Tansley review

Evaluating theories of drought-induced vegetation mortality using a multimodel–experiment framework

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Contents

Summary 305  VI.  Next-generation, traditional, and empirical models 316
I. Background 305  VII. A path forward 317
II. Model–experiment approach 306  VIII. Conclusions 318
III. Simulations of hydraulic failure and carbon starvation 310  Acknowledgements 318
IV. On thresholds vs duration of stress as drivers of mortality 311  References 318
V. Interdependence of hydraulic failure and carbon starvation 314
I. Background

Accelerating rates of vegetation mortality in association with drought and rising temperature have now been documented in all major global biomes (van Mantgem et al., 2009; Allen et al., 2010; Phillips et al., 2010; Beck et al., 2011; Carnicer et al., 2011; Peng et al., 2011; Liu et al., 2013; Williams et al., 2013). Mortality is expected to increase as a result of rising temperature and increasing drought frequency and severity (Breshears et al., 2005; Allison et al., 2009; Lewis et al., 2011; Dietze & Moorcroft, 2012; Williams et al., 2013), with large biogeochemical and biophysical climatic feedbacks expected to follow as a result of shifts in land carbon and energy balance (Bonan, 2008; Kurz et al., 2008).

A primary motivation for examining our understanding of drought-induced mortality is the large international demand for realistic land surface modeling to enable accurate climate projections (Bonan, 2008; Allison et al., 2009; Arora et al., 2013). Mortality of widespread plant functional types (PFTs) within models has a large impact on the prediction of terrestrial climate forcing and future climate in dynamic global vegetation models (DGVMs; Hurtt et al., 1998; Sitch et al., 2003; Friedlingstein et al., 2006; Parves & Pacala, 2008; Allison et al., 2009). The mortality algorithms within most DGVMs are relatively simple and represent neither the current understanding of how PFTs die during drought nor the internal status of carbon and water in vegetation under drought stress (Moorcroft, 2006; McDowell et al., 2011). The current limits to mechanistic mortality modeling are driven in part by the lack of direct experimental tests of mortality theory (McDowell & Sevanto, 2010) and evaluation against data. Forecasts of future mortality can also be extrapolated from historic, empirical relationships (e.g. Williams et al., 2013). Thus, we need to determine not only the dominant mechanisms driving mortality for fundamental understanding, but also the degree of empirical vs theoretical prediction that is required to accurately simulate mortality, ideally using a common evaluation framework (e.g. Luo et al., 2012).

In the current absence of a community benchmark effort for model predictions of mortality, an alternative and more immediate option is to examine our model-based understanding within the constraints of ecosystem drought manipulations (e.g. Galbraith et al., 2010; Powell et al., 2013). Multi-model evaluations thus far have revealed that accurate simulation of traditional fluxes (e.g., photosynthesis and transpiration) does not equate to accurate prediction of mortality, partly as a result of both hydraulic and carbon metabolism uncertainties during severe drought (Galbraith et al., 2010; Powell et al., 2013). Our study complements these through a similar model–experiment framework, but with a focus on the mechanisms of mortality.

There are multiple inclusive hypotheses regarding the underlying drivers of drought-induced mortality: hydraulic failure, or desiccation as a result of cessation of water transport; carbon starvation, or the lethal impairment of metabolism or failure to defend against biotic attack as a result of depletion of carbohydrate stores; and an interdependency of carbon starvation, hydraulic failure, and biotic attack (summarized in McDowell et al., 2011; Fig. 1). Failure to maintain a sufficient phloem turgor gradient to drive carbohydrate flow from sources to sinks can hasten mortality through carbon starvation (Sala et al., 2010) or hydraulic failure (McDowell et al., 2011) or both (Sevanto et al., 2013). Novel glasshouse and field observations have clearly demonstrated the importance of both carbon starvation and hydraulic failure in mortality (Adams et al., 2009; Breshears et al., 2009; Andergga et al., 2012; Plaut et al., 2012; Hartmann et al., 2013; Quirk et al., 2013; Sevanto et al., 2013).

Theories on drought-induced plant mortality scale biophysical and ecological principles (Waring, 1987; McDowell et al., 2008;
Raffa et al., 2008), including numerous water–carbon feedbacks (e.g. McDowell et al., 2011), making hypothesis testing challenging even with manipulative experiments. The original, ground-breaking models of internal hydraulic or carbohydrate dynamics (Thornley, 1972; Tyree & Sperry, 1988; Amthor & McCree, 1990) have been recently developed across plant (Sperry et al., 1998; Hölttä et al., 2006, 2009; Rasse & Tocquin, 2006), ecosystem (Williams et al., 2001; Mackay et al., 2003; Domec et al., 2012), and global scales (Hickler et al., 2006; Fisher et al., 2010). These types of models synthesize our understanding of the complex hydraulic-carbohydrate system of vegetation (e.g. Cowan & Troughton, 1971; McDowell, 2011) and can thus be employed to investigate complex, dynamical processes such as drought responses of forests (e.g. Williams et al., 2001).

We used a model–experiment approach as a framework to examine our collective knowledge regarding how trees survive and die during drought. We began with reviewing and clarifying the definitions of hydraulic failure and carbon starvation that represent our state-of-knowledge of plant mortality and are simultaneously compatible with the current framework of most process models and DGVMs. We then drove six models using input parameters from a replicated drought manipulation study in a mature piñon pine–juniper woodland (Pinus edulis–Juniperus monosperma) in central New Mexico, USA. It has been predicted through both a DGVM and an empirical model that the southwestern USA will experience almost 100% mortality of the dominant conifers by 2050 (Jiang et al., 2013; Williams et al., 2013). The models employed here represent individual plant-scale (two models), ecosystem-scale (two models), and two global-scale DGVMs. Models were employed to simulate either or both hydraulic failure and carbon starvation and their interdependencies. Additionally, the mortality predictions from the carbon starvation algorithms in the two DGVMs were compared with observations, traditional process-model mortality indices, and an empirical tree-ring model.

II. Model–experiment approach

1. Overall approach

Our objective was to examine our model-based understanding of drought-induced mortality. We simulated the response of pine and juniper trees to experimental drought (Plaut et al., 2012, 2013; Gaylord et al., 2013; Limousin et al., 2013) as a way of capturing the complex and often unmeasurable internal hydraulic and carbohydrate dynamics. Specifically, we examined multimodel simulations of the mechanistic processes of hydraulic failure, carbon starvation, and their interdependency, as well as more traditional simulations of mortality using net primary production (NPP), growth efficiency (NPP yr⁻¹ per leaf area), and an empirical model based on regional tree-ring datasets (Williams et al., 2013). We compared simulations with observations of transpiration (E) for evaluation, and additional parameters depending on the model. We did not make predictions about the future nor did we conduct formal comparisons of the models, because three of them lacked replicate simulations (their smallest scale was the plot scale). We identified consistencies and discrepancies across models and empirical observations.

We employed models that varied in structure and scale, from individual plants to a global level, in the approximate following order: FINNSIM (Hölttä et al., 2006, 2009), the Sperry model (Sperry et al., 1998), TREES (Loranty et al., 2012; Mackay et al., 2012), MuSICA (Ogée et al., 2003; Domec et al., 2012), ED(X) (Fisher et al., 2010; Xu et al., 2012), and CLM(ED) (Fisher et al., 2010; Bonan et al., 2012). The unique, common characteristic of the models used here is the ability to simulate internal plant hydraulics and/or carbon dynamics (Fig. 1). These capabilities are novel in woody plant, ecosystem, and global-scale modeling, and allow predictions of processes consistent with the postulated proximate drivers of plant death.

2. Definitions of hydraulic failure, carbon starvation, their interdependence, and mortality

We defined the process of hydraulic failure as the progressive loss of hydraulic conductivity (K) on an individual-plant basis (Fig. 1). The loss of K for all models was scaled and reported as the percentage loss of conductance (PLC; 0–100%). The advantages of PLC as a definition of hydraulic failure are that it is quantitative, measurable, scalable to PFTs, and it inherently accepts that static PLC-mortality thresholds do not exist (e.g. Sevanto et al., 2013). This definition assumes that conductance–vulnerability curves on soils, roots, and branches scale to whole-tree K. This definition

Fig. 1 A generalized simulation scheme for modeling plant hydraulic failure, carbon starvation, and their interdependence. The numbers within each box indicate inclusion by the following models: 1, Sperry model; 2, FINNSIM; 3, TREES; 4, MuSICA; 5, ED(X); 6 CLM(ED). Orange-bordered boxes and orange arrows indicate interdependencies, or bidirectional carbon–water fluxes, that are simulated by the models. Allocation of nonstructural carbohydrate (NSC) to defense, reproduction, respiration, and growth is not listed in priority order, because that remains a subject of debate. E, canopy transpiration; Gₖ, canopy-scale stomatal conductance; K, hydraulic conductance; PLC, percentage loss of conductance; Ψᵦ and Ψᵦroids and soil and root water potential; GPP, gross primary production; R, autotrophic respiration. *Biotic attack was not included in any of the models used in this study, but is included to highlight the need for this critical model development (red arrow). Feedbacks between biotic attack and plant physiology are not highlighted here.

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further assumes that PLC < 100% impacts the function of downstream foliage (e.g. Hubbard et al., 2001). Hydraulic failure has been previously defined at the distal tissue level as 100% PLC (Sperry et al., 1998; Davis et al., 2002), and at the whole-plant level as the PLC that results in insufficient hydration to maintain metabolism (McDowell et al., 2008, 2011). Defining hydraulic failure of the PLC continuum assumes that PLC < 100% may be sufficient to jeopardize water balance and metabolic function; analogous to metabolic impacts of a chronic > 50% reduction in mammalian cardiovascular circulation.

We defined the process of carbon starvation as the depletion of available nonstructural carbohydrates (NSC; Fig. 1). The advantages and assumptions of this definition are similar to those for PLC. Carbon starvation has been previously defined as prolonged zero photosynthesis (Martínez-Vilalta et al., 2002; Ward et al., 2005; McDowell et al., 2008), as strictly 100% NSC loss (Sala et al., 2010), and as the loss of carbohydrates available for maintenance of defense, metabolism, and turgor (McDowell, 2011; McDowell et al., 2011). Like PLC, the continuum definition of carbon starvation is quantitative and logical because partial NSC loss may be sufficient to lethally impair metabolism, defense, and turgor (McDowell, 2011; Hoch et al., 2003; Gruber et al., 2012; Richardson et al., 2013).

Interdependence of hydraulic failure and carbon starvation is defined as increasing PLC and associated xylem tensions causing declining carbon uptake, transport, or utilization, and subsequent feedbacks by which declining available NSC impacts PLC through xylem filling or water acquisition (modified from McDowell et al., 2011). No models simulated biotic attack in this study (Fig. 1), but the interdependence definition should ideally include water and carbon feedbacks on defense and subsequent biotic agent population dynamics.

Mortality was quantified in the field as the percentage loss of foliated crown and was measured annually (Gaylord et al., 2013). When pinion pine dies in association with bark beetle (Ips spp.) attack (as occurred in two of the three drought plots in 2008), the entire canopy progresses from green to orange (zero water content) in 4 wk (Breshears et al., 2009; Plaut et al., 2012; Gaylord et al., 2013). Juniper, by contrast, drops individual twigs and branches as drought progresses, maintaining individual survival for longer than pine but progressively losing leaf area (Gaylord et al., 2013). Trees were pronounced dead at 0% foliated canopy.

We defined mortality in the two DGVMs, ED(X) and CLM (ED), as a threshold minimum carbohydrate content per unit leaf area. Only ED(X) and CLM(ED) have explicit mortality predictions; the other models simulated physiological processes but did not have thresholds or triggers for mortality. Mortality predictions from these models have not previously been tested.

3. Modeling PLC and NSC

Loss of xylem conductivity with decreasing xylem water potential was represented using Weibull functions fit to PLC and water potential ($\Psi$) data for species- and site-specific measurements (see Plaut et al., 2012, and Supporting Information, Notes S1, Fig. S1)

$$\text{PLC} = 100 \left(1 - e^{-\frac{\Psi}{b}}\right)$$

Eqn 1

where $\Psi$ values are branch and root water potential values (MPa), $b$ is the critical $\Psi$ that leads to 63% of conductivity reduction and $c$ is a shape parameter (Sperry & Tyree, 1988; Pammenter & Van der Willigen, 1998). The Weibull function was the best fit to the vulnerability curve data (Plaut et al., 2012; and Notes S1, Fig. S1). These vulnerability curves are measured on branches and roots, allowing tissue-specific calculation of PLC from $\Psi$ measurements or estimates. PLC is both theoretically and practically useful for investigating hydraulic failure, and has the additional value of broad coverage of plant functional types in the literature (e.g. Maherali et al., 2004; Choa et al., 2012), thus enabling input into future DGVM simulations.

While our models shared Eqn 1 for simulating PLC, they differed in their treatment of below-ground hydraulics and stomatal regulation (Tables 1, S1). Sperry, TREES, MuSICA, and CLM(ED) had multiple depths of root water uptake and explicit soil–root hydraulic conductance, whereas ED(X) simulated a single soil water pool. ED(X) assumed soil $\Psi$ equaled root $\Psi$, whereas the smaller-scale models prevented root $\Psi$ from falling below the midday observed $\Psi$, FINNSIM used root $\Psi$ simulated by MuSICA. All models (except FINNSIM) assumed xylem refilling followed the species- and tissue-specific vulnerability curves (Eqn 1, Notes S1). In Sperry and TREES, the soil was assumed to immediately recover hydraulic conductance on rewetting, but not the xylem. Xylem refilling (or recovery via new xylem growth) was indicated when fluxes were underpredicted post-drought, and the models were recalibrated accordingly.

Modeling approaches for NSC are less well tested than for PLC because of our poor understanding of NSC storage in trees (Le Roux et al., 2001; McDowell & Sevanto, 2010; Sala et al., 2012; Richardson et al., 2013). Many models do not include a storage pool, and, for those that do, the controls on fluxes in and out of the storage pool are poorly constrained. Theoretical and empirical evidence suggests that over the lifetime of plants, allocation to storage is probably an equal priority to growth (Waring & Schlesinger, 1985; Chapin et al., 1990; Hoch et al., 2003; Rasse & Tocquin, 2006; Smith & Stitt, 2007; Sulpice et al., 2009; McDowell, 2011; Sala et al., 2012; Stitt & Zeeman, 2012; Wiley & Helliker, 2012). In our study, the models that simulated NSC (TREES, MuSICA, ED(X) and CLM(ED)) used various modifications to the general NSC overflow approach that included feedbacks to prevent growth or respiration from consuming all NSC (Table 1; similar to Rasse & Tocquin, 2006), which is consistent with evidence from many studies (reviewed in McDowell, 2011; Sala et al., 2012; Stitt & Zeeman, 2012), including extreme tests of carbon starvation via 100% shading (e.g. Marshall & Waring, 1985; Sevanto et al., 2013). TREES, MuSICA, and ED(X) decreased growth as carbohydrate storage declined, and CLM(ED) effectively did the same by lowering tissue turnover rate and homeostatically increasing storage fluxes as carbohydrate storage declined.
### Table 1 Key processes in mortality simulation

<table>
<thead>
<tr>
<th>Model/scale</th>
<th>$G_s$ control</th>
<th>C-H$_2$O points of interaction*</th>
<th>Internal water and carbon status</th>
<th>GPP and $R$ regulation in drought</th>
<th>Partitioning rules</th>
</tr>
</thead>
<tbody>
<tr>
<td>FINNSIM Plant</td>
<td>$E$ is given as input</td>
<td>$C$ cost of cavitation refilling</td>
<td>Phloem turgor; $C$ cost of cavitation refilling</td>
<td>GPP and $R$ are given as input</td>
<td>N/A</td>
</tr>
<tr>
<td>Sperry Plant</td>
<td>Darcy’s law</td>
<td>N/A</td>
<td>Steady state</td>
<td>N/A</td>
<td>Root : shoot $K = 1 : 1$</td>
</tr>
<tr>
<td>TREES Plant/</td>
<td>Darcy’s law, VPD</td>
<td>$g_s - A$; no refilling if NSC is zero; growth and $R$ decline with $K$; root uptake</td>
<td>Steady state for this analysis</td>
<td>Both are down-regulated</td>
<td>Maintenance $R$ first, NSC storage, root/shoot growth last</td>
</tr>
<tr>
<td>ecosystem</td>
<td></td>
<td></td>
<td>Initial NSC proportional to biomass; withdrawn for $R$ first, then growth</td>
<td></td>
<td></td>
</tr>
<tr>
<td>MuSICA Ecosystem</td>
<td>Ball-Berry–Tardieu–Davies</td>
<td>$g_s - A$; root uptake</td>
<td>Water capacitance scales with leaf area; $K$ with fine root length; hydraulic redistribution Single NSC pool; source kinetics</td>
<td>Both down-regulated except maintenance $R$</td>
<td>N/A (biomass prescribed in current simulations)</td>
</tr>
<tr>
<td>ED(X) Ecosystem</td>
<td>Ball-Berry</td>
<td>$g_s - A$ regulated via $K$; root uptake</td>
<td>Vulnerability curves, soil $Ψ$ drive PLC</td>
<td>Maximum carboxylation and maintenance $R$ reduced 50% if NSC is $&lt; 8%$ leaf biomass</td>
<td>Storage followed by maintenance $R$, turnover, and then growth</td>
</tr>
<tr>
<td>ED(X) Ecosystem</td>
<td>Ball-Berry</td>
<td>Root uptake</td>
<td>Single NSC pool regulated to approach target level; declines if GPP-$R$ turnover is negative</td>
<td>GPP reduced with moisture stress. No reduction of $R$</td>
<td>Maintenance $R$ followed by turnover, growth then storage</td>
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<td>ED(X) Ecosystem</td>
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</tr>
</tbody>
</table>

$G_s$, canopy conductance; $E$, evapotranspiration; PLC, percentage loss of conductance; NSC, nonstructural carbohydrates; GPP, gross primary production; $R$, respiration (maintenance unless indicated otherwise); $K$, hydraulic conductivity. ED(X) and CLM(ED) induce mortality at NSC $< 8\%$ and $10\%$ of leaf biomass, respectively. The other models lack mortality rules.

*The stomatal ($E$–GPP), xylem–phloem, and H$_2$O uptake/root carbon allocation interfaces (e.g. Fig. 1). N/A, not applicable.
Interactions between phloem function and xylem refilling (Zwieniecki & Holbrook, 2009; Secchi & Zwieniecki, 2012) were mechanistically investigated using a new, coupled xylem–phloem transport model FINNSIM (based on Hölttä et al., 2006, 2009). FINNSIM used the gross primary production (GPP) and growth from MuSICA plus scaled respiration estimates (see Notes S2a) to estimate fluxes among the NSC pool, phloem, and xylem. This was the only model to examine theoretical carbon costs of xylem refilling, but because it was run with MuSICA simulations for input, it was excluded from ensemble analyses.

ED(X) and CLM(ED) represent a class of DGVMs that simulate the biogeoclimatic, biogeography, and demographics of global plant functional types (Cox et al., 1998; Moorcroft et al., 2001; Woodward & Lomas, 2004; Sitch et al., 2008; Medvigy et al., 2009; Fisher et al., 2010; Oleson et al., 2010; Zaehle et al., 2010; Medvigy & Moorcroft, 2012). DGVM mortality predictions have not performed well in tropical drought simulation studies (Galbraith et al., 2010; Powell et al., 2013); ours is the first test in the temperate zone.

ED(X) and CLM(ED) are aggregated models and thus could not simulate individual trees, but rather simulated cohorts of average trees within each functional type, size, and demographic status (Moorcroft et al., 2001). Because these models simulated the entire drought and ambient plots, there are no replicates of these simulations and thus intermodel comparisons are not statistically possible. All the models used tree allometric equations (Notes S2a) for the root, stem and leaf structural carbon pools and measured leaf NSC (Notes S2b) at the site for initiating the carbon pools. To accommodate different model requirements for stand, soil or physiological inputs, we distributed all available data from the precipitation–manipulation experiment to each modeler (see Table S1 for variables). The data used for calibration and evaluation varied for the different models, but all models used $E$ for a common evaluation. Additional model details can be found in the Notes S3.

4. Field experiment

The study site is located within the Sevilleta National Wildlife Refuge, New Mexico (34°23′11″ N, 106°31′46″ W). The site is a piñon pine (Pinus edulis Englem.) and juniper (Juniperus monosperma Englem. (Sarg.)) savannah (Romme et al., 2009). These sympatric species are excellent models of drought responses because of their contrasting hydraulic strategies (McDowell et al., 2008). Piñon pine is relatively isohydric, maintaining midday leaf $\Psi$ within a narrow range despite large treatment and seasonal variations in soil $\Psi$ (Plaut et al., 2012). The pine’s stomatal closure during drought reduces photosynthesis (Limosin et al., 2013). Juniper is relatively anisohydric, allowing greater photosynthesis during drought by maintaining higher stomatal conductance and tolerating lower leaf $\Psi$ (Plaut et al., 2012; Limousin et al., 2013). Piñon pine is more vulnerable to drought than juniper (Breshears et al., 2005; Plaut et al., 2012), but has relatively similar midday $\Psi$, vulnerability curves, and other physiological traits similar to most members of the Pinaceae (Maherali et al., 2004; Choat et al., 2012). Juniper is representative of cavitation-resistant species in seasonally dry regions (Maherali et al., 2004; Choat et al., 2012).

The field site is located in the lower latitudinal and elevational ranges of both species (Romme et al., 2009). The climate, physical setting, and study design are described in detail elsewhere (Pangle et al., 2012; Plaut et al., 2012; Limousin et al., 2013). Briefly, mean annual temperature and precipitation are 12.7°C (SE 0.13) and 363 mm (SE 21.5), respectively (20 yr record), with a bimodal distribution of precipitation, with peaks in the winter and late summer (monsoon), and with a pronounced dry period during the spring and early summer. The experiment consists of three 40 m × 40 m (1600 m²) replicate plots of four treatments: water addition by overhead sprinklers; 45% precipitation removal using gutters (‘drought’); an infrastructure control with inverted gutters allowing 100% of ambient subcanopy precipitation to reach the soil; and ambient control. The plots were blocked based on aspect, and treatments were imposed in August 2007 (Pangle et al., 2012).

Simulations of one drought and one ambient plot (or individual trees within plots, depending on model) are considered to represent simulations of trees that died and those that survived, respectively, because of the large amount of mortality in the drought plot. The models used input data from the southeast-facing drought and control plots to simulate individual trees or groups of trees. This block was selected because it had the longest-running data, and a large amount of mortality occurred on this block (and on the north-facing block; Gaylord et al., 2013). Piñon pine in the drought plot exhibited 68% mortality by December 2008 (Plaut et al., 2012; Gaylord et al., 2013) and 100% mortality by May 2009 in association with beetle attack. Juniper trees exhibited limited canopy dieback in 2008, but by 2011, 30% of the mature trees had <15% green canopy remaining and one mature juniper was completely dead (for a total of 60% canopy loss by 2011, Gaylord et al., 2013). No trees died on the ambient plot. All models were run only for these two plots.

Models were parameterized with data from January 2007 to December 2010, including near-monthly measurements of pre-dawn $\Psi$, daily mean soil $\Psi$, half-hourly or daily $E$ (beginning in April 2007), half-hourly meteorological data (solar radiation, air and soil temperature, and precipitation) as well as standard metrics of stand density, tree diameter and height, biomass, leaf area, soil depth, texture, and nutrient content. Meteorological data were collected at midcanopy height. Soil temperature was measured at 5 cm depth and $\Psi$, was measured at 15 and 20 cm depths to ensure similar measurement depths across all soil profiles despite variation in depth to bedrock. In addition, leaf and stem samples were collected throughout the study and analyzed for NSC (Notes S2b). A list of variables used by the models is provided in Table S1.

5. Evaluation of $E$ simulations

Models were parameterized and evaluated individually against multiple datasets, but all models shared calibration using species-specific, sapflow-based $E$ (per unit sapwood area to avoid scaling issues) measured in spring 2007 when the drought infrastructure had not yet been installed and seasonal drought had not yet initiated (Plaut et al., 2012). Likewise, all models were evaluated against $E$ observations from August 2007 (the date of drought structure installation) to 2010 at least. $E$ is the
longest, most continuous, and potentially the most relevant observation in this study (Plaut et al., 2013), because it integrates whole-plant hydraulics and carbon uptake, and \( E \) is also a common output variable of most process models. Note that FINNSIM did not simulate \( E \) but utilized MuSICA's simulations as input.

Comparison of observed and simulated \( E \) demonstrates an example of the challenge of evaluating DGVMs, which are designed for regional to global application, at single sites. These large-scale models have fewer mechanisms that can be tuned (at the plot scale) than the fine-scale models, leading to variation in the simulation of \( E \) across the models (Table 2). The Sperry model performed best and also captured predawn \( \Psi \) observations with high accuracy (Fig. S2). The difference between Sperry and TREES simulations, which include the same fundamental hydraulic structure, is a result of recalculation of the Sperry model to \( \Psi \) measurements after rainfall events or new growing seasons, which TREES did not do. In addition to \( E \), MuSICA predictions of predawn and midday leaf \( \Psi \) averaged (\( r \) 0.88 in piñon and 0.95 in juniper). The error was attributed to insufficient knowledge of below-ground water uptake dynamics, and the assumption of complete refilling whenever xylem pressure became less negative. ED(X) predictions of daily total \( E \) improved after calibration of the slope of photosynthesis to stomatal conductance within the Ball–Berry model to fit pretreatment \( \Psi \) observations. The resulting model also captured soil \( \Psi \) reasonably well (\( r \geq 0.91, P < 0.01; \) Fig. S3). The CLM (ED) model was relatively successful at predicting the rapid response of canopy water use to variation in rainfall, but regression fits were not strong, in part because this was the only model to run both species together rather than separately. CLM (ED) simulation of \( E \) was limited by a soil \( \Psi \) stress factor that is superimposed on the Ball–Berry estimates of stomatal conductance. The stress factor is nonlinear with respect to water content, which drove the rapid increases and decreases in water use with small changes in soil water.

### III. Simulations of hydraulic failure and carbon starvation

#### 1. Hydraulic failure

We compared PLC simulations for both species and treatments to investigate model predictions of hydraulic failure before mortality. The models simulated significantly greater PLC in trees of both species that died during the simulation periods (located on the drought plot) than in those that survived (located on the ambient plot; Fig. 2, \( P < 0.001 \) for drought vs control, for both species, for all models; using semiparametric regression based on Wand et al., 2009). This is consistent with empirical observations of water uptake and stem native conductivity differences across treatments and species at this site (Plaut et al., 2013; P. Hudson et al., unpublished). Only ED(X) predicted that trees ever experienced 100% PLC. ED(X) assumed that root \( \Psi \) is equal to soil \( \Psi \), but this is false because soil \( \Psi \) dropped to \( c. \) −8.0 MPa, while piñon pine xylem \( \Psi \) does not fall much below −3.0 MPa at this site (Plaut et al., 2012; Limousin et al., 2013) or anywhere else in piñon pine's range (West et al., 2007; Breshears et al., 2009). ED(X) simulated reasonable PLC for juniper because the assumption that soil and root \( \Psi \) are equal is nearly met at this site (Plaut et al., 2012). We suspect that the ED(X) PLC estimates for pine may accurately represent below-ground xylem PLC because the soil \( \Psi \) simulations were accurate (Fig. S3) and thus crossover of the Sperry (e.g.) and ED(X) PLC simulations in Fig. 2 may represent the timing of complete loss of \( K \) from the soil to the roots.

Amongst the remaining models that simulated PLC, we found that hydraulic processes well beyond the simple tissue-level vulnerability relationships (Eqn 1, Notes S1) were critical to driving PLC. The largest drivers of intermodel variability were the setting of maximum \( K \) (because PLC is the loss of conductance relative to the maximum) and simulating root \( \Psi \). The Sperry model was the most highly calibrated one, in part because this was the second iteration of modeling at this site (after Plaut et al., 2012) and it was focused only on hydraulics. It used the maximum simulated hydraulic conductance averaged for surviving trees over the simulation period to set species-specific reference conductance. Predawn leaf \( \Psi \) was simulated to set the minimum root \( \Psi \) (Fig. S2) to avoid assuming the root and soil \( \Psi \) distribution. TREES used a similar approach to estimating root \( \Psi \), but, by contrast, it simply set maximum conductance to the single measured value (tree-specific) before drought treatment initiation in 2007. By using this single value, TREES most likely underestimated maximum conductance and hence simulated unrealistically low PLC (Fig. 2). ED(X) also used a single measured value (species-specific) of hydraulic conductance before drought treatment initiation in 2007 to set maximum conductance. In MuSICA, maximum conductance was calibrated through optimizing the distribution and hydraulic conductivity of fine roots relative to soil properties, to match the predawn \( \Psi \) data before drought. Root \( \Psi \) was then computed dynamically via hydraulic capacitance optimized to match the time lag between tree transpiration and root water uptake estimated from sap flow data.

#### 2. Carbon starvation

From treatment initiation until autumn 2011, dying trees had 38 and 44% lower GPP than surviving trees for pine and juniper, respectively (\( P < 0.001 \) for all models and species). Decreasing GPP with drought is, of course, expected, but it is also a required tenet of

![Table 2] Summary of model performance in comparison of simulated and observed \( E \) (per unit sapwood area)

<table>
<thead>
<tr>
<th>Model</th>
<th>( r, P )</th>
<th>Piñon pine</th>
<th>Juniper</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sperry</td>
<td>0.95, &lt;0.01</td>
<td>0.99, &lt;0.01</td>
<td></td>
</tr>
<tr>
<td>TREES</td>
<td>0.78, &lt;0.01</td>
<td>0.71, &lt;0.01</td>
<td></td>
</tr>
<tr>
<td>MuSICA</td>
<td>0.78, &lt;0.01</td>
<td>0.82, &lt;0.01</td>
<td></td>
</tr>
<tr>
<td>ED(X)</td>
<td>0.61, &lt;0.01</td>
<td>0.55, &lt;0.01</td>
<td></td>
</tr>
<tr>
<td>CLM(ED)</td>
<td>0.35, ( P = 0.87^a )</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\( ^a \) CLM(ED) simulated only pine.
carbon starvation (McDowell et al., 2008). The second tenet is that NSC declines. For the same period, all models simulated lower whole-tree NSC stores in trees that died than in those that survived (Fig. 2, \( P < 0.001 \) for both species). None of the models consistently captured the variation observed in leaf NSC measurements (Fig. 2; the highest \( r \)-value was 0.40 for all models); however, we note that comparing observations of leaf NSC to simulations of whole-tree NSC is not a fair test. The large variability amongst models appears to be the result of the wide range of approaches to simulating the dynamics of fluxes into and out of the NSC pool. TREES constrained NSC depletion through simulating maintenance respiration as a direct function of \( K \), but large changes in \( K \) still lead to similarly large declines in NSC. MuSICA also simulated low NSC values despite a conservative, source-driven respiration algorithm, with the lowest predicted NSC values found in August 2008 when maximum pine mortality was recorded. Notably, MuSICA allows NSC to decline to zero rather than imposing a minimum threshold. In contrast to smaller-scale models, ED(X) and, to a lesser degree, CLM(ED) predicted relatively small NSC fluctuations because allocation to storage was adjusted to maintain a target residual store of NSC relative to leaf biomass (similar to Fisher et al., 2010). To buffer depletion of NSC storage pools, these models simulate the replacement of tissues, such as foliage and roots, as approaching zero when photosynthesis becomes zero, and ED(X) also down-regulates respiration by 50% when carbon storage crosses a threshold. A noteworthy point is that the general model approach of constraining NSC consumption by reducing allocation to other processes (e.g. Fig. 1) inherently invokes a shift in NSC allocation priorities during drought, which remains a topic of actively growing research (Sala et al., 2012; Stitt & Zeeman, 2012; Wiley & Helliker, 2012).

IV. On thresholds vs duration of stress as drivers of mortality

A common question in the mortality field is: what are the thresholds beyond which mortality is unavoidable? A logical and still standing hypothesis is that 100% PLC and 0% NSC are thresholds for mortality, but there is no evidence to support the notion that these extreme depletions in hydraulic and carbohydrate metabolism are necessary to cause mortality (McDowell et al., 2011; Gruber et al., 2012). By contrast, 1 yr of near-zero stomatal conductance seems to be a shared temporal duration beyond which mortality becomes likely in mature conifer species (Breshears et al., 2009; Plaut et al., 2012; Lévesque et al., 2013).

Because the individual models all demonstrated consistent treatment and species results, we generated multimodel ensembles to investigate the consensus behavior of modeled durations and...
absolute thresholds associated with mortality, across a range of model assumptions and approaches (e.g. Sitch et al., 2008; Powell et al., 2013). No clear thresholds were detected when comparing the ensemble simulations to the dates of mortality in August 2008 (pine) and the end of 2011 (juniper, Fig. 3). Simulated piñon pine trees that died in August 2008, 1 yr after installation of the drought treatment, achieved a maximum PLC of c. 80% and a minimum NSC of 40% of their starting NSC pool just before mortality. These may be taken as hypothetical thresholds; however, surviving pine trees were simulated to have equally large (or larger) changes in 2011 (Fig. 3) during a regional drought, but did not die (see Section VI for further interpretation of this result). Therefore, there is no evidence from these simulations of a threshold PLC or NSC loss (e.g. 80% and 40% from this example) beyond which mortality is inevitable.

Juniper may be even less likely to have simple mortality thresholds. Juniper trees dropped foliage progressively during drought and exhibited gradual canopy loss from 2007 to 2013 and whole-tree mortality (defined as whole-canopy loss; Gaylord et al., 2013) during 2010–2013 (Plaut et al., 2013). The faster and larger drought responses simulated for piñon pine than for juniper (Fig. 3) were the result of model representations of isohydry and anisohydry for piñon pine and juniper, respectively (West et al., 2007; McDowell et al., 2008; Breshears et al., 2009). These ensemble simulation results are partially consistent with the original predictions of McDowell et al. (2008): rather than mechanisms being partitioned between species, the processes of hydraulic failure and carbon starvation appear to co-occur in both species as they were exposed to prolonged, ecosystem-scale precipitation reductions that lead to death. The relatively more isohydric piñon pine progressed down the path of hydraulic failure and carbon starvation ahead of the relatively anisohydric juniper. This result is consistent with iso-anisohydry death trajectories demonstrated empirically in glasshouse-grown seedlings (Mitchell et al., 2013).

All models simulated that trees of both species that died spent significantly more time with relatively high PLC values (Fig. 4, P<0.001 for all models and species, Kolmogorov–Smirnov test; Marsaglia et al., 2003). While the relative values for mean PLC varied substantially between models, these treatment and species results were consistent across all models (Fig. 4), with means for all models of 41 and 63% PLC for surviving and dying pine trees, respectively, and 21 and 32% PLC for surviving and dying juniper trees, respectively, from the date the drought treatment was initiated until death. This consistent result arose primarily from the large treatment differences in soil water availability and species differences in cavitation vulnerability.

Similar to PLC, each model’s simulations of NSC suggested trees that died spent greater amounts of time with lower NSC than trees that survived (Fig. 4, P<0.001 for all models and species). Using MuSICA as an example, piñon pine trees that eventually died in the drought plot had only 39% of their maximum NSC reserves, whereas pines that survived on the ambient plot averaged 54% over the same period. These treatment and species differences were also consistent across the models, with means for all models of 76 and 51% of maximum NSC for surviving and dying pine trees, respectively, and mean simulated NSC of 52 and 45% of the maximum for surviving and dying junipers, respectively, from the date of drought treatment onset to the time of death. This consistent result arose primarily because all models simulated a decline in both growth and respiration with drought and ensuing mortality, but this was insufficient to compensate for the even larger photosynthetic reduction (dying pines and junipers had 62 and 57% of the GPP of surviving trees, respectively; P<0.01 for both species), resulting in consistently declining NSC for all trees that ultimately died.

Closer examination of the ensemble model results suggests these models may more realistically simulate NSC trends for the isohydric than for the anisohydric species. In Fig. 5, we have corrected for temporal variation in NSC by plotting the difference between the NSC of dying trees and that of surviving trees, allowing visualization of the relative impact of drought and ensuing mortality on NSC in comparison to trees that survive. A significant trend of decreasing leaf NSC was observed in piñon pine trees

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**Fig. 3** Model ensemble simulations of percentage loss of conductance (PLC) and percentage nonstructural carbohydrate (NSC) loss for piñon pine and juniper trees in the ambient (surviving) and drought (dying) treatments. The models used are TREES, MuSICA, Sperry, ED(X), and CLM-ED. Ensemble means across all models were created by averaging the daily output for each model, which was the mean of individual tree simulations for Sperry, TREES, and MuSICA, and the daily simulations of the two stands for the dynamic global vegetation models (DGVMs). The mean standard error is shown on the right-hand side of each panel for clarity.
and this trend was moderately captured by the model ensembles ($r = 0.47$). The models also suggested a decline in NSC for dying junipers, but the observations exhibited a relatively stable NSC storage pool. This may be because of a mismatch of leaf and branch observations (19 and 31% of tree NSC, respectively; Notes S2a) vs whole-tree simulations, and a more rapid leaf shedding in the junipers than was simulated (Gaylord et al., 2013). Thus, a survival strategy of juniper appears to be hydraulic adjustment to reduce leaf area and maintain hydraulic function and NSC pools above critical values (Limousin et al., 2013). It is possible that shifts in relative NSC allocation and depletion between above- and below-ground biomass could have led to this apparent discrepancy between modeled and observed juniper NSC (Hartmann et al., 2013).
The consistent simulation across all models of greater PLC and reduced NSC in trees that died supports the co-occurrence of hydraulic failure and carbon starvation during drought-induced mortality at this site. This is logical, given that increasing PLC reduces gas exchange and prolongs zero photosynthesis and elevate heat stress (McDowell et al., 2008; Limousin et al., 2013). Chronically low gas exchange rates associated with high PLC could also impair embolism refilling capacity (Zwieniecki & Holbrook, 2009), reduce resin production and pressure (Herms & Mattson, 2009), and impair embolism refilling capacity (Zwieniecki & Holbrook, 2009). It is from these interactive hydraulic and carbon metabolism processes that the interdependency hypothesis of mortality has arisen (McDowell et al., 2011).

V. Interdependence of hydraulic failure and carbon starvation

There are many feedbacks between carbohydrate and hydraulic dynamics that can accelerate or buffer the rate of mortality during drought (Fig. 1; Hummel et al., 2010; McDowell et al., 2011; Mueller et al., 2011). Simulated PLC and NSC should, in theory, capture many of these feedbacks, regardless of the spatial or temporal scale of simulation. Consistent with this, correlation of the ensemble results of PLC and NSC simulations from Fig. 5 revealed that modeled periods of depleted NSC were associated with simulated increases in PLC (Fig. 6). In this analysis, the daily difference between ensemble predictions of the ambient (surviving) and drought (dying) trees is calculated for both NSC and PLC. The mean daily difference for 30 d periods was calculated to allow for temporal displacement between cause-and-effect relationships of PLC and NSC. Both species fall along the same trend. This result is consistent with an interdependency of mechanisms underlying vegetation mortality, starting with strong stomatal impacts on photosynthesis (Martinez-Vilalta et al., 2002; McDowell et al., 2011). Strictly quantifying the interdependence of these factors is a big empirical challenge, but it can be simulated using highly detailed process models such as FINNSIM.

Our goals for the FINNSIM simulations of whole-tree xylem and phloem function were, first, to investigate the hypothesis that phloem transport ceases during drought as a result of failure of the interdependent hydraulic-carbohydrate system (McDowell & Sevanto, 2010; Sala et al., 2010; McDowell, 2011) and, secondly, to apply the model to investigate potential mechanisms underlying the hydraulic results and carbohydrate costs of maintaining xylem function (Zwieniecki & Holbrook, 2009). Using driving parameters most consistent with the observations and results of the other models, FINNSIM simulated the failure of phloem transport (represented here as the phloem turgor gradient from top to bottom of the canopy – the most direct and measurable trait of phloem function) in both species during the seasonal drought in 2008 (Fig. 7). The model simulated juniper to have lower turgor than pine, and trees of both species that died had lower turgor than those that survived. For the relatively anisohydric juniper, photosynthesis continues down to −6 MPa (Limousin et al., 2013), which provides sugars to aid in maintaining phloem pressure (Hölttä et al., 2009; Sevanto et al., 2013), but the lack of water availability to the phloem with xylem \( \Psi \) exceeding −8 MPa during drought (Plaut et al., 2012) forced a complete cessation of juniper phloem function for extended periods (Fig. 7). By contrast, phloem transport was not predicted to be constrained by water availability in pinion pine as a result of its relatively isohydric behavior, which maintained xylem \( \Psi \) significantly higher (> −3MPa) than values that would impair phloem function. Pine phloem transport is constrained only by NSC availability, which becomes limiting
during extended periods of zero gas exchange (Limousin et al., 2013). It will require empirical tests to determine if such a decline in phloem function actually matters to survival when GPP is near zero and there is no photosynthate to transport.

We extended the FINNSIM simulations to examine xylem refilling and its potential impacts on hydraulics and carbohydrate balance. We varied the rate of refilling and the amount of sucrose irreversibly consumed in refilling, as the precise refilling mechanism and its associated metabolic costs are not known (Zwieniecki & Holbrook, 2009). The rate of refilling determined the progression of PLC over time (Fig. 8a). In some cases, no refilling rates were sufficient to repair the loss of conductance.

Faster refilling kept PLC lower (Fig. 8a), but increased the carbon costs of refilling, especially when we assumed some fraction of sucrose used in refilling was not recycled (empirical values on how much NSC is lost from refilling do not exist). Despite carbon loss to refilling, embolism repair consumed only a minor portion of the plant's carbon budget. Even under the unlikely scenario of the highest refilling rates and with all sucrose used in refilling lost (0% recycled), the carbon cost of refilling was at most 40% of the annual cost of leaf respiration (Fig. 8b,c), or 10% of the total NSC in the plant (Fig. 8d). These results suggest that the carbon cost of refilling is unlikely to be large relative to the entire plant carbon budget; however, it may be a large amount of carbon for plants undergoing the late stages of carbon starvation (McDowell, 2011). This extra cost could, in theory, be responsible for the overestimates of NSC by most models (Fig. 2), as these models all assumed no carbon costs for refilling or maintaining phloem function.

![Graph showing phloem turgor over time](image)

**Fig. 7** FINNSIM simulations of the phloem turgor gradient from the upper canopy to the base of the stem. Turgor is the simplest and most testable metric of phloem transport, and simulations of phloem flux rates are nearly identical to turgor gradient simulations. The timescale was reduced to focus on January–September 2008 to highlight the dynamics proceeding pine mortality in August 2008. The phloem turgor gradient declines and hence nonstructural carbohydrate (NSC) transport ceases earlier in juniper than in pinon pine, largely as a result of the larger decline in xylem water potential in junipers and hence water available to the phloem. This effect is magnified for droughted junipers that die by 2011. Droughted pines that die in 2008 show a reduced phloem turgor as a result of a lack of NSC-based solutes to drive transport; xylem water potentials are never sufficiently low to impair phloem transport in dying or surviving pines.

![Graph showing cumulative carbon cost of refilling](image)

**Fig. 8** Xylem refilling modeled by FINNSIM. (a) Proportion loss of conductance (PLC) as a function of refilling rate. (b) Cumulative carbon per plant (mol) used for refilling as a function of the recycling rate of sucrose. (c) Ratio of the cumulative refilling carbon costs relative to cumulative leaf respiration (Notes S2b, S3). (d) The ratio of cumulative carbon costs of refilling relative to the total amount of nonstructural carbohydrate (NSC) within the plants.
VI. Next-generation, traditional, and empirical models

The treatment and species differences across models for PLC and NSC (Figs 3–8) are consistent with mortality occurring through the interdependence of hydraulic failure and carbon starvation at the stomatal, xylem/phloem, and below-ground interfaces (McDowell et al., 2011). It is clear that simulating hydraulic failure and carbon starvation is insufficient to accurately predict mortality, however, because of the significant impact of attacking biotic agents during drought on mortality (Raffa et al., 2008). This is exemplified by the ED(X) simulations (Fig. 9a). ED(X) correctly simulated the piñon pine mortality that occurred in 2008 (simulations were within the 95% confidence interval of the observation) in the presence of a bark beetle outbreak (Ips species; Plaut et al., 2012; Gaylord et al., 2013) with an assumed NSC threshold, but incorrectly simulated mortality of the (still living) pine trees on the ambient plot during the record-setting, severe regional drought in 2011 (Mu et al., 2013) during which there was no local outbreak of beetles (Fig. 9a; Limousin et al., 2013). There are, however, models of pathogen population dynamics that utilize climate data and estimates of forest stress (e.g. Biesinger et al., 2000) that could potentially be coupled to the NSC or new defense modules in DGVMs (e.g. Fig. 1). This approach may be useful at our site. An anomalous January cold event (<−29.0°C on site) that exceeded the cold temperature survival threshold of Ips (~1°C; Chanler, 1966) occurred in 2011, whereas the coldest temperatures in 2007 and 2008 on site did not fall below −15.2°C. Thus, despite greater physiological carbon starvation and hydraulic failure than for trees that died in 2008, remaining pine trees survived the drought in 2011, indicating that the mortality thresholds (e.g. absolute values or duration of NSC or PLC values) may vary with the presence of attacking agents (Raffa et al., 2008). Furthermore, there is strong evidence from these same experimental plots that average NSC is a reasonable predictor of mortality ($\rho = 0.77$; L. T. Dickman, unpublished) and thus a logical link exists both within the model framework and from empirical data. For near-term predictions, such models can be linked to remotely sensed estimates of mortality, to serve as initiation for further insect outbreaks (Wulder et al., 2006).

At the far end of the spectrum of model complexity, approaches using empirical relationships between mortality and indices such as meteorological drought are appealing (e.g. Wulder et al., 2006; Williams et al., 2013). These approaches risk oversimplification and resulting loss of accuracy when run into the future; however, given the large amount of data that can go into empirical models, they may be highly accurate in the near term (<100 yr). To test if a simple, empirical approach could capture mortality in our study, we used a new empirical relationship between cold-season precipitation, summer evaporative demand, and tree-ring-based growth and mortality estimates (the Forest Drought Severity Index, FDSI) to predict mortality (Fig. 9a; Williams et al., 2013). An FDSI value of −1.41 was associated with widespread forest mortality in the 1590s in the southwestern USA (Betancourt et al., 1993; Brown & Wu, 2005), including for piñon pine trees, and thus we use −1.41 as a hypothesized value beyond which mortality may occur. Similar to ED(X), the FDSI approach correctly predicted piñon pine mortality in 2008, but incorrectly predicted mortality in 2011. FDSI is an annual metric, which is consistent with the observation that mature, field-grown conifers can survive c. 12 months without positive photosynthesis (Breshears et al., 2009; McDowell, 2011; Lévesque et al., 2013). Thus, both the highly mechanistic and highly empirical approaches suffer from similar errors of not accounting for all processes, in this case, bark beetle attack dynamics.

An intermediate approach is to apply the numerous traditional DGVM mortality indices (McDowell et al., 2011). These simpler algorithms are appealing because they are already in place in the DGVMs and can be measured relatively easily. In our rather unnatural experimental manipulation (precipitation reduction without concomitant temperature rise as typically occurs in drought; e.g. Breshears et al., 2005), the traditional mechanisms...
of constant background mortality, climate envelopes, heat stress, size and age thresholds, and shading were all ineffective to predict mortality because the trees did not cross any temperature, size, or shading thresholds during this study. Simulations of NPP and growth efficiency (production per unit leaf area; Waring & Pitman 1985, Notes S4) did capture the species and treatment trends correctly, but like the other indices, they overestimated survival because the assumed mortality thresholds were not exceeded in the simulations (Fig. 9b). Model predictions across the range of complexity spectrums can be integrated with models of biotic agents (both mechanistic and empirical), and all model types should then be evaluated at regional scales (e.g. Wulder et al., 2006) to ensure they can obtain the correct answers for the correct reasons. These conclusions are based on one study site with two sympatric species, but may be representative of a global science challenge owing to our limited knowledge of fundamental mortality mechanisms and the importance of biotic attack agents in mortality globally (Raffa et al., 2008; Bentz et al., 2010; McDowell et al., 2011; Hicke et al., 2012).

VII. A path forward

Our analysis has revealed that, regardless of scale, all models suggest that the duration of hydraulic impairment and low NSC stocks is associated with mortality; that the stomatal, phloem, and belowground carbon and water interdependences were all important during simulated drought and mortality; and that mechanistic, traditional, and empirical modeling approaches all have similar vulnerability to processes not yet considered, such as biotic agent populations. These results emerged despite the various ways that models simulated and parameterized the hydraulic and carbohydrate systems, partly because of a fairly common, emergent simulation framework (Fig. 1). This study used an international set of models, but only a single experiment with two species within the traditional Needleaf Evergreen Tree PFT (e.g. Jiang et al., 2013), and thus an obvious next step is a similar test in another PFT (e.g. Fig. 9a). Statistical and mechanistic population dynamics models of biotic agents (e.g. Hicke et al., 2007; Magori et al., 2009) should be considered for integration into DGVMs. Integrated landscape-scale models of vegetation susceptibility and insect population dynamics will allow the links among climate, forest vulnerability, and outbreaks to be investigated, and can subsequently be used to parameterize DGVMs. Models of biotic attack and forest vulnerability will require evaluation datasets that incorporate patterns of large-scale mortality, climate, species, soil conditions, and, most critically, attack rates of biotic agents, in order to capture the real-world heterogeneity in edaphic, species, and disturbance drivers (Luo et al., 2012). Spatially distributed datasets are simultaneously critical for DGVMs, for which the smallest scale of simulation is the stand and hence replicated tests require evaluation at larger spatial scales. Such mortality benchmarks do not yet exist outside of inventory data, but potential exists for using remotely sensed approaches (Wulder et al., 2006; Huang et al., 2010; Garrity et al., 2012; Kennedy et al., 2012; Meddens et al., 2012; Mu et al., 2013). These evaluation tests serve the
additional benefits of providing fundamental knowledge of climate–mortality relationships, from which near-term (c. 50 yr) mortality forecasts can be generated (e.g. Fig. 9a and Williams et al., 2013).

VIII. Conclusions

Next-generation models of vegetation physiology are advancing rapidly at scales ranging from individual plants to a global level. Here, all models predicted depletions in NSC pools and increases in PLC in both pinyon pine and juniper trees that died within 1–5 yr of a sustained c. 45% reduction in precipitation. Model results suggested that mortality depended on the time trees spent with extensive hydraulic failure or carbon starvation, rather than on specific thresholds per se. Interdependency of carbon and water was supported by each model. The consistency of these results is encouraging, but substantial research is required before model predictions are reliable in the absence of significant empirical constraints, that is, in future scenarios. Next-generation process models, traditional process model metrics of mortality, and empirical estimates of mortality all suffer from assumptions that were not met in this study, for example the presence of bark beetles. Models representing a wide range of alternative hypotheses must be applied and rigorously evaluated to progress our understanding of the processes underlying tree mortality. Representation of belowground hydraulic function, NSC dynamics, vegetation defense, and population dynamics of biotic attack agents emerged as critical mechanisms requiring better understanding and modeling. Reducing uncertainty in mortality modeling is critical to better forecasting of future terrestrial impacts as our climate continues to change.

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Supporting Information
Additional supporting information may be found in the online version of this article.

Fig. S1 MuSICA model simulations of PLC in piñon pine using different vulnerability curves to predict loss of xylem conductivity with decreasing xylem water potential.

Fig. S2 Modeled versus measured predawn leaf water potential via the Sperry model.

Fig. S3 Example of the prediction of soil water potential using ED (X) for an ambient plot at 15 cm soil depth.

Table S1 A summary of how empirical variables were utilized or simulated by models.

Notes S1 Vulnerability to Cavitation.

Notes S2 (a) Estimates of maintenance respiration and allometric calculations. (b) Measurement of non-structural carbohydrates (NSC).

Notes S3 Model-specific developments and application.

Notes S4 On growth efficiency as a predictor of mortality.

Notes S5 Additional References cited in the Supplemental Information.

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