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Integrating plant physiology and community ecology across scales through trait-based models to predict drought mortality

Author for correspondence:
Anna T. Trugman
Email: att@ucsb.edu

Anna T. Trugman

Department of Geography, University of California Santa Barbara, Santa Barbara, CA 93106, USA

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Summary

Forests are a critical carbon sink and widespread tree mortality resulting from climate-induced drought stress has the potential to alter forests from a carbon sink to a source, causing a positive feedback on climate change. Process-based vegetation models aim to represent the current understanding of the underlying mechanisms governing plant physiological and ecological responses to climate. Yet model accuracy varies across scales, and regional-scale model predictive skill is frequently poor when compared with observations of drought-driven mortality. I propose a framework that leverages differences in model predictive skill across spatial scales, mismatches between model predictions and observations, and differences in the mechanisms included and absent across models to advance the understanding of the physiological and ecological processes driving observed patterns drought-driven mortality.

I. Introduction

Process-based vegetation models (VMs) simulate plant physiological processes, such as photosynthesis and transpiration, and ecological interactions, such as competition for scarce resources, that govern the responses of forests to climate. VMs are also a tool that is central to assessing the sensitivity of terrestrial ecosystems to anthropogenic climate change. In practice, the actual physiological and ecological processes incorporated in a particular VM vary substantially depending on historical model development, experimental purpose, spatial scale and biome(s) of interest.

In recent years, the representation of climate stress-driven tree mortality in VMs has been identified as a major source of uncertainty in determining forest sensitivity to climate change due to the variety and empirical nature of mortality parameterisations, most of which couple mortality to low plant-growth efficiency (Bugmann *et al.*, 2019). By contrast, in live trees, plants harness gradients in water potential to transport water from the soil to their leaves and transpire this water through stomates into the atmosphere. During periods of water stress, the water potential in the hydraulic continuum declines until embolisms occur in xylem conduits and impair water transport. Efforts to more mechanistically represent the impacts of water limitation on plant growth and drought-driven mortality in VMs through explicitly modelling the hydraulic continuum have the capacity to advance VM predictive skill and constrain carbon cycle uncertainty associated with mortality predictions (Xu *et al.*, 2016; Trugman *et al.*, 2018b; Venturas *et al.*, 2018). However, the skilful prediction of drought-driven mortality remains elusive, even with the addition of plant hydraulic processes in VMs (Rowland *et al.*, 2021).

The limitations for simulating drought-driven mortality represent a major challenge for terrestrial carbon cycle prediction. Yet, deficiencies in VM performance also offer an opportunity to better understand the underlying mechanisms governing the forest dynamics in ecosystems surrounding us through a better understanding of where, when and why models fail. In this review, I summarise the strengths and limitations of process-based VMs. I review where and when studies have seen success in predicting drought-driven mortality using plant hydraulics, and where and when plant hydraulics alone have proven insufficient to capture observed mortality patterns. Finally, I identify ways in which differences in predictive abilities of VMs across scales and model formulations can be leveraged to resolve gaps in our understanding of the physiology and ecology underlying forest drought responses and drought-driven mortality.

II. Process-based vegetation model strength and limitations

Trees are incredibly diverse and complex organisms. Ecological interactions between trees that determine forest composition, structure and demographic rates layer on additional process complexity. Due to limits on both computational resources and theoretical knowledge, even the most complex VMs are a highly simplified representation of a real forest. The simplicity of VMs relative to the real world is a strength and enables researchers to use VMs not only as predictive tools for future scenarios, but also as platforms to understand current day ecological unknowns.

Simplicity (or model parsimony) allows VMs to become hypotheses testing tools that researchers can use to determine the suit of mechanisms sufficient to produce patterns observed in nature (Pacala *et al.*, 1996). In this context, the absence of known processes is as important as the processes that are included within a given model. For example, in a study focused on the physiological mechanisms underlying tree drought responses, the authors used a simple VM to test the hypothesis that hydraulic damage to xylem tissue during drought and the subsequent carbon costs of rebuilding damaged tissues to recover predrought function explained the widespread observed patterns of delayed tree mortality following drought events (Trugman *et al.*, 2018a). In another study, focused on the ecological interactions underlying tropical forest structure, the authors used a VM to test the hypothesis that gap-generating disturbances and subsequent asymmetric competition for light explained tropical forest tree size distributions (Farrior *et al.*, 2016). In Trugman *et al.* (2018a), drought-induced xylem damage is a critical process, but competition for light is not a processes included in the VM, whereas in Farrior *et al.* (2016), competition for light is necessary, while xylem damage is ignored. Because both models were able to reproduce the phenomena of interest, they were able to conclude that the included processes (xylem damage and recovery for Trugman *et al.*, 2018a, gap disturbances and competition for light for Farrior *et al.*, 2016) were more important than the excluded processes as mechanisms underlying lagged mortality and tree size distributions, respectively.

The level of complexity in many VMs has increased substantially over the past 2 decades to simulate physiological processes that occur on timescales of minutes and ecosystem dynamics that occur on the timescales of years to decades (Xu & Trugman, 2021). Advances in model capabilities in terms of the number of processes and sophistication with which processes are represented have escalated with the aim of simulating the complex world around us (Bonan & Doney, 2018). The need to add complexity is understandably urgent, given that VMs are an integral component of the land surface models that are used in climate change projections. However, complexification leads to barriers that inhibit the advancement of scientific understanding by making it increasingly difficult to attribute particular VM responses to underlying physiological or ecological mechanisms, and by increasing uncertainty in VM predictions due to uncertainty in underlying model parameters and equifinality issues during model validation (Table 1).

In summary, VMs are a frequently underappreciated and powerful hypothesis testing tool that cannot and should not fully capture reality. The utility of VMs in hypothesis testing also makes them a fundamental tool for guiding future measurements, ultimately improving both measurements and models (Medlyn *et al.*, 2015, 2016). Given major uncertainties associated with increasing VM complexity (Sitch *et al.*, 2008; Tang & Zhuang, 2008; Prentice *et al.*, 2015), the addition of new processes should ideally be done through several steps in which the proposed new mechanism is first evaluated using an idealised model (such as the examples of Trugman *et al.*, 2018a and Farrior *et al.*, 2016) and subsequently added into a more complex VM in a modular structure. Therefore, the VM can be run with or without the proposed new mechanism to see which processes representation gives the most parsimonious result compared with patterns observed in nature.

III. From leaf to ecosystem: cross-scale vegetation model predictions of drought-driven mortality

Approaches to modelling plant hydraulic transport are extremely diverse (detailed by Mencuccini *et al.*, 2019). However, hydraulically enabled VMs have several commonalities across formulations, including a description of hydraulic traits of tissues such as roots, stems and leaves, allometric parameters that scale up tissue-level properties to the whole plant, and processes linking plant function to carbon and water fluxes (Mencuccini *et al.*, 2019) (Fig. 1). Hydraulic modules diverge in their choices (hypotheses) including the leaf-level representation of stomata–environment interactions (Wang *et al.*, 2020), the precise physiological representation of plant hydraulic transport and water storage (or lack thereof) (Trugman *et al.*, 2018b; Mencuccini *et al.*, 2019), the coupling between stomata and hydraulics (Anderegg & Venturas, 2020), and phenological strategies such as drought deciduousness (Xu *et al.*, 2016). Depending on model purpose and scale, VMs may also represent complex hydrological processes that can strongly

Table 1 Potential modelling pitfalls.

Problem	Possible underlying issue	Example	What did we learn?
VM predictions do not match observations	Missing a mechanism or process in the VM that matters	*VM predicts that trees die where observations show tree persistence*. Love *et al*. (2019) used a VM to diagnose the controls of aspen dry range extent and found that growing season rainfall was insufficient to support aspen persistence where stands were observed growing around the region	Both hydrology and physiology are important. VM predictions of lethal plant stress based on physiological understanding and surface water budget provided a window into the subsurface and enable calculations of the necessary groundwater subsidy that aspen stands rely on to persist a dry range edge
	VM representation and/or scientific understanding of a process is incomplete or insufficient	*VM captures observed tree mortality patterns in controlled stand-level experiment but fails to capture mortality patterns at larger spatial scales*. Venturas *et al*. (2021) used a VM that skillfully simulated lethal stress in a stand-level experiment but found that model-prognosed stress explained little of observed variance in mortality at the regional scale	The lack of skilful mortality prediction at large spatial scales is likely to stem from multiple issues including incomplete scientific understanding of mortality processes (both ecological and physiological), subsequent missing mechanisms in VMs (Fig. 1), and imperfect observational data
	Observational data used to parametrise or validate the VM is imperfect and/or measurement error is undocumented	*Mortality data used during VM validation includes multiple co-occurring drivers with different underlying mechanisms, not all of which are included in the VM*. Stephenson *et al*. (2019) found that most tree mortality during an extreme drought in California was associated with bark beetles and did not necessarily correspond with the most physiologically stressed trees	VMs are important tools to help guide future measurements that should be made to discriminate among differing hypotheses represented by distinct processes within a single VM and/or across different VMs (Medlyn *et al*., 2016)
VM predictions match observations for the wrong reasons	Compensating errors in model specifications/Equifinality in VM parameterisations such that different sets of parameters for a single modelling system result in same or similar predictions	*A suite of VMs with different mortality formulations match observational data well but mortality modules that performed similarly during validation manifest sharply diverging trajectories in novel climate conditions*. Bugmann *et al*. (2019) used 15 VMs with different mortality schemes and found that VM sensitivity to future climate was highly dependent on differences in mortality formulation	**(1)** Systematic intercomparisons of specific VM processes (such as mortality) through increased modularity **(2)** VM intercomparisons using a hierarchy of model complexities **(3)** Challenging VMs with multiple tests and/or benchmarks (Fisher & Koven, 2020)

VM, vegetation model.

affect plant available water (PAW) and prognosis during and after drought (Tai *et al.*, 2018). Although important when understanding observed broad-scale mortality patterns (Trugman *et al.*, 2021), pests and pathogens, which often co-occur with drought and drive mortality events (Raffa *et al.*, 2008), are currently absent from VMs designed for regional- to global-scale simulations (McDowell *et al.*, 2020).

The recent inclusion of new stomatal optimisations (Sperry *et al.*, 2017) and the explicit representation of plant hydraulics in VMs encapsulates the hypothesis that the physiology of water limitation is important for predicting ecosystem fluxes, demographic outcomes and terrestrial carbon cycle dynamics in a water limited world. In many instances, hydraulically enabled VMs have seen success in explaining observed patterns in nature. For example, studies have found that an explicit representation of hydraulic processes improves simulated short-term fluxes of water and carbon (Eller *et al.*, 2020; Sabot *et al.*, 2020), inter-annual variations of vegetation dynamics in seasonally dry forests (Xu *et al.*, 2016), and mortality in controlled drought experiments using simulated plant hydraulic thresholds (Venturas *et al.*, 2018). However, when applied to regional-scale prediction, mortality thresholds derived from plant hydraulics have added relatively little skill in explaining observed patterns in mortality (Venturas *et al.*, 2021). Furthermore, model biases for hydraulically enabled VMs are not systematic. For example, the VM used in Venturas *et al.* (2021) overpredicted the observed mortality at the majority of forest inventory sites in a study of western United States (US) forests, whereas De Kauwe *et al.* (2020) substantially underpredicted observed mortality in a study of south-eastern Australia forests using a different VM but similar mortality criteria.

There are some possible reasons underlying poor VM performance and differing biases for regional-scale mortality prediction.

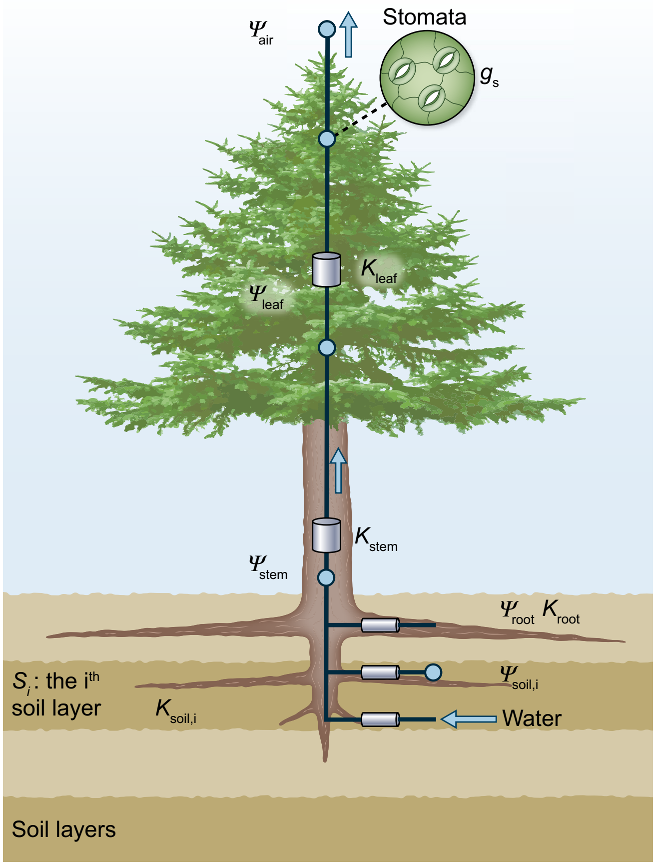

Fig. 1 Conceptual representation of basic elements in hydraulically enabled vegetation models in which water travels along a water potential (Ψ) gradient from the soil to the leaf through cohesion–tension theory, and is transpired through stomates into the atmosphere at a rate that is regulated by species-specific plant traits such as the conductance (K) of different tissues (root, stem, leaf) and stomatal conductance (g_s). S_i, i^{th} soil layer.

First, imperfect data, both for model inputs and validation, affect metrics of VM performance. For example, uncertainty in meteorological forcings and boundary conditions for soil and stand properties impact model-predicted soil moisture and plant stress (Guo *et al.*, 2006). In addition, different benchmarking datasets, such as forest inventory data and remote sensing vegetation indices, have different spatial and temporal resolutions and underlying data uncertainties (Table 1). Variations in model structure as a result of model purpose and computational considerations can result in different model predictions. For example, although both are hydraulically enabled, De Kauwe *et al.* (2020) used a big leaf model, whereas Venturas *et al.* (2021) used an individual-based stand model. Finally, the ecology, forest structure and functional diversity are important for VM prediction at the landscape scale, including direct effects such as the representation of functional diversity and community composition, and indirect effects through competition for scarce resources. Therefore, model biases may reflect multiple missing mechanisms that are required for predicting drought mortality under a unified framework at the global scale.

IV. Using mismatches in model prediction across scales, models and observations to tackle ecological and physiological blind spots

Concomitant overprediction of drought mortality in some biomes around the globe and underprediction in others by hydraulically enabled VMs provide a useful framework to develop a series of hypotheses mapping out how to improve both ecological understanding and model predictive skill of drought mortality at broad spatial scales. VM overprediction of drought mortality could occur for a number of reasons, several hypotheses that are mentioned in Venturas *et al.* (2021) and De Kauwe *et al.* (2020) that I detail further here use the US mountain west as a case study area (Fig. 2).

First, the PAW may be greater in reality compared with VM-simulated PAW, either due to subsurface water subsidies (Fig. 2a; H1), taproot access to deep soil or rock moisture (Fig. 2a; H2), or a combination of H1 and H2. Indeed, the western US is topographically complex, so stand water balance can be subsidised by lateral flow, and several studies have found that trees routinely tap bedrock water stores in the region (Goulden & Bales, 2019; Mackay *et al.*, 2020; McCormick *et al.*, 2021). Solving the subsurface problem and its role in drought-driven mortality is important and also not immediately resolvable, because ecological understanding is incomplete and the subsurface is hard to measure. Although we cannot immediately troubleshoot our lack of scientific understanding of the subsurface to advance mortality prediction, VMs are already being used to augment observations and improve the understanding of the subsurface (Table 1). For example, both Mackay *et al.* (2020) and Chitra-Tarak *et al.* (2021) used hydraulically enabled VMs to understand tree rooting strategies by parameterising the VMs with aboveground traits and estimated rooting depth using observed physiological diagnostics such as plant water potentials, growth and mortality dynamics, and isotopic data. Similarly, Tai *et al.* (2018) coupled a hydraulically enabled VM to a three-dimensional groundwater flow model and showed that the VM overpredicted mortality without accounting for subsurface flow. Therefore, observed patterns of mortality, combined with VMs as hypothesis testing tools, provide an unprecedented window into the subsurface that is fruitful for both basic science and prediction.

An incomplete understanding of within-species (intraspecific) trait variation (Fig. 2b, H4) could also explain the instances of VM overestimation of tree stress (Table 1). One example of incomplete process-based understanding that may matter for drought mortality prediction is that hydraulic traits have been shown to vary substantially within species (Anderegg, 2015), and variation is coordinated with aridity for some traits (Rosas *et al.*, 2019; Anderegg *et al.*, 2021). Yet, the extent to which intraspecific trait variation can accommodate climatic stress is not fully understood. Furthermore, within-species or within-functional type variation in climate stress is not generally represented in VMs due to incomplete understanding. However, model-predicted stress for trees parameterised with species mean traits would be higher compared with their *in situ* counterparts, if the model functional diversity was inadequate, or if the *in situ* trees had more drought-resistant traits compared with the recorded literature values. This could be for

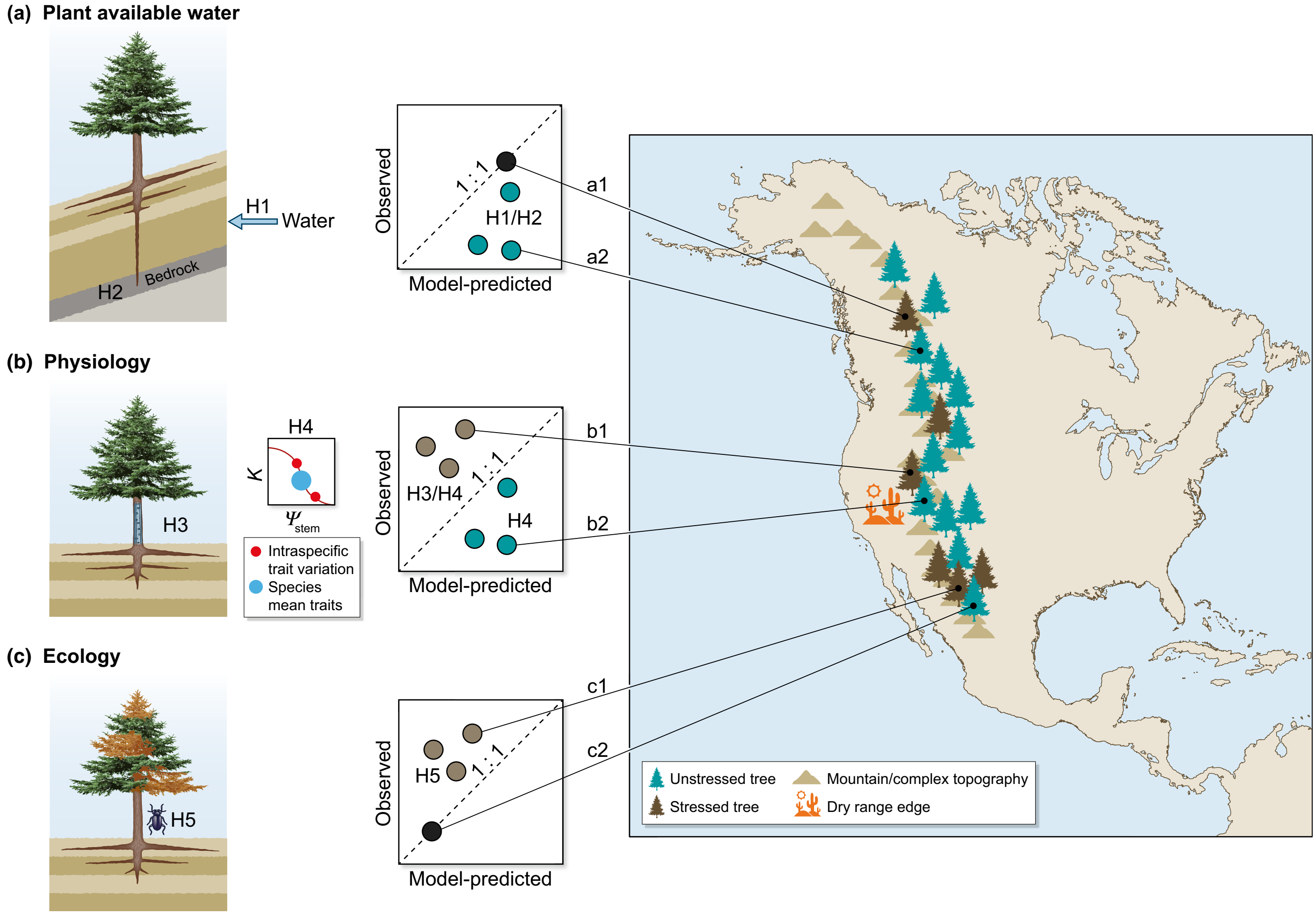

Fig. 2 A basic representation of plant hydraulics (illustrated in Fig. 1) in vegetation models (VMs) can be sufficient for mortality prediction in simple systems such as controlled drought experiments in which plant-specific traits are measured. (a–c) Illustration of several potential complicating mechanisms (using the western United States as an example system) when scaling from an individual tree to the landscape as a series of hypotheses (H1–H5). (a) Omission of processes that impact simulated plant available water such as subsurface water subsidies (H1) and/or taproot access to deep water (H2) may result in VM overprediction of tree stress and mortality relative to observations. Variations in subsurface water availability in which some trees have access to groundwater (a2) and others are exclusively rain fed (a1) in topographically complex landscapes can yield heterogeneous mortality responses not anticipated from VM processes. (b) Omission of physiological processes that impact simulated plant stress such as legacy drought damage (for example, extensive previous xylem embolism or cavitation fatigue, H3) could result in VM underprediction of mortality relative to observations (b1) and spatial biases across a region in VM performance, depending on the spatial patterns of drought frequency and severity. By contrast, omission of within-species (intraspecific) trait variation could result in either overprediction or underprediction of mortality, depending on whether the tree is more drought resistant (H4 green points) or drought vulnerable (H4, brown points) relative to the VM-parameterised traits. In this case, VM performance may differ across species' ranges, given the potential acclimation responses at dry range edges (b2, for example) not anticipated from VM-parameterised mean traits. (c) Omission of ecological processes such as pest- and pathogen-driven mortality (H5) may result in model underprediction of mortality relative to observations. Without a representation of the spatial dynamics of processes such as bark beetle outbreaks (as one prominent example of pest and pathogen-driven mortality), it is not possible to capture heterogeneous landscape mortality responses of attacked trees that ultimately die (c1) and those that survive (c2). Dashed lines represent the 1 : 1 line between hypothetical observations and model-simulated predictions. Ψ, water potential; K, conductance.

either physiological reasons corresponding with selection and/or aridity or simply because literature-reported trait measurements are sparse and not a good population sample. Although similarly not immediately resolvable, there is the substantial opportunity for VMs to aid in determining measurement locations that most effectively sample intraspecific trait variation.

Vegetation model underprediction of plant stress and mortality could occur for reasons rooted in physiology, such as lack of representation of hydraulic damage during drought (such as cavitation fatigue; Hacke *et al.*, 2001; Fig. 2b, H3) and subsequent legacy effects on the ecosystem dynamics (Anderegg *et al.*, 2015). Hypotheses, such as hydraulic damage during drought and the carbon cost of repair, could be implemented in a VM to see if the increases in model explanatory power merit widespread inclusion in VMs, according to principles of parsimony (Prentice *et al.*, 2015). Pest- or pathogen-driven mortality may also explain VM underestimation of observed mortality patterns (Fig. 2c, H5). However, data on pest and pathogen-driven mortality is sparse across many regions of the globe (Trugman *et al.*, 2021). Given the combined lack of observational data and representation of pest- and pathogen-driven mortality in the majority of VMs (McDowell *et al.*, 2020), progress needs to be made on both fronts. In VMs, initial semiempirical implementations of pest and pathogen outbreaks, perhaps targeting well known pest and pathogen 'functional types' (Dietze & Matthes, 2014), may be a tractable first step.

V. Conclusions

Vegetation models are an important hypothesis testing platform used to determine the suit of mechanisms sufficient to produce patterns observed in nature. Hydraulically enabled VMs have yet to see general success in predicting mortality at broad spatial scales, a critical aim for terrestrial carbon cycle prediction with climate change. However, progress has been made in advancing the understanding of the subsurface using VM experiments coupled with observations of aboveground diagnostics. Furthermore, there is significant potential for VMs to advance the understanding of intraspecific trait variation and pest- and pathogen-driven mortality through informing future measurements. Although the full suite of mechanisms required for regional-scale mortality prediction is still uncertain, VM experiments combined with observational validation in which new processes are systematically evaluated in idealised VMs and added to more complex VMs, using a modular structure that allows for factorial experimentation with or without the proposed new mechanism, is a promising future avenue of research. In many cases we can gain the most understanding when our models fail to meet expectations.

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ORCID

Anna T. Trugman https://orcid.org/0000-0002-7903-9711

References

Anderegg LDL, Loy X, Markham I, Elmer C, Hovendan M, HilleRisLambers J, Mayflied M. 2021. Aridity drives coordinated trait shifts but not decreased trait variance across the geographic range of eight Australian trees. *New Phytologist* **229**: 1375–1387.

Anderegg WRL. 2015. Spatial and temporal variation in plant hydraulic traits and their relevance for climate change impacts on vegetation. *New Phytologist* **205**: 1008–1014.

Anderegg WRL, Schwalm C, Biondi F, Camarero JJ, Koch G, Litvak M, Ogle K, Shaw JD, Shevliakova E, Williams AP *et al.* 2015. Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. *Science* **349**: 528–532.

Anderegg WRL, Venturas MD. 2020. Plant hydraulics play a critical role in Earth system fluxes. *New Phytologist* **226**: 1535–1538.

Bonan GB, Doney SC. 2018. Climate, ecosystems, and planetary futures: the challenge to predict life in Earth system models. *Science* **359**: eaam8328.

Bugmann H, Seidl R, Hartig F, Bohn F, Brůna J, Cailleret M, François L, Heinke J, Henrot A-J, Hickler T *et al.* 2019. Tree mortality submodels drive simulated long-term forest dynamics: assessing 15 models from the stand to global scale. *Ecosphere* **10**: e02616.

Chitra-Tarak R, Xu C, Aguilar S, Anderson-Teixeira KJ, Chambers J, Detto M, Faybishenko B, Fisher RA, Knox RG, Koven CD *et al.* 2021. Hydraulically-vulnerable trees survive on deep-water access during droughts in a tropical forest. *New Phytologist* **231**: 1798–1813.

De Kauwe MG, Medlyn BE, Ukkola AM, Mu M, Sabot MEB, Pitman AJ, Meir P, Cernusak LA, Rifai SW, Choat B *et al.* 2020. Identifying areas at risk of drought-induced tree mortality across South-Eastern Australia. *Global Change Biology* **26**: 5716–5733.

Dietze MC, Matthes JH. 2014. A general ecophysiological framework for modelling the impact of pests and pathogens on forest ecosystems. *Ecology Letters* **17**: 1418–1426.

Eller CB, Rowland L, Mencuccini M, Rosas T, Williams K, Harper A, Medlyn BE, Wagner Y, Klein T, Teodoro GS *et al.* 2020. Stomatal optimization based on xylem hydraulics (SOX) improves land surface model simulation of vegetation responses to climate. *New Phytologist* **226**: 1622–1637.

Farrior CE, Bohlman SA, Hubbell SP, Pacala SW. 2016. Dominance of the suppressed: power-law size structure in tropical forests. *Science* **351**: 155–157.

Fisher RA, Koven CD. 2020. Perspectives on the future of land surface models and the challenges of representing complex terrestrial systems. *Journal of Advances in Modeling Earth Systems* **12**: e2018MS001453.

Goulden ML, Bales RC. 2019. California forest die-off linked to multi-year deep soil drying in 2012–2015 drought. *Nature Geoscience* **12**: 632–637.

Guo Z, Dirmeyer PA, Hu Z-Z, Gao X, Zhao M. 2006. Evaluation of the Second Global Soil Wetness Project soil moisture simulations: 2. Sensitivity to external meteorological forcing. *Journal of Geophysical Research* **111**: 1–11.

Hacke UG, Stiller V, Sperry J, Pittermann J, McCulloh KA. 2001. Cavitation fatigue. Embolism and refilling cycles can weaken the cavitation resistance of xylem. *Plant Physiology* **125**: 779–786.

Love DM, Venturas MD, Sperry JS, Brooks PD, Pettit JL, Wang Y, Anderegg WRL, Tai X, Mackay DS. 2019. Dependence of aspen stands on a subsurface water subsidy: implications for climate change impacts. *Water Resources Research* **55**: 1833–1848.

Mackay DS, Savoy PR, Grossiord C, Tai X, Pleban JR, Wang DR, McDowell NG, Adams HD, Sperry JS. 2020. Conifers depend on established roots during drought: results from a coupled model of carbon allocation and hydraulics. *New Phytologist* **225**: 679–692.

McCormick EL, Dralle DN, Hahm WJ, Tune AK, Schmidt LM, Chadwick KD, Rempe DM. 2021. Widespread woody plant use of water stored in bedrock. *Nature* **597**: 225–229.

McDowell NG, Allen CD, Anderson-Teixeira K, Aukema BH, Bond-Lamberty B, Chini L, Clark JS, Dietze M, Grossiord C, Hanbury-Brown A *et al.* 2020. Pervasive shifts in forest dynamics in a changing world. *Science* **368**: eaaz9463.

Medlyn BE, De Kauwe MG, Zaehle S, Walker AP, Duursma RA, Luus K, Mishurov M, Pak B, Smith B, Wang YP *et al.* 2016. Using models to guide field experiments: *a priori* predictions for the CO_2 response of a nutrient- and water-limited native Eucalypt woodland. *Global Change Biology* **22**: 2834–2851.

Medlyn BE, Zaehle S, De Kauwe MG, Walker AP, Dietze MC, Hanson PJ, Hickler T, Jain AK, Luo Y, Parton W *et al.* 2015. Using ecosystem experiments to improve vegetation models. *Nature Climate Change* **5**: 528–534.

Mencuccini M, Manzoni S, Christoffersen BO. 2019. Modelling water fluxes in plants: from tissues to biosphere and back. *New Phytologist* **222**: 1207–1222.

Pacala SW, Canham CD, Saponara J, Silander JA, Kobe RK, Ribbens E. 1996. Forest models defined by field measurements: estimation, error analysis and dynmaics. *Ecological Monographs* **66**: 1–43.

Prentice IC, Liang X, Medlyn BE, Wang YP. 2015. Reliable, robust and realistic: the three R's of next-generation land-surface modelling. *Atmospheric Chemistry and Physics* **15**: 5987–6005.

Raffa K, Aukema BH, Bentz B, Carroll AL, Hicke JA, Turner MG, Romme WH. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. *BioScience* **58**: 501–517.

Rosas T, Mencuccini M, Barba J, Cochard H, Saura-Mas S, Martínez-Vilalta J. 2019. Adjustments and coordination of hydraulic, leaf and stem traits along a water availability gradient. *New Phytologist* **223**: 632–646.

Rowland L, Martínez-Vilalta J, Mencuccini M. 2021. Hard times for high expectations from hydraulics: predicting drought-induced forest mortality at landscape scales remains a challenge. *New Phytologist* **230**: 1685–1687.

Sabot MEB, De Kauwe MG, Pitman AJ, Medlyn BE, Verhoef A, Ukkola AM, Abramowitz G. 2020. Plant profit maximization improves predictions of European forest responses to drought. *New Phytologist* **226**: 1638–1655.

Sitch S, Huntingford C, Gedney N, Levy PE, Lomas M, Piao SL, Betts R, Ciais P, Cox P, Friedlingstein P *et al.* 2008. Evaluation of the terrestrial carbon cycle, future plant geography and climate-carbon cycle feedbacks using five Dynamic Global Vegetation Models (DGVMs). *Global Change Biology* **14**: 2015–2039.

Sperry JS, Venturas MD, Anderegg WRL, Mencuccini M, Mackay DS, Wang Y, Love DM. 2017. Predicting stomatal responses to the environment from the optimization of photosynthetic gain and hydraulic cost. *Plant, Cell & Environment* **40**: 816–830.

Stephenson NL, Das AJ, Ampersee NJ, Bulaon BM, Yee JL. 2019. Which trees die during drought? The key role of insect host-tree selection. *Journal of Ecology* **107**: 2383–2401.

Tai X, Mackay DS, Sperry JS, Brooks P, Anderegg WRL, Flanagan LB, Rood SB, Hopkinson C. 2018. Distributed plant hydraulic and hydrological modeling to understand the susceptibility of riparian woodland trees to drought-induced mortality. *Water Resources Research* **54**: 4901–4915.

Tang J, Zhuang Q. 2008. Equifinality in parameterization of process-based biogeochemistry models: a significant uncertainty source to the estimation of regional carbon dynamics. *Journal of Geophysical Research: Biogeosciences* **113**: 1–13.

Trugman AT, Anderegg LDL, Anderegg WRL, Das AJ, Stephenson NL. 2021. Why is tree drought mortality so hard to predict? *Trends in Ecology & Evolution* **36**: 520–532.

Trugman AT, Detto M, Bartlett MK, Medvigy D, Anderegg WRL, Schwalm C, Schaffer B, Pacala SW. 2018a. Tree carbon allocation explains forest drought-kill and recovery patterns. *Ecology Letters* **21**: 1552–1560.

Trugman AT, Medvigy D, Mankin JS, Anderegg WRL. 2018b. Soil moisture stress as a major driver of carbon cycle uncertainty. *Geophysical Research Letters* **45**: 6495–6503.

Venturas MD, Sperry JS, Love DM, Frehner EH, Allred MG, Wang Y, Anderegg WRL. 2018. A stomatal control model based on optimization of carbon gain versus hydraulic risk predicts aspen sapling responses to drought. *New Phytologist* **220**: 836–850.

Venturas MD, Todd HN, Trugman AT, Anderegg WRL. 2021. Understanding and predicting forest mortality in the western United States using long-term forest inventory data and modeled hydraulic damage. *New Phytologist* **230**: 1896–1910.

Wang Y, Sperry JS, Anderegg WRL, Venturas MD, Trugman AT. 2020. A theoretical and empirical assessment of stomatal optimization modeling. *New Phytologist* **227**: 311–325.

Xu X, Medvigy D, Powers JS, Becknell JM, Guan K. 2016. Diversity in plant hydraulic traits explains seasonal and inter-annual variations of vegetation dynamics in seasonally dry tropical forests. *New Phytologist* **212**: 80–95.

Xu X, Trugman AT. 2021. Trait-based modeling of terrestrial ecosystems: advances and challenges under global change. *Current Climate Change Reports* **7**: e2020JG006228.