measurements (i.e., flux towers), fundamental errors in model structure, or the difficulty in physically deriving these estimates using ecophysiological parameters measured at the leaf scale. Modeling studies focused on parameter uncertainty show that uncertainty in ecophysiological parameters can be greater than uncertainty in flux-tower measurements (Mitchell et al., 2009). This suggests that one of the first steps in improving ecosystem models' carbon cycling capabilities is to better understand the uncertainty introduced by ecophysiological parameterization and also investigate the role of C allocation parameters, which these prior studies did not include (Booth et al., 2012; Mitchell et al., 2009; Zaehle et al., 2005).

Allocation determines the partitioning of carbon fixed in photosynthesis to plant respiration or biomass, and whether C is fixed as biomass above or below ground in longer- or shorter-lived organs. Allocation thus influences not just tree growth, but terrestrial biogeochemistry via litter quality and decomposition rates (Friedlingstein et al., 1999), and forest uptake of water and nutrients from the soil. There is no consensus on how to model carbon allocation, and so it represents a primary limitation in our understanding of the carbon cycle. A number of approaches to modeling allocation exist, ranging in complexity from computationally efficient empirical methods – to allocation estimates based on competition for resources between individual trees (see Franklin et al. (2012) for a detailed review). Improving our ability to model forest C allocation will improve our understanding of forests' role in the terrestrial carbon balance.

How C allocation is modeled, both in model structure and parameterization, may be particularly important for estimating ecosystem carbon cycling response to drought and climate variability (Bloom et al., 1985; Farrior et al., 2015). In addition, hydrologic variables, including evapotranspiration and streamflow, may be highly sensitive to forest structure and its responses to climate. Drought stress is typically accompanied by declines in net C assimilation and most carbon cycling models account for this response. How reductions in net C assimilation are translated into changes in growth, however, can impact subsequent ecosystem function (De Kauwe et al., 2014; Litton et al., 2007). Declines in allocation to roots or leaves under increasing CO₂ levels could decrease subsequent forest access to water and C assimilation capacity (Farrior et al., 2015). Shifting the proportion of net assimilation allocated to roots in response to drought on the other hand, could alter subsequent sensitivity to drought and forest water use (Schenk and Jackson, 2002). Recent droughts in the Western US highlight the need for improved understanding and prediction of forest carbon cycling responses (Allen et al., 2015) and the local and downstream impacts of associated changes in forest water use (Asbjornsen et al., 2011; Grant et al., 2013). Hydrologic models have been used to estimate changes in evapotranspiration and streamflow, but do not account for potential changes in forest structure and its impact on water use. Coupled hydrology and ecosystem growth models provide a more

mechanistically complete estimate by accounting for interactions among forest structure, climate, and water use (Abdelnour et al., 2013; Birkinshaw et al., 2011). To the authors' knowledge, however, little work has examined how ecophysiological parameter and allocation uncertainty in coupled ecohydrologic models might alter these estimates. This paper aims to characterize ecophysiological uncertainty by examining how it interacts with forest carbon allocation and to also provide a first order estimate of its influence on basin hydrology.

We apply a process-based, coupled ecohydrologic model to ask: (1) how do estimates of mature forest carbon stores vary across different assumptions about forest allocation of Net Primary Productivity (NPP); (2) how do uncertainties in ecophysiological parameters interact with differences in forest carbon allocation strategies to influence estimates of forest carbon stores; and (3) how do differences in carbon allocation strategies influence annual and low monthly streamflow estimates? To answer these questions, we assess the uncertainty of modeled carbon storage and streamflow estimates due to allocation assumptions and ecophysiological parameter uncertainty for relatively wet and dry forested regions. We limit this analysis to two conifer varieties that are widely studied in the western US: *Pinus ponderosa* (PIPO) and *Pseudotsuga menziesii* (PSME). By focusing on two well-studied conifers, we capitalize on existing field-based studies that provide a range of estimated ecophysiological parameter values and a variety of measurements for mature forest C pools of foliage, fine roots and stemwood. We use measured C pool estimates to assess whether vegetation models are reasonable and where possible, constrain model parameters. We investigate the implications of variability in C pool partitioning on low flow and annual streamflow estimates in the California Sierra Nevada (SIERRA) and the western Oregon Cascades (CASCADES), using well-instrumented case study watersheds in these two regions.

2. Modeling strategy

2.1. Approach

In order to examine uncertainty in vegetation parameterization and its effect on watershed scale streamflow estimates, we apply a coupled process-based carbon cycling and hydrology model for (1) a spatially lumped and (2) a spatially distributed representation of the landscape. In the lumped approach a single model patch is used to represent an average forest stand and allows us to perform computationally intensive parameter sensitivity analysis. The spatially distributed approach is then used to for a more limited sensitivity analysis of parameter effects on streamflow estimates that require accounting for within watershed heterogeneity and lateral water fluxes. We compare three carbon allocation strategies where partitioning of net assimilation is based on: (1) fixed coefficients (FIX), (2) allometric scaling (AGE), and (3) resource limitation (RESOURCE) (described in more detail below). All are relatively simple models of allocation strategies that may be appropriate for describing the average allocation behavior of a forest at the stand or regional scale (Franklin et al., 2012). At the stand-scale, we quantify the uncertainty in model estimates for foliage, fine root, and stemwood C pools to individual ecophysiological parameters for each allocation strategy and each species. Model estimates are also compared to field observations taken from literature for each organ. A subset of ecophysiological parameters whose stand-scale C pool estimates fall within the range of measured values are used to model watershed streamflow. We conduct this analysis focusing on two species located at two sites that have similar wet-winter/dry-summer climates, but have key climatic differences such as total annual precipitation and energy received.

Table 1

Ecophysiological parameters and the range for each species and location (SIERRA, CASCADES) across which this study tests sensitivity of model estimates of vegetation carbon accumulation and streamflow estimates. Parameter ranges were tested across all three allocation strategies except for the three allocation-specific parameters AGE_a, RES_a, and RES_b. “Alias” corresponds to the abbreviations used in Fig. 3.

	Units	Alias	SIERRA (PIPO)	CASCADES (PSME)
Allocation				
New fine root to new leaf C allocation	–	Rf:L	0.35–5.5	0.8–6.8
New coarse root to new stem C allocation	–	Rc:St	0.17–0.85	0.15–0.5
New stem to new leaf C allocation	–	St:L	0.6–4.8	1.0–5.3
Annual turnover proportion of leaf, fine/coarse root, stem and non-structural C and N pools	yr ⁻¹	M	0–10%	0–10%
Annual turnover of stem, coarse root and coarse woody debris C and N pools	yr ⁻¹	Mstem	0–10%	0–10%
AGE allocation shape parameter determining rate of change in the fraction of C allocated to foliage	–	AGE _a	0.15–0.6	0.15–0.6
RESOURCE allocation shape parameter determining maximum value of C allocated to fine roots	–	RES _a	0.5–0.9	0.5–0.9
RES. allocation shape parameter determining rate of change in the fraction of C allocated to fine roots	–	RES _b	2.0–3.0	2.0–3.0
Photosynthesis				
Canopy average Specific Leaf Area	m ² kg C ⁻¹	SLA	1.5–4	5–12
Maximum Stomatal Conductance	m s ⁻¹	g _s	0.001–0.05	0.001–0.05
Respiration Increase per 10C increase in temperature	–	Q10	1.5–3.0	1.5–3.0
C:N ratios				
Foliage C:N	kg C kg N ⁻¹	C:N _L	21–53	31–53
Fine Root C:N	kg C kg N ⁻¹	C:N _{FR}	50–200	26–200
Litter C:N	kg C kg N ⁻¹	C:N _{LTR}	49–134	50–100

We focus on 14 ecophysiological parameters that control photosynthesis, fractional allocation, and carbon/nitrogen ratio requirements of plant organs (Table 1). We constrain the range of these parameters by species-specific values found in literature. Average total fine root, stemwood, and foliage estimates over the final 10-years of model spin up are used for estimates of mature forest C-stores. We sum these fine root, stemwood and foliage estimates to estimate total plant C.

The uncertainty in mature C-store estimates to allocation strategy is evaluated by comparing the distribution of total C estimates across the vegetation ecophysiological parameter space for each allocation strategy. We use simple statistical analysis (*t*-test) to compare magnitudes of stores (leaf, stem, root and total plant C) for each allocation strategy. We also measure the influence of individual ecophysiological parameters on C estimates. First, C estimates for each organ are plotted and visually assessed to determine whether C estimates vary linearly across individual ecophysiological parameters' space (not shown). For linear relationships, ordinary linear regression models are used to calculate the significance of the particular parameter for C estimates; the slopes for significant relationships (*p*-values < 0.1) are compared across allocation strategies and between species.

The influence of vegetation parameter uncertainty on watershed streamflow estimates is evaluated at the watershed scale in the western Oregon Cascades (CASCADES) and in the California Sierra Nevada (SIERRA).

2.2. RHESSys model

We use the Regional Hydro Ecologic Simulation System (RHESSys) (Tague and Band, 2004), a process-based model that calculates carbon (C), nitrogen (N) and water fluxes over variable terrain. It has been used to investigate a range of hydrologic and ecologic questions in western United States mountain watersheds (Christensen et al., 2008; Garcia et al., 2013; Tague et al., 2013b). Model performance has been evaluated in these and other snow-dominated mountainous regions, and comparisons with measured streamflow (Tague et al., 2013a; Tague and Peng, 2013), tree-rings (Vicente-Serrano et al., 2015), and flux tower data (Zierl et al., 2007) show that the model captures inter-annual variations in carbon flux and daily to monthly streamflow patterns with reasonable accuracy.

RHESSys uses a spatially explicit framework to model processes at their representative scale; subdividing processes allows

for greater computational efficiency. The largest spatial unit is the watershed (10–100 km²), which is delineated by a topographically enclosed area that drains to a stream gage. The watershed is divided into hillslopes, subunits that drain to a single stream reach, and it is in this unit that explicit routing of hydrologic fluxes occurs. Zones are nested within hillslopes and are delineated by spatially-explicit patterns (i.e., elevation bands) and climate station data interpolated across variable terrain (Running and Nemani, 1987). Biogeochemical cycling and vertical hydrologic fluxes are calculated and coupled within the smallest stand-scale spatial unit, the patch. This patch unit is defined by similarities in elevation and vegetation and soil types, and we conduct our uncertainty analysis to ecophysiological parameters at this smallest spatial sub-unit. RHESSys can have multiple strata layers within a patch, and our model representations include two: an overstory and an understory. Radiation attenuation, canopy interception and storage are calculated through the strata layers as a function of LAI and gap fraction. Transpiration from plants and evaporation from water stored in leaves, litter and soil are calculated using the Penman-Monteith formulation (Monteith, 1965). Stomatal conductance is calculated with the Jarvis model (Jarvis, 1976), and is a function of daily radiation, vapor pressure deficit, soil moisture, and air temperature values.

Carbon and nutrient cycle sub-modeling is similar to other carbon cycling models including BIOME-BGC (Thornton, 1998), the Community Land Model (CLM) (Oleson et al., 2010), and the Terrestrial Ecosystem Model (TEM) (Raich et al., 1991), such that there is a daily partitioning of net photosynthate to respiration costs and above and below ground carbon pools on a daily timestep. RHESSys uses daily climate drivers and vegetation ecophysiological parameterization to estimate daily fluxes of vegetation carbon, nitrogen and water fluxes. Gross Primary Productivity (GPP) is calculated with the Farquhar equation, and net photosynthesis is calculated as the difference between GPP and net respiration (*R_n*). *R_n* accounts for the maintenance and growth respiration of woody, foliar, and fine root biomass. Maintenance respiration (*R_m*) is a function of temperature and nitrogen content of each of the live carbon stores. It is calculated following Ryan (1991) as:

$$(1)R_m = R_0 * Q_{10}^{(T-20)/10}$$

Stomatal conductance and consequently GPP are limited by water availability, providing a feedback from the hydrology model to the ecosystem carbon cycling model. The carbon cycling model in turn influences hydrology through changes to plant structural

attributes, such as LAI, that control interception, transpiration, and surface evaporation fluxes through the shading of the forest floor.

The nitrogen dependent respiration rate, R_0 , is calculated as $R_0 = N * 0.218 \text{ kg C kg N}^{-1} \text{ day}^{-1}$, where N represents the amount of nitrogen in each plant organ pool and the empirical value of 0.218 from Ryan (1991) is the respiration cost of C per kg of N. This nitrogen dependent cost is scaled by temperature using Q_{10} following Tjoelker et al. (2001); Q_{10} is a unitless factor expressing change in respiration with a 10°C change in temperature. Both R_0 and Q_{10} are calculated daily. Q_{10} increases or decreases respiration costs depending on the temperature in relation to a threshold value of 20°C ; below 20°C a higher Q_{10} decreases respiration costs, and above that threshold higher Q_{10} increases respiration costs.

The fraction of net photosynthate distributed to plant organs is calculated using one of three allocation strategies:

(1) Fixed fraction (FIX): An empirical approach where proportions of net photosynthate allocated to leaves versus fine roots, for example, remains constant. FIX is commonly used by DGVMs (Ostle et al., 2009) and is most appropriate for forests that are in a steady state condition and when drivers that typically vary in space and time are averaged over a large region. FIX does not account for changes in allocation that can occur with changes in environmental conditions or plant structure (Dieleman et al., 2012).

(2) Allometric scaling (AGE): A semi-mechanistic allometric approach that depends on the photosynthetic capacity of the plant as represented by LAI, and based on an approach developed by Dickinson et al. (1998). AGE preferentially allocates assimilated carbon to foliage in developing canopies, thereby accelerating the rate at which a stand achieves its maximum LAI, thus its photosynthetic capacity. An empirical factor, AGEa, adjusts the maximum amount of C that is preferentially allocated to the leaf. The fraction of C allocation to leaf, f_{leaf} , is calculated as:

$$f_{\text{leaf}} = \exp(-1.0 * \text{AGEa} * \text{LAI}) \quad (2)$$

Higher values of AGEa lower the fraction of available carbon preferentially allocated to foliage. Once a mature canopy is achieved, the fraction of C allocated to stemwood and roots increases.

(3) Resource scaling (RESOURCE): A second semi-mechanistic allocation approach, which increases the fraction of C preferentially to roots when the availability of water and nitrogen in the soil limits the rate of photosynthesis from meeting the potential. Potential photosynthesis is calculated based on daily radiative forcing and temperature conditions (Landsberg and Waring, 1997). This approach should be sensitive to drought conditions. The fraction of C preferentially allocated to roots, f_{root} , under RESOURCE allocation is calculated as:

$$f_{\text{root}} = \text{RESa} / (1.0 + \text{RESb} * \text{LIM}) \quad (3)$$

Where LIM is the ratio of actual photosynthate to potential photosynthate. Empirical parameters RESa and RESb adjust the magnitude of f_{root} and its sensitivity to LIM.

To study uncertainty in C store estimates due to individual ecophysiological parameters, we focus on values that effect: (1) turnover and mortality, where a fraction of the plant pool is replaced or removed annually; (2) C and N ratios, which define nutrient requirements for new growth, plant respiration rates, photosynthetic capacity, and litter quality; and (3) photosynthetic controls of canopy radiation absorption and carbon assimilation rates. We focus specifically on the 14 parameters listed in Table 1. The range in parameter values is generally taken from a comprehensive review of observation based estimates of ecophysiological parameters (White et al., 2000). Ranges are constrained to those observed for evergreen-needle-forests and further constrained by values specific to our two species of interest, *Pseudotsuga menziesii* (PSME) and *Pinus ponderosa* (PIPO). Because maximum stomatal

conductance rates are not listed in White et al. (2000), we select a range of values based on measurements reported in literature (Bond and Kavanagh, 1999; Hubbard et al., 2001; Van Wijk et al., 2000).

Background mortality in RHESSys includes whole plant mortality and stemwood mortality (Mstem). Stemwood mortality moves a fraction of C from the live and dead stemwood and coarse root C pools to coarse woody debris daily (the values listed in Table 1 represent an assigned percent that is divided by 365 for a daily percent removal). It is a coarse approximation of the self-thinning process that occurs with increasing forest density during stand succession. Ecosystem models generally assume that background mortality occurs at a rate of 1–2% per year, and we test the uncertainty of C storage to a range of values between 0 and 5%. Because Mstem measurements are generally unavailable we test annual values equal to background mortality, 0–5%. We also test the uncertainty of C pool estimates to empirical parameters embedded within AGE and RESOURCE allocation schemes.

For each of the 14 ecophysiological parameters, we use a Monte-Carlo approach and sample from a uniform distribution of values within the species-specific literature-based ranges reported in Table 1. We note that literature-based ranges define parameter uncertainty due to a variety of factors including measurement limitation, and spatial heterogeneity within and between locations due to plasticity and local adaptation in plant traits. We randomly assemble individual parameter values to create 2000 sets of co-varied ecophysiological parameters. Each co-varied parameter set is used to spin up vegetation in a single model patch for the three allocation schemes within each watershed. We compare patch estimates of C stores to field-derived measurements taken primarily at the individual level within a forest stand (studies presented in Table 1), with the exception of remote sensing derived estimates taken from Hudiburg et al. (2009). Prior to vegetation spin up, soil C/N stores are spun up to a stable state requiring approximately 3000 years of model calculated growth (Thornton and Rosenbloom, 2005). Forest spin up is conducted with plant C initialized at zero after soil C/N stores are stabilized. ‘Spin up’ refers to achieving a steady state of estimates related to carbon cycling that are calculated with models driven by simple climate forcing (Baisden and Amundson, 2003; Manzoni and Porporato, 2009). Spin up was conducted by repeating the available climate records at each site (approximately 40 years of daily data, Table 2) for the appropriate duration. The spin up duration is based on the age of forests established in SIERRA and CASCADES, the sites where watershed scale analysis is conducted—100 and 300 years for PIPO and PSME, respectively. Study site characteristics are described in additional detail below.

Literature-derived bounds of plant organ C pools and LAI for mature forests composed of PIPO or PSME (Table 2) are used to select two ‘acceptable’ ecophysiological parameter sets per allocation strategy for each site. ‘Acceptable’ parameter sets were those for which estimates for stemwood, leaf, and fine root C pools, the sum of these three pools, and LAI values fell within the measured ranges presented in Table 2. It is important to note that many of the measurements are indirect and estimated using allometric equations. Typically, stemwood C is estimated from measurements of diameter at breast height (DBH) and tree height. Foliage estimates were calculated using LAI derived from plot scale LICOR estimates or sapwood area and specific leaf mass. Fine root stores were generally estimated using soil cores during peak growing season or allometric equations. Biomass carbon is estimated by multiplying biomass measurements reported as total mass by 0.5. We include LAI in our validation because coupled models frequently use it to scale estimates of evaporation and transpiration, thus it potentially has a large influence on estimates of the hydrologic budget. We use LAI measurements measured via LICOR or remote sensing.

Table 2
Key physical and climate characteristics of the study watersheds.

	CASCADES	SIERRA
Location	H.J. Andrews Experimental Forest, Oregon, United States	Sagehen Experimental Forest, California, United States
U.S. Geological Survey gage number	14161500	10343500
Coordinates (NAD27)	Latitude 44° 12' 35" Longitude 122° 15' 20"	Latitude 39° 25' 54" Longitude 120° 14' 13"
Elevation range (m)	410–1630	1800–2650
Drainage Area (km ²)	64	26
Climate record	1958–2008	1960–2005
Mean Annual Precipitation (mm)	2250	850
Mean winter <i>T</i> (JFM) (°C)	−0.9/5.2	−9.5/3.7
Mean spring <i>T</i> (AMJ) (°C)	4.0/14.0	−2.5/13.8
Mature Carbon Stores		
Leaf (kg C m ^{−2})	0.45–1.0 ^{1,2}	0.25–0.8 ^{3,4}
Stem (kg C m ^{−2})	16–45 ^{1,5}	3.4–10.0 ^{4,6}
Fine Root (kg C m ^{−2})	0.25–1.7 ^{7,8}	0.25–1.2 ^{3,6}
LAI	8–12	2–8

¹ Smithwick et al. (2002).

² Grier and Logan (1977).

³ Campbell et al. (2009).

⁴ Johnson et al. (2008).

⁵ Hudiburg et al. (2009).

⁶ Law et al. (2001).

⁷ Keyes and Grier (1981).

⁸ Nadelhoffer and Raich (1992).

We test how uncertainty in vegetation parameters influences streamflow estimates across allocation strategies at the watershed scale. Modeling all vegetation parameter sets at the watershed scale is ideal, however, it is too computationally expensive. We select parameter sets that fall within published uncertainty bounds of plant organ C pools (Table 2) and that yield estimates that are the most and least dynamic in their response to climate drivers to try to characterize the likely range of response given parameter uncertainty. The “most” and “least” dynamic parameter sets are selected based on the coefficient of variation (CV) in average annual leaf area index (LAI) as a proxy for the responsiveness of the vegetation to climate drivers. Each watershed is spun up to maturity with two sets of ecophysiological parameters per allocation strategy. In order to also account for uncertainty in hydrologic estimates from soil parameterization, each ecophysiological parameter set is spun up with two soil parameter sets meeting basic streamflow metrics that account for accuracy in high and low flows (NSE) and have less than 15 percent error in average daily magnitude.

2.3. Watershed characteristics

We test the sensitivity of allocation schemes in two western US watersheds: Sagehen Creek Experimental Forest in the Sierra Nevada, CA (SIERRA) and the H.J. Andrews Experimental Forest in the western Oregon Cascades (CASCADES). Table 2 summarizes basin and climate characteristics, though we provide additional climate descriptions below. RHESSys has recently been implemented in both watersheds and additional details of soil calibration processes and hydrologic model validation can be found in Garcia et al. (2013) and Tague and Peng (2013) for CASCADES and SIERRA, respectively.

2.3.1. Sagehen Experimental Forest (SIERRA)

Sagehen Creek is a 26-km² watershed located in the central Sierra Nevada mountain range (Table 2). Sagehen has a Mediterranean climate with warm, dry summers and cold, wet winters—snowfall accounts for a significant portion of the annual precipitation. Daily records of precipitation and minimum/maximum temperature are used to drive the RHESSys model. Climate data is taken from the Sagehen East Meadow weather sta-

tion (elevation 1932 m), available through the U.S. National Climate Data Center. Precipitation and temperature data are spatially distributed through the basin with elevation-based scalars (Tague and Peng, 2013).

Sagehen is characterized by both the montane and sub-alpine vegetation ranges of the Sierra Nevada floristic province (Barbour et al., 2007). It is dominated by mixed conifer forest and non-forested areas are composed of montane meadows. We approximate conifer allocation using published data for ponderosa pine, for which a large body of literature exists. Though this simplifies watershed species type, our knowledge of species-specific ecophysiological parameters for conifers remains limited, so this is a first order approximation that may capture the success of species derivatives. Canopy fraction is assigned based on observations (Vaillant, 2008); a patchy grass understory of average annual LAI of 0.2 is assigned to all forested and non-rock areas throughout the watershed.

2.3.2. H.J. Andrews Experimental Forest (CASCADES)

The wetter watershed, the H.J. Andrews Experimental Forest, is a 64-km² watershed located in the western Oregon Cascades (Table 2). Its average annual precipitation of 2250 mm is more than twice that received at SIERRA. Approximately 75% of its total precipitation falls from November to April and its temperatures are generally warmer than SIERRA (Table 2) so less of its total precipitation falls as snow. Climate data is taken from the CS2Met station located at an elevation of 430 m (Daly and McKee, 2015). Temperature is spatially adjusted using regionally specific lapse rates calculated using minimum and maximum temperatures recorded at CS2Met and the Vanilla Leaf station (elevation 1273 m). The HJ Andrews is primarily composed of Douglas-fir (*P. menziesii*) with a shrubby understory vegetation (*P. rhododendron*).

Soil drainage and storage characteristics are one of the key sources of uncertainty in hydrologic modeling and can – especially in water-limited ecosystems – strongly influence plant water availability. To account for soil uncertainty in modeling at the watershed scale, we select two parameter sets from previous soil calibrations at each site. Details for soil calibration at CASCADES and SIERRA are described in Garcia et al. (2013) and Tague and Peng (2013), respectively. Soil parameter sets were selected based on compar-

Table 3
Median and standard deviation (in parentheses) of 10-year averages of mature forest C pools and average annual LAI across (A) all ecophysiological parameter sets and (B) for parameter sets that fall within literature constraints listed in Table 2.

	CASCADES					SIERRA				
	Stem C kg m ⁻²	Foliage C kg m ⁻²	Fine Root C kg m ⁻²	Total C kg m ⁻²	Mean Ann LAI	Stem C kg m ⁻²	Foliage C kg m ⁻²	Fine Root C kg m ⁻²	Total C kg m ⁻²	Mean Ann LAI
(A)										
AGE	32.5 (7.1)	1.1 (0.2)	0.4 (0.07)	34.0 (6.9)	9.3 (1.0)	3.2 (5.9)	1.8 (0.5)	1.4 (0.3)	6.4 (5.8)	4.7 (1.3)
FIX	10.6 (7.3)	0.7 (0.3)	0.9 (0.3)	12.4 (7.4)	6.0 (2.6)	3.0 (5.3)	0.8 (0.4)	1.7 (0.9)	5.7 (5.4)	2.0 (1.2)
RES	19.0 (4.4)	1.1 (0.3)	0.6 (0.1)	20.7 (4.5)	9.9 (2.3)	3.5 (6.0)	0.9 (0.5)	1.2 (0.3)	5.9 (6.1)	2.6 (1.7)
(B)										
	35.7 (4.3)	0.9 (0.05)	0.3 (0.02)	37.0 (4.2)	9.8 (0.7)	5.9 (1.7)	1.1 (0.06)	0.9 (0.05)	7.9 (1.7)	4.1 (0.3)
	22.0 (4.4)	0.9 (0.07)	0.7 (0.2)	23.6 (4.3)	9.8 (1.1)	5.0 (1.5)	0.7 (0.1)	0.7 (0.2)	6.1 (1.5)	2.2 (0.5)
	21.2 (2.9)	0.9 (0.06)	0.7 (0.07)	22.8 (2.9)	9.8 (1.1)	6.0 (1.9)	0.7 (0.1)	0.9 (0.05)	7.7 (1.9)	2.0 (0.4)

ison with daily streamflow records. We evaluate soil parameter streamflow performance across the new vegetation parameters using the same criteria: the Nash-Sutcliffe efficiency (NSE) of daily streamflow (Nash and Sutcliffe, 1970), and daily water balance bias averaged over the validation period. Soil parameter sets in Garcia et al. (2013) and Tague and Peng (2013) had NSE values greater than 0.6 (where 1.0 is optimal) and average percent daily bias less than 10. Two of these previously calibrated soil parameter sets were selected based on soil available water capacity, which influences the sensitivity of forest ET to climate drivers (Garcia and Tague, 2015). These soil parameters were used to spin up vegetation stores across each basin using the max CV and min CV for each allocation strategy within PIPO and PSME.

3. Results

3.1. Influence of parameter uncertainty and allocation strategy on total C

Total C estimates vary considerably across ecophysiological parameter uncertainty and with carbon allocation strategies (Fig. 1), and are significantly different between the CASCADES and SIERRA sites. At CASCADES, total C estimates varied more across allocation strategy than as a result of ecophysiological uncertainty. Notably, the AGE strategy estimates higher total C than FIX or RESOURCE across all parameter sets. On average, the RESOURCE strategy estimates slightly higher total C relative to FIX (Fig. 1, Table 3A) across all parameter sets. SIERRA shows more similarity in estimates of total C across the different allocation schemes. Sensitivity to ecophysiological parameters for SIERRA is limited to a relatively narrow range of parameters, with many parameters producing similar total C (e.g., as shown by highly skewed distribution of total C across parameter space (x-axis) on Fig. 1).

Constraining parameter sets by literature estimates reduces variability in model estimates of all three C pools (leaf, stem and root) for both sites (Table 3B). All allocation strategies produce estimates within observation ranges for some subset of ecophysiological parameters (Table 4).

We explore implications for C pool estimates for a modeling instance when stemwood mortality (Mstem) is not included. In the modeling scenario that does not account for Mstem, CASCADES' maximum literature-derived stemwood C estimate is exceeded by 40, 92, and 98 percent of parameter sets in FIX, RESOURCE and AGE strategies, respectively. For SIERRA, total C estimates without Mstem exceeded the maximum total amount derived from literature estimates by four to six times and 93–99% of param-

Table 4
Fraction of parameter sets meeting C-store bounds after 100 (PIPO) and 300 (PSM) years of model spin up.

	SIERRA	OREGON
AGE	8%	24%
FIX	18%	4%
RESOURCE	13%	14%

ter sets exceed that maximum (Fig. 2d). With Mstem, SIERRA's fine root and foliage C pool estimates also exceeded maximum literature values. Inclusion of Mstem lowers median values of total C by two to ten magnitudes across allocation strategies at both sites (Table 3). Inclusion of Mstem increased the number of ecophysiological parameter sets that met literature-defined C pool estimates of foliage, stem and fine roots for mature forests to 4–24% (Table 4).

The model captures key differences between SIERRA and CASCADES in terms of size and relative proportion of carbon stores – in particular, the proportionally greater fine root and leaf C stocks at SIERRA relative to total C, as compared to root/leaf C stocks at CASCADES (Fig. 1). Estimates of individual plant components also show substantial variation with allocation and parameter uncertainty. For CASCADES, allocation strategy is the dominant influence on the magnitude of stemwood and fine root C estimates (Fig. 2a,c), and the impact of parameter uncertainty is small relative to the impact of allocation (standard deviations reported in Tables 4, 5, Fig. 1). The impact of allocation strategy is greatest for stemwood, and consequently also for total C, which is primarily comprised of stemwood carbon. Total C is highest for the AGE strategy, followed by RESOURCE. FIX leads to slightly greater fine root carbon and slightly lower leaf C, relative to RESOURCE and AGE strategies. At SIERRA, the impact of allocation strategy was relatively small for all organ pools and the effect of parameter uncertainty was greater, particularly for fine root and leaf C estimates. However there is an interaction effect between allocation strategy and sensitivity to uncertainty in ecophysiological parameters, with the FIX strategy showing greater uncertainty of fine root C to range in parameters (Table 3A).

Total C is generally higher in CASCADES, however SIERRA's fine root and foliage carbon pools are proportionally greater than CASCADES' leaf/root pools (Table 3A, Fig. 2). SIERRA's median fine root estimates across all allocation strategies and median foliage values for AGE and FIX strategies exceed estimates for CASCADES. Differences in our two sites' total C can be largely attributed to stem C estimates where median values for 300-year old CASCADES

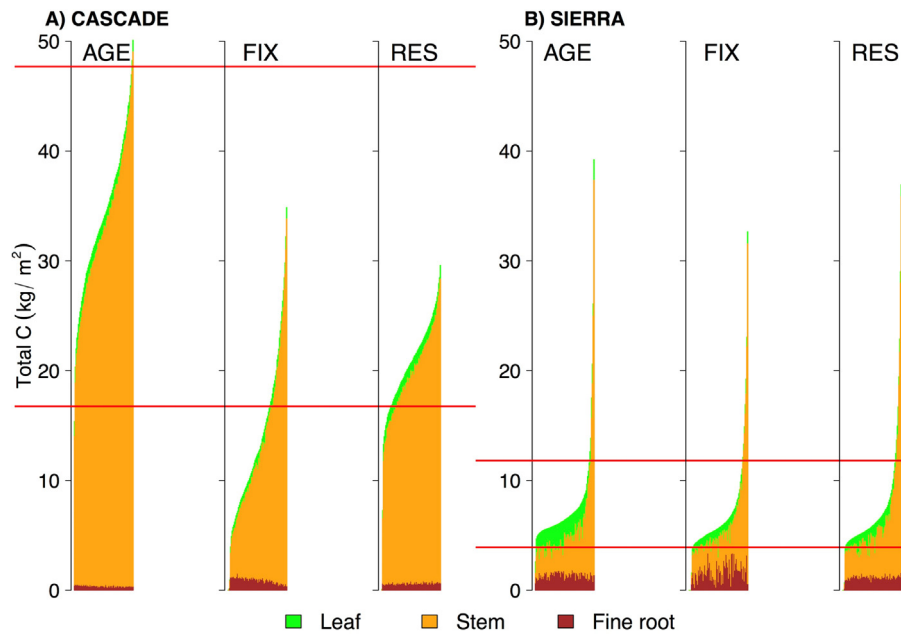


Fig. 1. Leaf, stem and fine root C pool estimates for (A) CASCADES and (B) SIERRA across 2000 ecophysiological parameter sets. Estimates of the three carbon pools are summed to approximate total C, then ranked in order of ascending magnitude across allocation strategies AGE, FIX and RESOURCE (“RES”). Red lines indicate literature defined observational range of total C. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

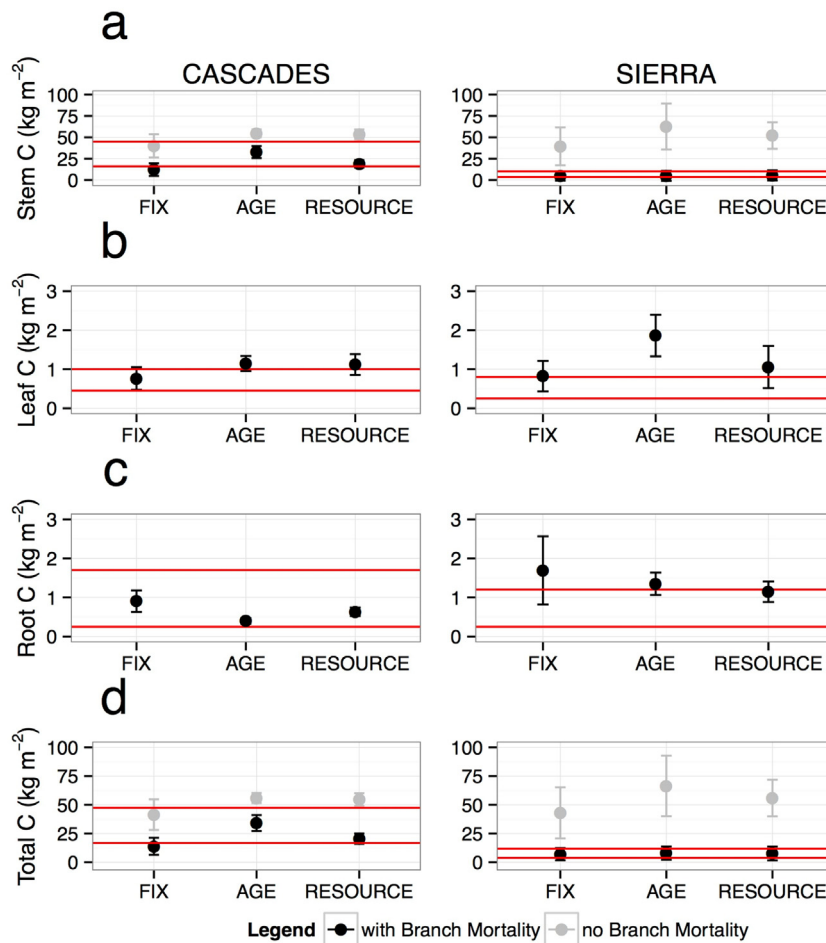


Fig. 2. C stocks in (a) stemwood, (b) foliage, (c) fine root pools, and (d) total average forest carbon for mature forest stands across all ecophysiological parameters and allocation schemes. Distributions show mean values (points) and dashes indicate ± 1 standard deviation. Panels (a) and (d) include estimates for two model conditions: inclusion of branch mortality (black) and no branch mortality (grey). Panels (b) and (c) present only the “with” branch mortality results. Red lines in panels indicate observation-based limits calculated using measurements in Table 1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 5
Normalized sensitivity of total C, leaf and fine root C pool estimates to individual ecophysiological parameters. We report only calculated values with significance of $p < 0.01$.

CASCADES	Total C			Leaf			Fine root		
	AGE	FIX	RES	AGE	FIX	RES	AGE	FIX	RES
ALLOCATION									
Rf:L	0	−0.84	0	0	−0.71	0	0	0.47	0
Rc:St	0	0.18	0.092	0	0	−0.06	0	−0.05	0.043
St:L	0	0.72	0.27	0.02	−0.12	−0.42	0	−0.21	0.17
Mb	−0.19	−0.15	−0.14	−0.05	−0.05	−0.04	−0.07	−0.04	−0.08
M	0	0	0	0	0	0	0	0	0
Agea	0.89	0	0	−0.65	0	0	−0.78	0	0
Resa	0	0	−0.65	0	0	−0.41	0	0	0.75
Resb	0	0	0.47	0	0	0.16	0	0	−0.53
C:N Ratio									
C:N,leaf	0	0		0	0	0	−0.08	0	0
C:N,Rf	0.07	0.14	0.008	0	0.071	0.052	0	0.083	0.028
C:N,litter	0	0	0	0	0	0	0	0	0
Photosynthesis									
SLA	0.58	0	0.078	−0.67	−0.13	−0.31	−0.68	0	−0.04
Q10	0.11	0.19	0.094	0	0.12	0	0	0.11	0
gs	0.03	0.12	0.099	0	0.05	0.041	0.018	0.06	0.025
SIERRA	Total C			Leaf			Fine root		
	AGE	FIX	RES	AGE	FIX	RES	AGE	FIX	RES
Allocation									
Rf:L	0	−0.19	0	−0.03	−0.45	0	0	0.65	0
Rc:St	0	0	0	0	−0.21	−0.30	0	−0.20	−0.06
St:L	0	0	0	0	−0.70	−0.99	0	−0.64	−0.10
Mb	−0.76	−0.84	−0.93	0.03	0	0	0.039	0	0
M	0	0	0	0	0	0	0	0	0
AGEa	0.15	0	0	−0.63	0	0	−0.39	0	0
RESa	0	0	0.6	0	0	−0.44	0	0	1.1
RESb	0	0	0	0	0	0.24	0	0	−0.69
C:N Ratio									
C:N,leaf	0	0	0	0.09	0	0.122	0.0885	0	0
C:N,Rf	0	0	0	0	0	0	0	0.101	0
C:N,litter	0	0	0	0	0	0	0	0	0
Photosynthesis									
SLA	0.148	0	0	−0.6	0	0	−0.38	0.102	0.09
Q10	0.22	0.28	0.23	0.09	0.184	0	0.09	0	0.12
gs	0	0.16	0.16	0.05	0.131	0.08	0.04	0.153	0.12

are 3–10 times larger than 100-year old SIERRA (Table 3A) when stemwood mortality is accounted for.

3.2. Sensitivity of C estimates to ecophysiological parameterization

We use a simple linear model to compare how all individual ecophysiological parameters influence C pool estimates of total, leaf, and fine root C estimates for each allocation strategy. We identify significant relationships ($p < 0.1$), then compare their normalized slopes as a measure of sensitivity of each C pool estimate to individual parameters (Fig. 3; Table 5). We note that the C:N ratios showed relatively little influence on C-estimates and are removed from Fig. 3 in order to highlight allocation and photosynthetic parameters that more strongly influenced C estimates.

Total C estimates for SIERRA are most sensitive to branch mortality across all allocation strategies. After branch mortality, photosynthetic parameters were the strongest controls of total C. The sensitivity of total C to Q_{10} has the second strongest relationship with total C under AGE and FIX allocation strategies, and is a strong control for RESOURCE also. A higher Q_{10} value increases total C. As shown in Eq. (1), air temperature and Q_{10} interact in such a way that below 20 °C, higher Q_{10} values have lower maintenance respiration (Rm); above 20 °C Rm is more sensitive to increasing

temperature with higher Q_{10} (Eq. (1)). Higher maximum stomatal conductance (gs) was significantly related to higher total C for FIX and RESOURCE. Though AGE did not have a significant relationship to gs, total C increased with higher SLA.

CASCADES' total C estimates are significantly more sensitive to a greater number of ecophysiological parameters than SIERRA across all allocation strategies. As with SIERRA, total C estimates are sensitive to Q_{10} , gs and branch mortality (Mb), although sensitivity is slightly less. The total C under the AGE strategy shows a strong sensitivity to SLA. For AGE and RESOURCE allocations, total C is most sensitive to AGE_a and RES_{a,b} respectively. These allocation-specific parameters adjust the size/resource limitations of when fractional photosynthate of C is preferentially allocated to leaves and roots. Total C increases for RESOURCE with the smaller fractional allocation to roots (Eq. (3)). Similar to RESOURCE, when the amount of C that is preferentially allocated to foliage is decreased (by increasing AGE_a), total C increases (Eq. (2)). Total C for FIX and RESOURCE was also sensitive to allocation parameters Rc:St and St:L, which strongly influence stemwood estimates (Table 5). For both PSME and PIPO, total C is negatively correlated with Mstem and positively related to assimilation parameters.

The sensitivity of foliage and fine root pool estimates to ecophysiological parameter uncertainty is similar between sites. For both sites, under the AGE allocation strategy SLA significantly influ-

Table 6
Specific parameter sets for vegetation modeling applied to whole-watershed spin up.

LAI CV all parameters	SIERRA (PIPO)					
	AGE		FIX		RESOURCE	
	0.04–0.2		0.05–0.55		0.05–0.5	
	Max CV	Min CV	Max CV	Min CV	Max CV	Min CV
LAI CV	0.12	0.07	0.20	0.17	0.19	0.11
Average LAI	2.9	3.2	2.7	2.6	3.6	3.0
Root (f): Leaf	0.8	0.6	0.4	0.6	0.6	0.5
Root (c): Stem	4.6	1.9	2.9	2.7	2.1	2.7
Stem: Leaf	51.2	31.6	23.5	22.4	27.1	22.9
Leaf C:N (kgC kgN ⁻¹)	151.6	181.4	187.7	197.5	143.9	58.0
C:N _{FR} (kgC kgN ⁻¹)	68.3	81.8	122.3	83.8	111.9	87.2
Litter C:N (kgC kgN ⁻¹)	2.5	2.7	3.6	3.9	4.0	3.9
SLA (m ² kgC ⁻¹)	0.4	0.4	0.4	0.1	0.3	0.1
Branch Mortality (yr ⁻¹)	0.04	0.03	0.04	0.014	0.026	0.014
Total Mortality (yr ⁻¹)	0.6	0.6	0.1	0.1	0.2	0.2
Age Curve (Da)	0.7	0.8	0.7	0.8	0.7	0.8
Resource Curve (Wa)	2.4	2.9	2.3	2.1	2.4	2.8
Resource Curve (Wb)	2.9	4.3	1.0	0.9	3.9	2.1

LAI CV all stats	CASCADES (PSME)					
	AGE		FIX		RESOURCE	
	.006–0.09		.002–0.05		0.002–0.04	
	Max CV	Min CV	Max CV	Min CV	Max CV	Min CV
LAI CV Max/Min	0.064	0.025	0.027	0.018	0.038	0.020
Average LAI	8.4	8.2	8.1	9.0	9.3	8.1
Root (f): Leaf	5.5	3.3	1.9	3.6	5.3	1.8
Root (c): Stem	0.3	0.3	0.4	0.4	0.2	0.3
Stem: Leaf	2.1	1.9	3.0	1.9	3.1	3.7
Leaf C:N (kgC kgN ⁻¹)	44.2	53.0	32.5	32.2	47.3	41.8
C:N _{FR} (kgC kgN ⁻¹)	34.5	60.9	183.1	178.0	110.9	159.8
Litter C:N (kgC kgN ⁻¹)	99.1	98.1	86.5	79.7	70.8	72.0
SLA (m ² kgC ⁻¹)	11.1	10.7	10.6	11.7	11.6	11.0
Branch Mortality (yr ⁻¹)	0.021	0.006	0.035	0.006	0.034	0.021
Total Mortality (yr ⁻¹)	0.004	0.004	0.005	0.004	0.003	0.004
Age Curve (Da)	0.2	0.2	0.2	0.2	0.2	0.2
Resource Curve (Ra)	0.7	0.8	0.8	0.8	0.8	0.8
Resource Curve (Rb)	2.1	3.0	2.8	2.3	2.4	2.6

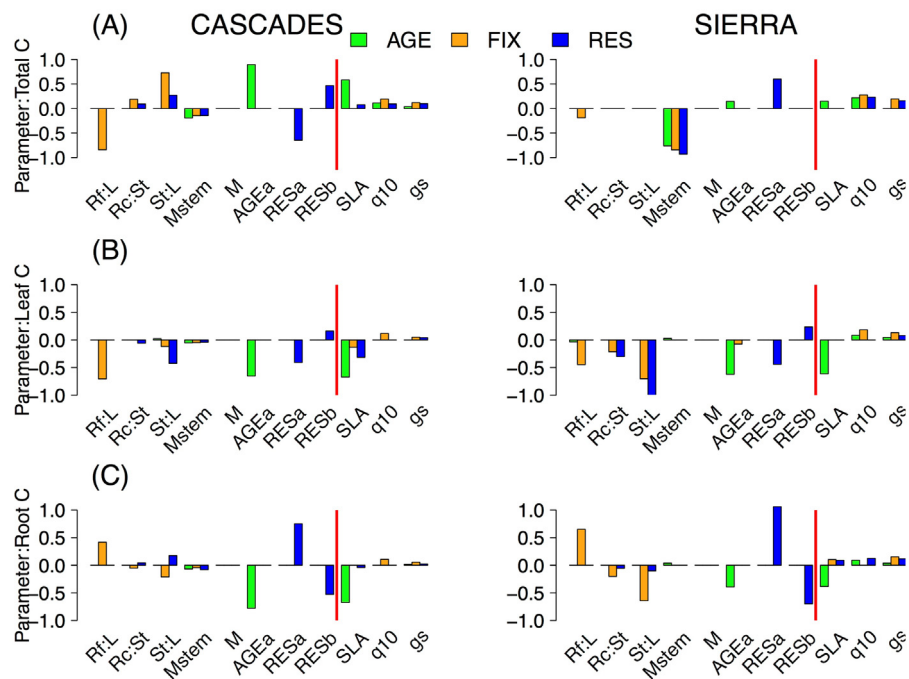


Fig. 3. Normalized slopes for the ecophysiological parameters showing significant relationships between (A) total C, (B) leaf, and (C) fine root pools. Red lines separate parameter groups controlling fractional allocation (left) and photosynthetic capacity (right). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

ences fine root and leaf C pools. For this allocation strategy, SLA has a negative relationship with foliage and fine roots, and a positive relationship with total C. SLA translates leaf C into LAI, thus influencing light availability – with higher SLA, there is higher C production. Higher values of SLA for AGE result in higher LAI values being achieved more quickly with growth, so allocation shifts to stemwood sooner (Eq. (2)). For the RESOURCE and FIX allocation strategies, fine root and leaf pools are most strongly influenced by parameters that explicitly influence allocation to those pools: RESa and RESb for RESOURCE; Rf:L, Rc:St, and St:L for FIX.

3.3. Influence of parameter uncertainty and allocation strategy on streamflow estimates

We select two ecophysiological parameter sets per allocation scheme at each site to investigate the watershed scale effect of uncertainty in modeling vegetation. We focus on the subset of ecophysiological parameters that result in mature organ C model estimates falling within literature-derived field observations. From that subset of ‘acceptable’ vegetation configurations, we select two parameter sets based on inter-annual change in LAI as bounding estimates. Specifically, we choose parameters that produce the maximum and minimum LAI CV (CVmax and CVmin). Rather than try to select ecophysiological parameter sets that best fit a set of measured carbon stocks, we select for two parameter sets that result in the greatest and least variability in change in LAI that still fall within measured carbon pools. All parameter sets that fall within the literature-derived measurement range (Table 2) are provided as Supplementary material. Fig. 4 shows total C pools for all parameter sets. We note that spin up of vegetation over each watershed was done separately for each parameter set.

We note that differences in total C estimates between parameter sets may differ by as much as 100–300% across allocation strategies for CASCADES. Differences in total C are smaller (20–100%) for SIERRA. Differences in average annual LAI for CVmax and CVmin parameters are not significant at both sites (Table 6). Table 6 reports specific ecophysiological parameters used to model vegetation in the streamflow analysis.

Table 7

Watershed scale daily streamflow statistics for 1980–2000 across 6 realizations of mature vegetation for each species type and location. NSE represents the Nash Sutcliffe Efficiency.

	CASCADES	SIERRA
NSE	0.55–0.66	0.2–0.4
logNSE	0.71–0.78	0.6–0.65
Percent Daily Bias	–10–10	–20–20

Table 7 summarizes daily streamflow statistics for 1980–2000 across all basins with the CVmax and CVmin vegetation. Daily streamflow performance of SIERRA degrades relative to its original calibration values in NSE (originally >0.6) and in percent daily bias (<15%), but monthly NSE values are greater than 0.8; thus model performance is sufficient for analysis of monthly and annual streamflow results. Results of the average calculation using the two soil parameter sets for each species and allocation strategy are presented below.

Fig. 5A plots total annual streamflow estimates calculated between 1980 and 2000 for each ecophysiological parameter set. Median values of total annual streamflow across vegetation parameters and allocation strategy at SIERRA range from 240 to 420 mm (Table 8). Both the highest and lowest streamflow totals occur when using AGE, thus annual streamflow estimates are particularly sensitive to ecophysiological parameters when the AGE strategy is used for SIERRA. Figures showing time series of annual streamflow are included in Supplementary material.

We test whether the distribution of annual streamflow estimates are significantly different between ecophysiological parameter sets within each allocation strategy using a two-sample *t*-test. For SIERRA, annual streamflow totals differ significantly ($p < 0.01$) between ecophysiological parameters for PIPO's AGE and FIX. For CVmax parameters or for CVmin parameters, annual streamflow estimates are significantly different between AGE and FIX and between AGE and RESOURCE, but not between FIX and RESOURCE when using pairwise two-sample *t*-tests. For CVmax parameters, annual streamflow is lower with AGE allocation, relative to FIX or RESOURCE. For CVmin parameters, annual streamflow is greater with AGE allocation relative to FIX or RESOURCE. There

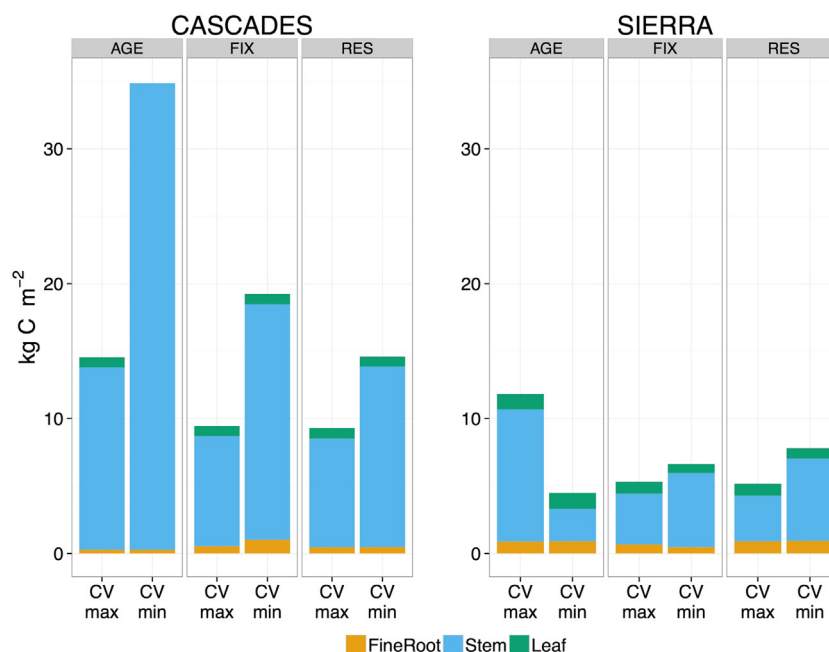


Fig. 4. Average 20-year carbon stocks that result from the vegetation parameters applied to whole watersheds.

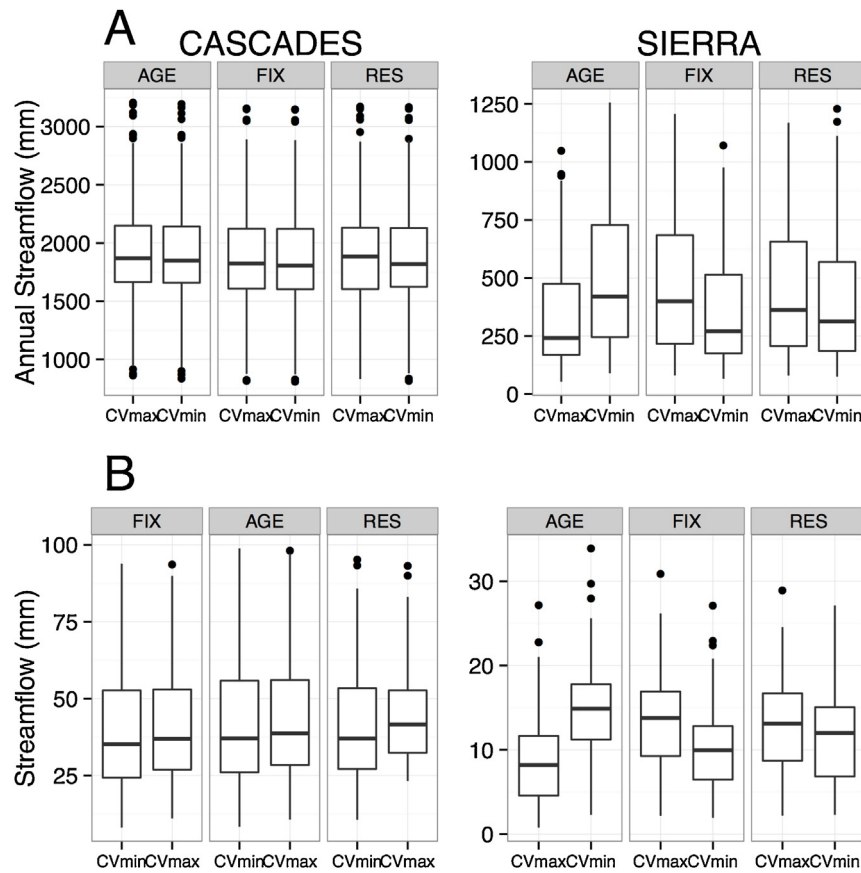


Fig. 5. Distribution of (A) total annual and (B) low monthly streamflow estimates from 1980 to 2000 for each vegetation parameter set (CVmax/CVmin) falling within C-store criteria. Low flows are for September and August in OREGON and SIERRA, respectively.

Table 8

Median and standard deviation of (A) total annual and (B) minimum monthly streamflow from 1980 to 2000 in a mature forest (CASCADES:September; SIERRA: August).

	CASCADES		SIERRA	
	CVmax	CVmin	CVmax	CVmin
(A) Annual				
AGE	1870 (520)	1850 (520)	241 (240)	420 (305)
FIX	1825 (520)	1810 (520)	400 (300)	270 (250)
RESOURCE	1880 (520)	1820 (520)	360 (290)	310 (290)
Observed	1670 (480)		430 (250)	
(B) Minimum flow				
AGE	22 (20)	21 (21)	8 (5)	15 (6)
FIX	21 (20)	20 (20)	13 (6)	10 (5)
RESOURCE	24 (16)	21 (20)	13 (6)	12 (6)
Observed	16 (8)		8 (5)	

is no significant effect of either ecophysiological parameter set or allocation for CASCADES.

Inter-annual variability in annual streamflow is considerably different between CVmax and CVmin at SIERRA for AGE and RESOURCE strategies. Interestingly, interannual variation in annual streamflow is lower for CVmax (the ecophysiological parameter set that increases interannual variation in LAI) relative to CVmin for the AGE allocation strategy. For FIX, interannual variation in annual flow is less for CVmax relative to CVmin. For other allocation strategies and for CASCADES, interannual variation in streamflow is not changed by ecophysiological parameters. For both sites, CVmax vegetation parameters resulted in higher annual streamflow estimates for FIX and RESOURCE allocation schemes relative to CVmin (Table 8).

Using observed streamflow records, we calculate the month

of average lowest total streamflow to be September and August for SIERRA and CASCADES, respectively. Only the ecophysiological parameters used in SIERRA's AGE and FIX allocation strategy result in significantly different distributions of low monthly flows (Fig. 5B). For SIERRA, there is a 30 and 100 percent difference in low monthly flow estimates for FIX and AGE, respectively (Table 8). For CVmax parameters, the lowest monthly streamflow is lower with AGE allocation, relative to FIX or RESOURCE. For CVmin parameters, lowest monthly streamflow is greater with AGE allocation relative to FIX or RESOURCE. As with annual flow, AGE allocation strategy at SIERRA shows a greater difference in low monthly flow estimates between CVmax and CVmin parameters. Total low monthly flow estimates demonstrate little sensitivity to vegetation parameters or allocation strategy at CASCADES (Table 8).

4. Discussion

This research demonstrates that considerable variability in forest C pool estimates may be attributed to allocation strategy and ecophysiological parameters and that – in more semi-arid regions – this variability may influence streamflow estimates in coupled ecosystem models. Our analysis summarizes the difference in model sensitivity to parameter uncertainty at the two sites. These differences reflect not only differences in species as captured by the ecophysiological parameters that we selected, but also differences due to distinctive climate drivers. Differences in the conditions under which we compare C estimates for these two conifers include climate used to drive their growth, especially precipitation regime, and the age of the forest stand: 100-year old PIPO estimates are derived for a northern Sierra Nevada catchment and 300-year old PSME estimates are calculated for a western Oregon Cascade catchment.

Within SIERRA or CASCADES, model estimates of mature forest carbon stores (and in some cases streamflow) are strongly influenced by both allocation strategy and ecophysiological parameter uncertainty. However, these within-site effects are small relative to model estimates of between site differences. Regardless of parameter set or allocation strategy used, the model estimates greater total C stores in CASCADES (12.4–34 kg/m²) relative to SIERRA (5.7–6.4 kg/m²), which is consistent with observations (Hicke et al., 2007; Hudiburg et al., 2009). Model estimates also yield a greater proportion of leaves and roots relative to stemwood for the more water-limited SIERRA environment relative to CASCADES, which is consistent with field measurements (Table 2) and studies that show preferential allocation to roots during drought (Bloom et al., 1985; Chmura et al., 2011; Gessler et al., 2004). Recent work has also found a strong relationship between cold climates and higher proportions of total forest biomass allocated to roots (Reich et al., 2014). The SIERRA site is both colder and drier than CASCADES. These results suggest that the ability of process-based models to capture large-scale regional differences in carbon cycling and streamflow may be robust to uncertainty in ecophysiological parameter setting and allocation strategy. Similarly, the model accurately captures the substantial differences in annual and low summer streamflow between the two sites for all allocation strategies and parameter sets. The within site effects of parameter uncertainty and allocation strategy, however, are more substantial. Table 9 summarizes these more salient results that we discuss in more detail below.

tion strategy, however, are more substantial. Table 9 summarizes these more salient results that we discuss in more detail below.

4.1. Allocation strategy influence on mature forest C estimates

For both sites, all allocation strategies produced reasonable estimates of forest C for some set of ecophysiological parameters. Thus, available literature based estimates of carbon stores were not sufficient to determine which allocation strategy was most appropriate. Nonetheless, different allocation strategies produced varied responses for both sites that provide insights into the role of carbon allocation. In the allocation strategies where allocation fractions vary with size or resource limitation (AGE and RESOURCE), total C estimates were higher at both sites. At both sites, FIX on average has smaller estimates of total C (12.4 and 5.7 kg/m² at CASCADES and SIERRA, respectively) and there is less variability across ecophysiological parameters in those estimates compared to AGE and RESOURCE (Table 3). FIX's smaller total C estimates likely reflect that it does not allow allocation to respond to climate; AGE and RESOURCE respond to environmental limitations by increasing partitioning to resource-gathering organs (leaves and fine roots), which enables harvesting more light/water/nutrients when these resources are limited. Our model estimates suggest that these strategies will tend to increase biomass accumulation over time. Many global dynamic vegetation models use the FIX allocation strategy for carbon cycling (Ostle et al., 2009), and our study's results suggest that such model estimates of carbon sequestration may be conservative. Perhaps more importantly, these results suggest that using a FIX strategy will likely overestimate the impact of climate related stressors such as droughts, that are expected to increase in the Western US's future (Ashfaq et al., 2013). Our results argue for including a more responsive allocation approach.

There were key, but site specific, differences in model estimates between AGE and RESOURCE allocation strategies. For the wetter CASCADES site, AGE produced higher stem and total C, thus had substantial impacts on carbon sequestration. AGE tends to preferentially allocate C to leaves under lower LAI conditions, thus the higher carbon sequestration resulting from the AGE strategy in CASCADES may reflect the relative importance of leaves and maximizing light interception for that site. In SIERRA, AGE and RESOURCE resulted in similar total C but AGE tended to increase

Table 9
Summary of key findings.

- Model estimates of the differences in carbon and water fluxes between CASCADES and the drier, colder SIERRA site were robust across ecophysiological parameter and allocation strategy uncertainty.
- Within site estimates of carbon varied substantially with allocation strategy but these differences were not sufficient to allow observations to determine which strategy was most appropriate.
- FIX allocation strategy tended to lead to lower estimates of carbon stores for both sites.
- Total C, and thus carbon sequestration, was much more sensitive to allocation strategy in CASCADES (relative to SIERRA), with the AGE strategy leading to substantially higher total C estimates in CASCADES.
- Proportion of carbon in roots and leaves was sensitive to allocation strategy in SIERRA, with higher leaf carbon with AGE strategy in SIERRA.
- A critical, and often overlooked, ecophysiological parameter is stem mortality.
- Temperature-sensitive parameters controlling productivity rates (i.e., Q_{10}) were the strongest controls of carbon estimates across sites and allocation strategies.
- Parameter sensitivity (e.g., most and least sensitive parameters) differed across allocation strategy.
- For streamflow, ecophysiological parameter uncertainty had a greater impact on estimates than allocation strategy – although there were interaction effects between ecophysiological parameter uncertainty and allocation strategy.
- Ecophysiological parameterization's influence on streamflow is considerably greater at SIERRA than at CASCADES

leaf carbon. Although this had little impact on carbon sequestration for the SIERRA site, the higher LAI associated with AGE had implications for streamflow estimates as discussed below. In reality, carbon allocation is likely to be more complex than either AGE or RESOURCE (Franklin et al., 2012) and further research is needed to develop approaches that can be utilized in watershed scale models. Given current state-of-the art, however, our results suggest that either approach (AGE vs. RESOURCE), with its ability to adapt to conditions, will tend to produce more similar – and likely more realistic estimates – of carbon sequestration than assuming the FIX approach.

4.2. Ecophysiological influence on mature forest C estimates

Though responses to uncertainty in individual parameters varied with site, there were many similarities across sites and allocation strategies. Our results show that overlooking a key physical mechanism such as branch mortality can lead to model inability to capture ecosystem measurements (Mitchell et al., 2009). We significantly overestimate total carbon by not accounting for branch mortality (when MSTEM is set to 0). Branch mortality approximates the self-thinning that occurs in maturing forest stands, and is typically represented in more complex stand-level models (Pretzsch, 2006; Sands and Landsberg, 2002) as varying through time with stem density. Our approach of applying a static branch mortality fraction is relatively simple and does not reflect how stem thinning occurs over time (Kane et al., 2014; Lutz and Halpern, 2006). Nonetheless, our model results reveal that including this simple approximation of branch thinning captures observed ecosystem carbon storage better than its exclusion and reduces the number of parameter sets that exceed field-derived C estimates from approximately 90%–80% and reduced the magnitude of exceedance by half (Fig. 2). Branch mortality was also a strong control on estimates for all carbon stores in CASCADES and for total C in SIERRA for all allocation strategies. Vegetation models used for regional carbon estimates typically do not include stemwood mortality, though there are recent exceptions (Hudiburg et al., 2013). DGVMs that do not account for branch mortality are likely to lead to an overestimation of regional C sequestration. Branch mortality is likely to be a sensitive parameter, thus field estimates that can reduce uncertainty in this parameter or better link it with existing models of stand development are likely to be a fruitful avenue for improving carbon cycling models.

In addition to branch mortality, temperature-sensitive parameters controlling productivity rates (i.e., Q_{10}) were the strongest controls of carbon estimates across sites and allocation strategies. We note that although Q_{10} has a positive relationship with total C under historical climate conditions at both sites, warmer temperatures could shift the relationship between them to be negative. Previous modeling studies have demonstrated the importance of including temperature-sensitive Q_{10} in understanding changes in forest NPP in response to climate change (Wythers et al., 2013). Because temperatures in the western US are projected to increase, our results highlight the importance of improving estimates of Q_{10} in modeling studies in order to better extrapolate possible implications of warmer temperatures on C assimilation.

4.3. Influence of vegetation uncertainty on streamflow estimates

Ecophysiological parameterization's influence on streamflow is considerably greater at SIERRA than at CASCADES (Fig. 5). This is in contrast to the impact of ecophysiological parameterization on total C estimates where the effect is much greater in CASCADES (Fig. 1). Allocation strategy has a noticeable impact on streamflow estimates for SIERRA such that annual streamflow estimates for AGE strategy are statistically distinct from RESOURCE and FIX;

the different estimates of LAI by AGE versus RESOURCE/FIX are more important in this water-limited environment and efforts are needed to assess whether AGE or RESOURCE produce more realistic results.

In general, the influence of ecophysiological parameters is greater than allocation strategy on model estimates of streamflow. We compared results for two ecophysiological parameter sets (CVmax and CVmin) that maximize and minimize differences in year-to-year variation in mature forest structure, as represented by LAI. In RHESys, LAI influences hydrology estimates through estimating intercepted rain evaporation losses, intercepted snow sublimation losses, transpiration rates, and effects on accumulation and melt. The inter-annual variation of LAI at SIERRA exceeded CASCADES's change in vegetation by an order of magnitude across all allocation strategies (Table 6). The higher annual coefficient in variation of LAI at SIERRA reflects a more water-limited system with higher year-to-year variation in productivity. Remote sensing of forest productivity in the Sierra shows substantial interaction variation and a strong correlation with water availability (Trujillo et al., 2012; Tague and Peng, 2013). In CASCADES, there is sufficient winter precipitation or snowmelt to recharge soil in the spring, and sufficient LAI to utilize all of this water each year. Thus, there is less inter-annual variation in water use and less sensitivity to year-to-year differences in LAI.

CASCADES demonstrated only minor sensitivity to vegetation parameterization in its estimates of total annual and low monthly streamflow. The negligible difference in annual streamflow estimates with PSME are surprising because vegetation parameters used to model watershed scale streamflow resulted in magnitudes of accumulated C differing by 50–200% across allocation strategies (Fig. 4) at the stand scale. We emphasize that our analysis focuses only on mature forest and the uncertainty in allocation and ecophysiological parameters may be different in post-disturbance conditions. Decades of paired catchment studies have established a strong relationship between forest biomass and streamflow (Andréassian, 2004 Brown et al., 2005), thus we might expect that differences in mature forest biomass may influence streamflow.

5. Conclusions

Model estimates of mature forest carbon stores and streamflow can be strongly influenced by allocation strategy and uncertainty in ecophysiological parameters. In general, we find that the influence of allocation strategy or uncertainty in ecophysiological parameterization on carbon and streamflow estimates differs depending on the site. Thus, whether or not an improved understanding of how plants allocate carbon is essential for coupled ecophysiology models depends on the location and goal of the model application. For the estimation of total carbon in wet, highly productive sites like CASCADES, improved understanding of how plants allocate carbon could have a substantial impact on estimates. On the other hand, if the goal of the model application is hydrologic estimation, understanding allocation is less critical. However for water limited sites like SIERRA, measurements that reduce uncertainty in ecophysiological parameters would improve streamflow estimates. Despite using species-specific organ-scale carbon estimates, we were not able to invalidate any of the three allocation strategies we considered. Because the Pacific Northwest's forest growth potential is frequently heralded as a CO₂ mitigation strategy – providing a larger C sink amongst mid-latitude temperate forests – understanding the influence of allocation on those estimates is critical.

Acknowledgements

We acknowledge support from the Center for Scientific Computing from the CNSI, MRL: an NSF MRSEC (DMR-1121053) and

NSFCNS-0960316. This work was supported by funding from the U.S. Geological Survey through the Western Mountain Initiative (award number G09AC00337) and the Department of Agriculture, National Institute of Food and Agriculture (award number 2011-67003-30346). EG also acknowledges support from NSF grant EF-1340649 to the University of Washington.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolmodel.2016.09.021>.

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