

Interactive comment on “Challenges and opportunities in modelling savanna ecosystems” by Rhys Whitley et al.

Anonymous Referee #3

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This paper presents a helpful and informative review of some of the major challenges in quantifying and predicting structural and functional dynamics of savanna ecosystems with numerical models. The paper focuses on terrestrial biosphere models that mainly aim to predict water, energy, and carbon fluxes and balances as they interact with the atmosphere. This is a worthwhile focus but the title should probably be modified to reflect this specific focus. The manuscript has a lot of valuable content, and offers constructive advice regarding ways to improve TBM performance for savanna ecosystems. However the paper is less comprehensive than, I'd argue, it should be given its aims. Also the paper omits some important theory and themes in savanna ecology, and misrepresents some of the broad geographic context of global savannas. This review focuses on those elements and recommends revisions in those directions.

0) Regarding Root Water Uptake: This is a worthwhile focus for improvements of TBMs

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but the authors have a rather specific read on the relevant literature. A few key citations I'd recommend are below, offering expanded perspectives on how to proceed with improving root water uptake in TBMs. Key considerations go beyond just prescribing rooting depth but also: dynamic uptake in response to soil water availability in the vertical profile, adaptive adjustments of the root distributions in response to water availability over seasonal and multi-year timescales, hydraulic redistribution along pressure gradients and via roots, soil water limitation function limiting productivity and evapotranspiration and associated water demand and water potential along the root to leaf and atmosphere continuum. I, too, caution against weighting root water uptake by fine root distribution because many plants are able to sustain water uptake and transpiration from deep taproots that access the saturated zone or deep unsaturated zone water sources even when fine roots (all concentrated near the surface) are in very dry soil layers. Furthermore, plant capacitance (storage) is important for accurately representing plant water potential, especially when water supply is limited or when root-to-leaf transport resistances inhibit water delivery to the site of transpiration at the leaf. Reinder A. Feddes, Holger Hoff, Michael Bruen, Todd Dawson, Patricia de Rosnay, Paul Dirmeyer, Robert B. Jackson, Pavel Kabat, Axel Kleidon, Allan Lilly, and Andrew J. Pitman, Modeling Root Water Uptake in Hydrological and Climate Models Bulletin of the American Meteorological Society 2001 82:12, 2797-2809. Lai, C.-T. & Katul, G. (2000) The dynamic role of root-water uptake in coupling potential to actual transpiration. Advances in Water Resources, 23, 427-439. Steudle, E., 2000. Water uptake by plant roots: an integration of views. Plant and Soil, 226(1), pp.45-56. Vrugt, J. A., M. T. vanWijk, J. W. Hopmans, and J. Šimunek (2001), One-, two-, and three-dimensional root water uptake functions for transient modeling, Water Resour. Res., 37(10), 2457–2470, doi:10.1029/2000WR000027.

1) A host of other processes of importance and interest in savannas are missed. For example, pulse response processes, stand-scale vegetation composition, plant-scale competitive interactions, stand-scale vegetation structure, landscape patterning of vegetation, nutrient cycling and interactions with herbivores, and more are all given lit-

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tle if any attention. Arguably many of those processes are important for representing savanna-atmosphere interactions, and for assessing savanna responses to global change factors. Given that this paper is intended to be a review of key processes that need to be considered to accurately model savanna ecological responses to global change factors, I would encourage additional discussion of these missed processes and their implications and importance for the stated aims.

2) Savanna ecologists would be underwhelmed by the three dynamic processes that are highlighted: phenology, root water uptake, and fire, given that these have long been the focus of their work going back many decades (e.g. Walter 1973). For example, the seminal work by Brian Walker (1981) is surprisingly absent from the present review even though this was foundational work identifying the importance of root zone separation and differential uptake zones for grass/herbaceous and woody PFTs in the savanna matrix. This was nicely tested in the Scholes and Walker (1993) book which is also missed. It is surprising that competitive interactions and differential resource access are not noted here, nor differential response of PFTs and species to single and multifactor drivers of CO₂, drought, warming, and increasing VPD. While I agree that the three features highlighted in the present paper are essential and yet poorly represented (if at all) in TBMs, such models will still not be up to the task of predicting responses to global changes without representation of a host of other factors. Walter H (1973) *Vegetation of the earth in relation to climate and the eco-physiological conditions*. New York: Springer Scholes, R. J., and B. H. Walker (1993), *An African Savanna: Synthesis of the Nylsvley Study*, Cambridge Univ. Press, New York. Walker, B. H., D. Ludwig, C. S. Holling, and R. M. Peterman (1981), Stability of semi-arid savanna grazing systems, *J. Ecol.*, 69, 473– 498.

3) Grazing and browsing are of central importance in many of the world's savannas, strongly influencing vegetation cover, loss of productivity and biomass, species composition, and affecting site fertility but this driver is hardly mentioned, receiving just one or two sentences. A bit more on this subject would seem warranted for such a review.

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4) Corresponding to the above, a nod to the alternate stable states literature is missing here, including Walker '81, Noy-Meir 1975, and others mentioned below. Noy-Meir I (1975) Stability of grazing systems: an application of predator prey graphs. *Journal of Ecology*, 63, 459–481. Jeltsch F, Weber GE, Grimm V (2000) Ecological buffering mechanisms in savannas: a unifying theory of long-term tree-grass coexistence. *Plant Ecology*, 161, 161–171. Scheffer M, Carpenter SR (2003) Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends in Ecology & Evolution*, 18, 648–656. van de Koppel J, Rietkerk M, Weissing FJ (1997) Catastrophic vegetation shifts and soil degradation in terrestrial grazing systems. *Trends in Ecology & Evolution*, 12, 352–356. Westoby M, Walker B, Noy-Meir I (1989) Range management on the basis of a model which does not seek to establish equilibrium. *Journal of Arid Environments*, 17, 235–239. Williams, C.A. & Albertson, J.D. (2006) Dynamical effects of the statistical structure of annual rainfall on dryland vegetation. *Global Change Biology*, 12, 1-16.

5) Discussion of the global context and diversity of savanna attributes and strategies is lacking and in some ways misleading. Section 2.1, particularly Line 169+: The language here misrepresents the growth and longevity strategies of woody plants in Africa. Many of the woody species in at least southern Africa do indeed have deep roots but groundwater is deep (probably deeper than in much of Australia) so there is less potential to rely on near surface (<10 m) water sources. The Archibald and Scholes '97 paper does not mention roots once, and says nothing about strategies of water access. The Higgins '11 paper also offers little on root water uptake. Both of those papers do indeed discuss and quantitatively document phenological dynamics, but neither indicates that the full woody component of southern African savannas is deciduous (indeed *Acacia* sp. often retain leaves consistently through the dry season). However both represent only southern African ecosystems at best (really, Kruger Park). Yet this statement is as grandiose as generalizing from these studies to all African and South American savannas! That's stretching it a bit, no? A much broader literature must be invoked if the authors truly want to discuss geographic patterns of root water uptake, and diversity in savanna traits and properties. Furthermore, this must consider not just phenology

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but also water availability in the unsaturated and saturated zones, and not confuse mesic and arid savanna types. The present interpretation seems to conflate shallow groundwater availability or its absence with a difference in plant strategy. However, woody species of savannas around the world “favour a long-term strategy of conservative growth that is insured against an unpredictable climate”, not just those in Australia. To include more on the global biogeography of savannas relevant to a modeling context I'd recommend some additional reading (and citation of) works in: Hill, Michael J. and Hanan, Niall P. eds (2011). *Ecosystem Function in Savannas: Measurement and Modeling at Landscape to Global Scales*. (CRC Press, Boca Raton, Florida) 559 pp.

6) The Pulse-Reserve paradigm in dryland ecology is noticeably absent from this review despite the well-known importance of rainfall pulses in organizing complex ecological and biophysical dynamics in water-limited environments. Many plant and ecosystem phenological dynamics are organized around rainfall pulses, including leaf-out and senescence, up- and down-regulation of productivity, respiration and decomposition bursts, reproduction and establishment events, and so forth. “Pulse” is not mentioned once in the current review. Chesson P, Gebauer RLE, Schwinning S et al. (2004) Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. *Oecologia*, 141, 236–253. Huxman, T.E., Snyder, K.A., Tissue, D., Lefler, A.J., Ogle, K., Pockman, W.T., Sandquist, D.R., Potts, D.L. & Schwinning, S. (2004) Precipitation pulses and carbon fluxes in semiarid and arid ecosystems. *Oecologia*, 141, 254-268. Jenerette, G.D., Scott, R.L. & Huxman, T.E. (2008) Whole ecosystem metabolic pulses following precipitation events. *Functional Ecology*, 22, 924-930. Noy-Meir, I. (1973), Desert ecosystems: Environment and producers, *Annu. Rev. Ecol. Syst.*, 4, 25– 44. Ogle, K. & Reynolds, J.F. (2004) Plant responses to precipitation in desert ecosystems: integrating functional types, pulses, thresholds, and delays. *Oecologia*, 141, 282-294. Williams, C.A. & Albertson, J.D. (2004) Soil moisture controls on canopy-scale water and carbon fluxes in an African savanna. *Water Resources Research*, 40, 1-14. Williams, C.A., Hanan, N.P., Scholes, R.J. & Kutsch, W. (2009) Complexity in water and carbon dioxide fluxes following rain pulses in an African sa-

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vanna. *Oecologia*,

7) Section 3.1: Possibly also mention potential for additional measurements to inform root water uptake dynamics (maybe around L590): -experimental use of isotopes to trace root water uptake dynamics (see work of Todd Dawson's lab for example). -standard field-measured sapflow and leaf gas exchange are surprisingly not mentioned but can be particularly useful when coupled with detailed soil moisture profile measurements, where changes over time directly indicate the effects of water uptake. -weighing lysimeter studies, while very intensive, have also been used to detect whole plant uptake. -groundwater wells would also be enormously helpful and are so often missed in ecological and even hydrological studies in savannas (and other ecosystems), yet are critical for characterizing the availability and dynamics of deep water sources. -groundwater maps, where available, are low hanging fruit for incorporation into spatial applications of TBMs. -another key thing that is missing is detailed mapping of C3 and C4 vegetation types (grasses/herbaceous), and their separate phenologies. -remotely sensed surface temperature is another valuable constraint on ecosystem water status (I think Damian Bonal was working on this and published on it).

8) Conclusions go uncomfortably beyond what is supported in this paper and stray from the paper's clear focus on how to improve TBM performance for savannas. For example: “Projected higher temperatures and rainfall variability, potentially promoting 645 more frequent fires, could favour C4 grasses in mesic savanna, while drier conditions are 646 expected to increase tree mortality in semi-arid savanna. Conversely, increases to 647 atmospheric CO₂ are expected to favour C3 trees, reflecting woody encroachment that is 648 already observed in many savannas globally (Donohue et al., 2009). Climate change 649 therefore has the potential to alter the carbon balance, which may have major feedbacks 650 on global climate and biogeochemical cycling.”

9) Again, it is recommended that the authors expand the scope of highlights to also emphasize ecosystem structural and compositional dynamics that are of central importance to TBM processes: particularly differential resource acquisition (primarily water)

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and competitive interactions. E.g. around L694... model and data efforts should also target those attributes of savannas. Perhaps the authors roll all of that into “phenology” but I’d argue that this is a mistake, where phenology is only one component of vegetation dynamics. The underlying competitive interactions, mortality and growth dynamics, and how these shift in response to a suite of climate, atmospheric compositional, soil fertility, land use and other global change factors could receive more attention in this review.

Some Details:

Why is root-water hyphenated? Do you mean ground-water or soil-water? Probably just drop the hyphen throughout.

Line 69+: not just “environmental conditions” but also biophysical and ecological conditions... that is, the ecosystem properties are themselves changing and this must be represented.

Line 96: “confronting task” reword, unclear

L100: “underperformed for savanna ecosystems” is too vague... what, specifically, lacks accuracy? “under” relative to what, other PFT or biome types, compared to data?

L105: “physical [and biological]”... most of these are not physical parameters.

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