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Linking resource- and disturbance-based models to explain tree–grass coexistence in savannas

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Summary

Savannas cover a significant fraction of the Earth's land surface. In these ecosystems, C_3 trees and C_4 grasses coexist persistently, but the mechanisms explaining coexistence remain subject to debate. Different quantitative models have been proposed to explain coexistence, but these models make widely contrasting assumptions about which mechanisms are responsible for savanna persistence. Here, we show that no single existing model fully captures all key elements required to explain tree–grass coexistence across savanna rainfall gradients, but many models make important contributions. We show that recent empirical work allows us to combine many existing elements with new ideas to arrive at a synthesis that combines elements of two dominant frameworks: Walter's two-layer model and demographic bottlenecks. We propose that functional rooting separation is necessary for coexistence and is the crux of the coexistence problem. It is both well-supported empirically and necessary for tree persistence, given the comprehensive grass superiority for soil moisture acquisition. We argue that eventual tree dominance through shading is precluded by ecohydrological constraints in dry savannas and by fire and herbivores in wet savannas. Strong asymmetric grass–tree competition for soil moisture limits tree growth, exposing trees to persistent demographic bottlenecks.

I. Introduction

Tree cover is a fundamental structural property of many ecosystems and plays an important role in driving ecosystem functions (Hoffmann *et al*., 2002; Jackson *et al*., 2002; Brudvig & Asbjornsen, 2009). Despite this overriding importance, a comprehensive model that explains global tree cover patterns remains elusive. In savannas and woodlands, which are poised in the continuum between forests (which are completely tree-dominated) and grasslands (which lack trees), an additional – and related – challenge is posed by the issue of tree–grass coexistence, a challenge referred to as the ‘savanna problem’ (Sarmiento, 1984; Higgins *et al*., 2000; D’Odorico *et al*., 2006; Mills *et al*., 2006; Kulmatiski & Beard, 2022). On the face of it, this challenge may appear no different from any other coexistence problem, that is the ‘paradox of the plankton’ (Hutchinson, 1961). After all, explaining how multiple species coexist when competing for a limited number of resources is one of the central challenges of ecology, and many different mechanisms have been proposed to meet this challenge (Chesson, 2000). What makes the savanna problem intriguing is the juxtaposition of two very different plant growth forms: trees and grasses. Given that some nonzero amount of tree cover is present in most tropical grassy ecosystems (Parr *et al*., 2014), what prevents trees from forming a closed canopy, thereby shading and excluding grasses?

In a comprehensive review, nearly two decades old, Sankaran *et al.* (2004) outlined the dominant explanations for tree–grass coexistence in savannas. They broadly divided these explanations into competition-based and demographic categories (Sankaran *et al*., 2004). Competition-based explanations focus on resource partitioning (specifically, soil moisture) and/or trade-offs between competitive ability and demographic rates in trees and grasses. Here, we label these models as ‘resource’ models. Demographic explanations minimize the role of resources and competition and focus more on disturbance and environmental variation. While the former often assume that coexistence represents a stable equilibrium, the latter treat savannas as ‘disequilibrium’ systems that will tend toward a grassland or forest state in the absence of stochastic environmental variation or disturbance (Sankaran *et al*., 2004). Given the dominant role of fire in these models, we label them ‘disturbance’ models.

Sankaran *et al.* (2004) reviewed the evidence for several quantitative and conceptual models within each of these broad categories and concluded that no single approach was free of limitations. For example, they suggested that (based on the evidence available at the time) partitioning of soil moisture between trees and grasses was only likely to hold under a limited set of environmental conditions (Sankaran *et al*., 2004). Conversely, it was unclear why trees would fail to eventually dominate grasses in savannas with low rates of disturbance or herbivory (Sankaran *et al*., 2004). A key critique raised by Sankaran *et al.* (2004) was the general lack of recognition in competition-based models that tree–grass interactions differ in strength across tree life stages (Scholes & Archer, 1997). Demographic models, for their part, often fail to incorporate the effects of competition, even though competitive effects have been well documented (Sankaran *et al*., 2004; Riginos, 2009).

Sankaran *et al.* (2004) proposed a framework that integrates the two approaches, recognizing the importance of both shifting competitive interactions between trees and grasses across tree life stages and explicitly incorporating demographic bottlenecks at multiple stages. The framework was intended as a conceptual tool for developing new synthetic models. A key challenge that remains is resolving the disagreement about whether trees or grasses are the dominant life form. Competition-based models tend to treat grasses as competitively dominant (e.g. Walker *et al*., 1981), while demographic models implicitly assume that trees will outcompete grasses once established, except when limited by disturbance or herbivory (e.g. Higgins *et al*., 2000). Settling this issue is essential for resolving the problem of coexistence.

Following the review by Sankaran *et al.* (2004, 2005) proposed that rainfall plays a dominant role in setting the upper boundary of tree cover. Below a certain mean annual precipitation (MAP) threshold (*c.* 650 mm yr^{-1}), tree canopies do not close, allowing grasses to coexist with trees in a stable equilibrium; that is, MAP imposes an upper boundary (the ‘Sankaran curve’) for tree cover below the threshold. Above this threshold, however, tree canopy closure is possible, but fire and herbivory can prevent trees from excluding grasses (Sankaran *et al*., 2005). In the climatically determined savannas below 650 mm yr^{-1}, it was assumed that water limitation prevents tree canopy closure. This raises a new set of questions: are trees competitively dominant to grasses under all conditions, even when water is limiting? What is the actual mechanism preventing trees from excluding grasses? Does niche partitioning occur, or is tree biomass independent of tree–grass interactions, implying self-limitation by trees? What is the relative importance of competition for water vs light? Are demographic bottlenecks needed at all as a key ingredient allowing tree–grass coexistence in dry savannas?

In this review, we propose that these questions have not yet been convincingly answered. We systematically revisit and review published models of tree–grass coexistence, both pre-dating and following Sankaran *et al.* (2004), and reassess the empirical evidence for the key assumptions embedded in those models, leading to a synthetic modeling framework for tree–grass coexistence. We argue that grasses consistently outperform trees in terms of soil moisture acquisition and that niche partitioning is therefore necessary to allow trees to persist under water limitation. We propose that the tree advantage in light acquisition becomes increasingly important as soil moisture increases, but that ecohydrological limitations on leaf area (and therefore shading) prevent grass competitive exclusion *via* light limitation under dry conditions. Finally, we argue that despite the importance of niche partitioning, grasses compete intensely with trees, limiting their growth and exposing them to pervasive bottlenecks imposed by fire and herbivores.

II. Tree–grass coexistence models

1. Foundational models

We identify and review eight different mathematical/numerical models that generate tree–grass coexistence (Table 1). The list is not

Table 1 Summary of key tree–grass coexistence models outlining the dominant coexistence mechanisms, key resources, drivers considered, treatments of rooting depth and demographic processes, and key limitations (Y/N, process present/absent, respectively).

Category	Model	Dominant mechanism(s)	Key contribution(s)	Dominant FT	Competition Water	Competition Light	Rooting depth	Demography	Fire/ Herb.	Key limitation(s)
Resource-based	Walker *et al*. (1981)	Niche separation	Recognition of importance of rooting differences	Grasses	Y	N	Y	N	N[†]	Assumes exclusive use layer for trees, no aboveground competition
	Van Wijk & Rodriguez-Iturbe (2002)	Trade-offs between: (1) rainfall frequency and stress/survival; and (2) colonization ability and stress	Acknowledgment of key role of stochasticity	Neither	Y	N	N[‡]	N	N	No explicit interaction between trees and grasses; assumes higher settlement probability for trees under low stress; assumes priority effects are key
	Scheiter & Higgins (2007)		Identification of aboveground competition as an important factor; recognition that herbivory and fire mainly impact shoots	Trees aboveground, neither belowground	Y	Y	N	N	N	Competitive effects of roots are decoupled from shoots, and lack environmental context; no ecohydrological trait differences between trees and grasses
	Xu *et al*. (2015)	Trade-off between water use efficiency and drought tolerance	Explicitly models competition for water and shading effects	Grasses	Y	Y	N[‡]	N	N	Assumes that trees have a competitive advantage under dry conditions
	Donzelli *et al*. (2013)	Competition for both water and N	Departs from the common assumption that water is the only limiting resource	Trees (for N) and grasses (for water)	N	Y	N	N	N	Root characteristics that make grasses superior competitors for water are likely to play a key role in N acquisition
Disturbance-based	Higgins *et al*. (2000)	Variability, storage effects, disturbance	Highlights the importance of variability	Trees	N	N	N	Y	Y	Does not explicitly incorporate competitive interactions for soil moisture between trees and grasses
	D'Odorico *et al*. (2006)	Stochastic fire regimes	Emphasizes the importance of stochastic processes	Trees	N	N	N	N	Y	Does not explicitly incorporate competitive interactions for soil moisture between trees and grasses
Hybrid	Jeltsch *et al*. (1996)	Fire and grazing	Explicitly integrates competition for soil moisture and disturbance into single framework	Grasses	Y	N	Y	Y	Y	Treatment of soil moisture is overly simplified

[†] A version of the model considers fire and herbivory, but these elements are not essential for coexistence to occur in this model.
[‡] Rooting depth is considered but does not play a role in facilitating coexistence.

exhaustive, but we consider these models as a 'foundational' quantitative set because they capture the range of mechanisms that have been proposed to explain coexistence. The ultimate foundational model is Walter's two-layer model (Walter, 1971), which proposed that niche partitioning along a soil depth axis allows trees and grasses to coexist. Grasses are assumed to outcompete trees for soil moisture in topsoil layers, but trees persist in the system by having exclusive access to soil moisture in subsoil layers (Walter, 1971). Walker *et al.* (1981) and others (Walker & Noy-Meir, 1982; Eagleson & Segarra, 1985) operationalized this idea through mean-field (i.e. not spatially explicit) systems of differential equations, both with and without other factors such as fire and herbivory. Crucially, they showed that a stable tree–grass equilibrium could occur in the absence of herbivores and disturbance.

The two-layer model gradually fell out of favor as a general explanation for tree–grass coexistence (Sankaran *et al.*, 2004). Objections have largely focused on a lack of generalized empirical support for rooting separation by soil depth between trees and grasses (Sankaran *et al.*, 2004). A key objection to the model is the observation that the rooting profiles of trees and grasses often exhibit substantial overlap (Scholes & Walker, 1993; Higgins *et al.*, 2000; Sankaran *et al.*, 2004; February & Higgins, 2010), with little evidence for a zone of exclusive use for trees (Scholes & Walker, 1993; February & Higgins, 2010). The relegation of the two-layer model gave rise to a search for alternative coexistence models along two parallel tracks: (1) resource-based models that did not rely on rooting separation and (2) disturbance-based models that de-emphasized the importance of resources.

A particularly influential work in the debate about tree–grass coexistence was the synthesis based on the work at the Nylsvley site in South Africa by Scholes & Walker (1993), and the later review by Scholes & Archer (1997). The Nylsvley work has informed assumptions and provided parameter estimates for a wide range of savanna models (e.g. Rodriguez-Iturbe *et al.*, 1999; Van Wijk & Rodriguez-Iturbe, 2002; Xu *et al.*, 2015). Notably, Scholes and Walker found little evidence for rooting separation between trees and grasses at Nylsvley and argued for a 'disequilibrium' model of savannas, in which disturbance and herbivory play dominant roles, preventing mature trees from displacing grasses (Scholes & Walker, 1993).

2. Alternatives to niche partitioning: other resource-based models

The assumption of rooting overlap between trees and grasses was incorporated into several subsequent 'resource-based' models. Van Wijk & Rodriguez-Iturbe (2002) developed a cellular automata model of tree–grass dynamics that generated tree–grass coexistence in the absence of belowground niche partitioning. The model is driven by stochastic rainfall, which drives soil moisture dynamics and plant water access. The model assumes a greater sensitivity to moisture stress and higher mortality for trees relative to grasses under drought conditions, but trees are assumed to have a higher colonization potential than grasses under wet conditions. This persistence-colonization trade-off generates coexistence in a spatially explicit framework. There are no explicit competitive interactions for the key limiting resource (water), and site occupancy is essentially treated as a priority effect. A lack of competition for resources is potentially problematic because unlike other plant species coexistence problems, almost complete spatial overlap (and therefore competition) is a defining feature of tree–grass interactions in savannas. The assumption that trees have a higher colonization potential under wet conditions (Van Wijk & Rodriguez-Iturbe, 2002) also lacks empirical support. Grass and tree canopies in savannas are continuous and discontinuous, respectively, suggesting that grasses readily colonize vegetation gaps before trees do.

An alternative trade-off in the absence of belowground niche partitioning was proposed by Xu *et al.* (2015). In their model, grasses are assumed to maintain higher transpiration rates per unit of plant biomass and translate transpired water into biomass more efficiently than trees because they allocate a higher relative fraction of their assimilated carbon to leaf tissue. Despite this, trees outperform grasses under dry conditions (Xu *et al.*, 2015), during which their rate of decline is assumed to be lower. Overall, the model assumes a trade-off in growth across a soil moisture gradient, with grasses growing faster under wet conditions but losing biomass at a faster rate than trees growing under dry conditions (Xu *et al.*, 2015). When driven by a stochastic (i.e. realistic) rainfall regime, the alternation of wet and dry conditions generates coexistence. A limitation of the model is that the low rate of decline for tree biomass under dry conditions is based on wood decay rates (Xu *et al.*, 2015). This is problematic because drought-stressed trees are fundamentally different from slowly decaying wood, because they can experience sudden, large-scale biomass losses (Fensham *et al.*, 2009; Case *et al.*, 2019). Recent work has found that savanna grasses can recover from extreme drought within a single growing season (Donaldson *et al.*, 2020; Wilcox *et al.*, 2020), so the assumption that trees outperform grasses in terms of biomass maintenance under dry conditions lacks support. Second, a key assumption of the model's stochastic rainfall generator is that the rainfall intensity (i.e. daily total rainfall) declines as a function of mean annual precipitation (Xu *et al.*, 2015), but this assumption is not generally supported across the African savanna biome (Supporting Information Fig. S1). The relationship between rainfall intensity and mean annual precipitation is messy, but it is certainly not negative (Fig. S1). This assumption leads the model to predict that grass cover should increase with rainfall intensity at the expense of trees (Xu *et al.*, 2015) when empirical data for savannas occurring on sandy soils (the system for which the model was designed) support the opposite pattern (Case & Staver, 2018).

Unlike the models described so far, which all assume a single limiting resource (soil moisture), Scheiter & Higgins (2007) partitioned trees and grasses into aboveground and belowground portions, with shoots competing for light and roots competing for soil moisture and/or nutrients. There is a compelling rationale for this division: herbivores and disturbance tend to have a far greater impact on aboveground biomass than on roots, disrupting root : shoot ratios, with consequences for plant growth rates and survival (Higgins *et al.*, 2000; Holdo, 2006; Grady & Hoffmann, 2012). In addition, it can be argued that a general model of tree–grass dynamics should account for conditions where light is limiting. Savannas, particularly tropical savannas, are generally considered to be high-light environments (Hoffmann & Franco, 2003; Ratnam *et al.*, 2011), and therefore, models either tend to focus on soil moisture as the key limiting resource (Yu & D'Odorico, 2015) or subsume the role of light into a single-resource category that could also include water and nutrients (D'Odorico *et al.*, 2006). Scheiter & Higgins (2007) incorporated the effects of fire and herbivory into their model, but we consider the model as a 'resource model' because, like the Walker *et al.* (1981) model, it predicts tree–grass coexistence in the absence of fire and herbivores. While incorporating flexibility in root : shoot ratios (and the effects of these varying ratios on growth), this model lacks flexibility in other potentially more critical ways. Unlike Xu *et al.* (2015), Scheiter & Higgins (2007) do not model resources explicitly, and competition coefficients are therefore assumed to be fixed across resource availability gradients. This precludes incorporating the trade-offs in tree vs grass performance across moisture gradients that are key features of the Xu *et al.* (2015) and Van Wijk & Rodriguez-Iturbe (2002) models. Competitive effects of grasses on trees for soil moisture are also assumed to be driven by grass root biomass (Scheiter & Higgins, 2007) and therefore do not account for variation in transpirational demand imposed by grass shoots (and *vice versa*). While we recognize that these simplifying assumptions are reasonable in a heuristic model that does not specify the nature of the belowground resource, explicitly accounting for soil moisture and key features of the transpirational pipeline is essential for understanding tree–grass coexistence.

A different type of two-resource model was proposed by Donzelli *et al.* (2013), who used resource ratio theory to mathematically prove that trees and grasses could theoretically coexist in a system where both water and nitrogen (N) are limiting. Following Tilman (1982), a necessary (but not sufficient) condition for two species to coexist when competing for two resources is that they exhibit a trade-off in R^* values for the two resources (i.e. trees must have a lower R^* value for N if grasses are more drought tolerant or *vice versa*). With their dense root networks, grasses can more effectively reduce soil moisture to lower values than trees, so for a resource ratio framework involving competition for water and N to be a plausible explanation for tree–grass coexistence, trees would have to have a lower R^* value for soil N than grasses. The same traits that allow grasses to efficiently exploit the rooting zone for water, however, should allow them to reduce soil N to low levels (Tilman & Wedin, 1991). C_4 grasses also tend to have a higher N-use efficiency than C_3 plants such as trees (Taylor *et al.*, 2010). Furthermore, an experimental comparison of belowground competitive effects of grasses on N-fixing and nonfixing tree species showed that both tree functional types experienced > 90% reductions in seedling biomass as a result of grass competition (Cramer *et al.*, 2012). This reinforces the strong competitive effect of grasses for belowground resources and suggests that the effect is independent of tree N status.

3. Disturbance-based models

Disturbance-based models provide an alternative means of circumventing the rooting-depth problem. Unlike previous (mostly resource-based) models, which tended to treat the tree–grass problem from an 'aggregated biomass' perspective, the Higgins *et al.* (2000) model recognized key differences between the two functional types, particularly the importance of accounting for the punctuated nature of tree demographic transitions and variation in demographic rates with tree size. The model assumes that trees are ultimately dominant to grasses and that, in the absence of environmental variability, savannas would eventually become forests. Tree dominance is impeded by low seedling establishment rates and fire, which limit recruitment into mature size classes. Both of these processes are variable and stochastic. Even though establishment rates are low, reproductive potential persists in the system because seed-producing adults are long-lived (Higgins *et al.*, 2000). Saplings and smaller adult trees are top-killed by fire but tend to persist *via* resprouting. Both of these aspects, as well as soil seed banks (Witkowski & Garner, 2000), contribute to a storage effect, a key feature of savannas (Higgins *et al.*, 2000). A strength of this model is its strong reliance on empirical relationships parameterized with field data and its recognition of a fundamental aspect of savanna tree ecology: establishment of new individuals is rare, but once established, trees experience very low mortality rates.

Despite this realistic treatment of tree demography, however, the competitive interactions between trees and grass lack a clear mechanistic basis. Once established, trees are assumed to be competitively dominant to grasses, but tree effects on grass production are undefined and appear to be independent of soil moisture availability. Grasses and soil moisture are assumed to have no effect on tree growth but affect tree establishment (Higgins *et al.*, 2000). Others have suggested that the competitive dominance shifts from grasses to trees as the latter transition from seedlings to adulthood (Scholes & Archer, 1997), but in the absence of specific mechanisms, and particularly in the absence of rooting depth niche partitioning, it is not clear why and how this should occur.

The Higgins *et al.* (2000) model, like the Van Wijk & Rodriguez-Iturbe (2002) and Xu *et al.* (2015) models, made environmental stochasticity a central factor in our understanding of savanna dynamics. Another example of this was provided by D'Odorico *et al.* (2006), who developed a minimalist tree–grass–fire model to show that fire alone can generate coexistence. A challenge for this model is that it makes assumptions about tree–grass interactions that tend to oversimplify the system. As is the case in Higgins *et al.* (2000) model, trees are assumed to be dominant to grasses, and a tree-dominated system emerges in the absence of disturbance, but tree–grass interactions are not explicitly incorporated into the model (D'Odorico *et al.*, 2006).

4. Hybrid models and derived models

An early model that challenged the two-layer paradigm was the model proposed by Jeltsch *et al.* (1996), with subsequent modifications in Jeltsch *et al.* (1998). This cellular automata model incorporated differences in tree–grass rooting profiles in topsoil and subsoil layers (and differences in the ability to exploit water between the two functional types) as well as disturbance effects. The model predicted that coexistence was unlikely to occur in the absence of disturbance, with fire preventing the system from developing into a woodland (Jeltsch *et al.*, 1996). The original model predicted tree–grass coexistence, but with trees only occurring in a clumped spatial pattern (Jeltsch *et al.*, 1996). A limitation of the model lies in its treatment of rooting depth and soil moisture dynamics. Although the model accounts for two soil layers, water movement from topsoil to subsoil is not modeled explicitly but is rather fixed in relation to rainfall. As a result, changes in grass biomass do not affect the amount of water infiltration into subsoil layers. The categorical treatment of soil moisture in the model and the lack of water movement between soil layers may explain the lack of tree–grass coexistence in the absence of fire.

In addition to this foundational set of models, others have been proposed that invoke additional mechanisms that can impact coexistence. We refer to these models as 'derived' because in every case, coexistence can occur (*via* previously hypothesized mechanisms) even when the new factors of interest are excluded. Yu & D'Odorico (2015) proposed that hydraulic lift by trees expands the range of conditions under which savannas may exist as a stable state by favoring grasses. Hydraulic lift was theoretically shown to strengthen the savanna state, but coexistence itself emerges as a result of belowground niche partitioning (and exclusive access to deep layers by trees), as in the Walker *et al.* (1981) model. Ratajczak *et al.* (2017) proposed a coexistence model based on a system of Lotka–Volterra equations. Although it does not specifically address competition mechanisms between trees and grasses, this model showed that if savanna trees are weak competitors with grasses, a self-reinforcing savanna community can persist. If savanna trees exhibit strong competition with grasses, the model predicts a community transition to forest species, which are more competitive than savanna trees and also shade out grasses (Ratajczak *et al.*, 2017). Beckage *et al.* (2009) explored how positive feedbacks between savanna trees and fire stabilize the savanna state, but the feedbacks were not essential for coexistence. Finally, van Langevelde *et al.* (2003) highlighted the importance of considering the divergent effects of two different herbivore guilds (browsers and grazers) and fire on tree : grass ratios, but the basis for coexistence was similarly provided by the Walker *et al.* (1981) model. A key contribution of this model was its emphasis on herbivory, which plays a lesser role than fire in other disturbance-based models (Higgins *et al.*, 2000; D'Odorico *et al.*, 2006). Empirical work shows clearly that herbivory is a fundamental driver of vegetation patterns in savannas (Staver & Bond, 2014; Hempson *et al.*, 2015; Staver *et al.*, 2021), and its inclusion is therefore necessary in models of tree–grass dynamics.

III. Reassessment of rooting depth and resource partitioning

As reviewed thus far, the various existing models combine strengths and limitations. The original two-layer tree–grass coexistence model was relegated to a large extent because the assumption of an exclusive use layer was often not supported for trees by empirical work in the tropics and subtropics (Scholes & Walker, 1993). In temperate grassy ecosystems, by contrast, the two-layer model has been more consistently supported (Sala *et al.*, 1989; Weltzin & McPherson, 1997; Nippert & Knapp, 2007a). In a later literature review on the topic, however, Ward *et al.* (2013) concluded that there was in fact considerable support for the two-layer model across a wide range of savanna types across both tropical and temperate latitudes, particularly in dry ecosystems.

Beyond this renewed support for the original conception of the two-layer model, we propose that the emphasis on exclusive use (and maximum rooting depth) is unnecessary. Holdo (2013) used a simple model with multiple soil layers to show that shallow- and deep-rooted plant strategies can coexist stably without differences in maximum rooting depth, provided that rainfall is treated (realistically) as stochastic. In this model, shallow-rooted species are competitively dominant to deep-rooted species, which are able to persist because large infiltration events occasionally exceed the uptake capacity of shallow-rooted plants. This model theoretically showed that subtle differences in root distribution as a function of depth can have important effects on water uptake (Holdo, 2013). When the assumption of exclusive use is no longer necessary to achieve coexistence, the empirical support for niche partitioning becomes more compelling. Second, earlier studies finding an extensive tree–grass rooting overlap relied mostly on patterns of root biomass distribution (Scholes & Walker, 1993; Mordelet *et al.*, 1997; Hipondoka *et al.*, 2003), but these do not necessarily reflect the functional patterns of water uptake (Asbjornsen *et al.*, 2008; Nippert & Holdo, 2015; Kulmatiski & Beard, 2022). A wide range of field studies conducted over the past decade have found clear tree–grass functional differences in water uptake as a function of depth, with trees relying on deeper soil moisture when available, while grasses consistently utilize water in the top 20–30 cm of the soil (Kulmatiski & Beard, 2013a,b, 2022; Holdo & Nippert, 2015; Holdo *et al.*, 2018; Case *et al.*, 2020). These patterns hold across precipitation gradients (Holdo *et al.*, 2018; Case *et al.*, 2020; Kulmatiski & Beard, 2022) and soil texture differences (Case *et al.*, 2020; Kulmatiski & Beard, 2022). In a recent paper, Kulmatiski & Beard (2022) reinforce the idea that functional rooting depth differences are a key component of tree–grass coexistence, despite the occurrence of substantial zones of overlap (and therefore competition) in water uptake. Paradoxically, they suggest that the deep strategy (i.e. trees) generally extracts more water from the ecosystem than the shallow strategy. This finding, however, is based on modeling work that, similar to Holdo (2013), puts aside tree–grass differences in root transport capacity, drought tolerance, transpiration, and water use efficiency to focus exclusively on rooting differences (Kulmatiski & Beard, 2022). Importantly, grasses outperform trees in all of these metrics (Wargowsky *et al.*, 2021; O'Keefe *et al.*, 2022; Belovitch *et al.*, unpublished), thus helping tilt the competitive advantage toward grass dominance. We argue that the two-layer model is alive and well but that it needs to incorporate the full range of differences in tree and grass ecohydrological traits (Ward *et al.*, 2013).

IV. Trees: competitively dominant or simply survivors?

Disturbance-based models assume that niche differentiation and ecohydrological traits (and therefore resources) play a lesser role in tree–grass coexistence (Sankaran *et al.*, 2004). A corollary of this assumption is that trees are ultimately dominant to grasses: in the absence of herbivory and disturbance, grasses rapidly reach their carrying capacity (100% cover). For trees, the process is slower, but the disturbance-free 'endgame' would be a tree-dominated landscape that excludes grasses (Higgins *et al.*, 2000; D'Odorico *et al.*, 2006; Beckage *et al.*, 2009). Trees are therefore (implicitly or explicitly) assumed to be competitively dominant (Table 1). Understanding competitive interactions and the tree–grass dominance hierarchy, however, cannot be achieved in the absence of an explicit consideration of resource use.

The key limiting resource in dry savannas is water. Scholes & Walker (1993) argued that water acts as an 'on–off switch' for growth and that N is the key limiting resource. Even if this interpretation is correct, the switch-like role of water allows us to treat it as the *de facto* limiting resource, supported by most resource-based models (Walker *et al.*, 1981; Van Wijk & Rodriguez-Iturbe, 2002; Holdo, 2013; Xu *et al.*, 2015; Yu & D'Odorico, 2015). There is ample evidence for grasses being competitively dominant to trees when competing within the same soil layers, across a wide range of soil moisture conditions (Walker *et al.*, 1981; Walker & Noy-Meir, 1982; February *et al.*, 2013; Campbell & Holdo, 2017). Grasses have finer roots than trees (Nippert *et al.*, 2012; Ma *et al.*, 2018; O'Keefe *et al.*, 2022), resulting in a higher specific root length and greater absorptive surface area per volume of soil (Ma *et al.*, 2018), higher fine-root conductivity (Wargowsky *et al.*, 2021), and whole-plant transpiration rates per unit mass (Belovitch *et al.*, unpublished). The root diameter imposes a trade-off: grasses have a larger absorptive capacity than trees in topsoil fine roots, but trees have a greater capacity for long-distance (i.e. deep) transport (Nippert & Knapp, 2007a). This is a result of the greater relative investment by trees in coarse roots than in grasses, with coarse (i.e. thick) roots playing a more important transport than acquisitive role (Tobin *et al.*, 2007; Rewald *et al.*, 2012). This is why trees are sometimes able to readily utilize groundwater, but grasses, despite often having deep roots, are not (Nippert *et al.*, 2012). Xu *et al.* (2015) assumed that grass transpiration per unit biomass exceeds tree transpiration across the full range of soil water potentials that plants experience, an assumption that is supported by recent empirical evidence (Belovitch *et al.*, unpublished). These water use differences manifest as strong competitive effects of grasses on trees across a wide range of tree life stages. Under both field (February *et al.*, 2013) and glasshouse conditions (Campbell & Holdo, 2017), competition is highly asymmetric, with grasses exerting a strong competitive effect on tree seedlings while exhibiting little or no competitive response to them.

When water is a key limiting resource, how can trees persist in the face of intense competition from grasses? In a rainfall manipulation and grass removal experiment in South Africa, February *et al.* (2013) showed that any 'excess' water added to plots accrued to grasses only (in terms of biomass production), with no measurable effect on tree growth. Only grass removal had an effect on tree growth (February *et al.*, 2013), supporting a strong competitive role for grasses. Such effects have been interpreted as being incompatible with niche partitioning by some (e.g. Barron-Gafford *et al.*, 2017), but that is not necessarily the case. In this and other field studies, tree growth is never reduced to zero by grass competition (Riginos, 2009; Laris *et al.*, 2021). So, why do trees continue to grow when grasses are so dominant? The two-layer hypothesis provides an explanation: even when grass biomass is high, 'excess' precipitation allows trees to persist. Grass biomass tracks some running average of recent rainfall (both grass biomass and net primary productivity are strongly linearly related to MAP (Sala *et al.*, 1988)), but rainfall beyond this average overwhelms grass uptake capacity and leads to deeper infiltration (Kulmatiski & Beard, 2013b). Coupled with rooting differences, this allows trees to persist in grass-dominated landscapes. This was elegantly demonstrated by experiments manipulating the size of rainfall events conducted in both South Africa (Kulmatiski & Beard, 2013b) and North America (Holdrege *et al.*, 2021): large rainfall events led to deep soil infiltration and enhanced tree growth rates relative to grass growth.

Although niche partitioning allows trees to persist and grow above a threshold value of MAP, the slow growth rate imposed by grass competition exposes trees to biomass-reducing (or mortality-inducing) disturbances such as fire or browsing. It has long been recognized that fire and browsing delay tree escape from fire (Bond & van Wilgen, 1996) or browsing traps (Staver & Bond, 2014), but the added effect of grass competition on tree growth has largely remained absent in models of savanna dynamics (Riginos, 2009). Higgins *et al.* (2000) showed that small variations in tree growth can exert an outsize influence on tree–grass coexistence. We propose that slow tree growth is a key feature of savannas (Fig. 1), part of the reason for savanna persistence (i.e. tree canopy closure and grass competitive exclusion can take a long time to occur, allowing fire and/or herbivory to maintain the savanna state before the system becomes forest), and often driven by competitive effects of grasses. Studies across a wide range of savanna sites have demonstrated strong tree growth responses to grass removal (Riginos, 2009; February *et al.*, 2013; Laris *et al.*, 2021), although these findings are not universal and may in fact be soil-dependent (Knoop & Walker, 1985). We suggest that stronger grass competition occurs on fine-textured soils than on coarse-textured soils because on fine soils, niche partitioning is more constrained by limited deep infiltration (Knoop & Walker, 1985; Case *et al.*, 2020).

V. A common problem: what sets the upper limit for tree cover?

A challenge for all models is as follows: if trees can survive and grow (however slowly) despite grass competition even in dry savannas, what prevents them from eventually completely covering the landscape and shading out grasses? Most models minimize the role of light limitation in dry savannas, under the argument that tree cover is too low for light to be a limiting resource (Yu & D'Odorico, 2015). Shading effects are assumed to lower grass stomatal conductance (and therefore indirectly, transpiration rates), but grasses are not competitively excluded (Xu *et al.*, 2015; Yu & D'Odorico, 2015). Grasses could theoretically be excluded, however, unless some form of resource limitation prevents trees

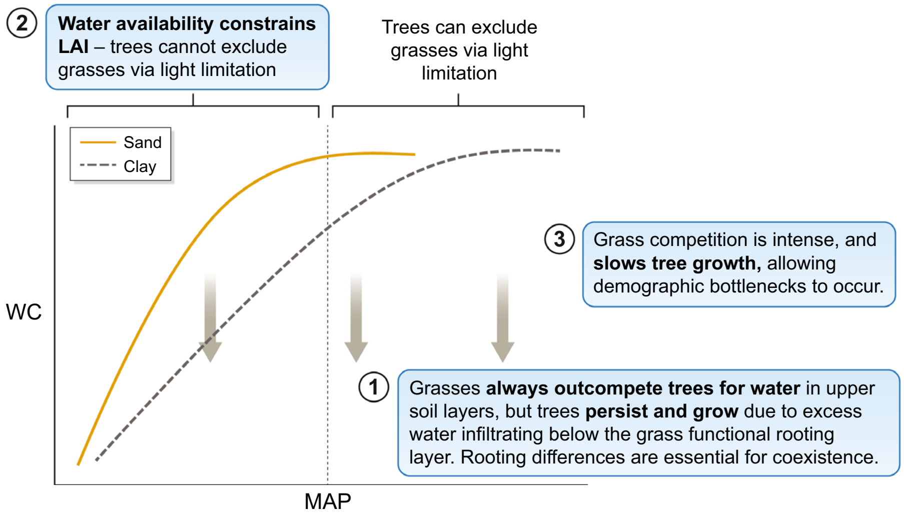

Fig. 1 Key elements of a tree–grass coexistence model. Empirical work shows that mean annual precipitation (MAP) imposes an upper boundary on woody cover (WC) below a certain threshold (Sankaran *et al*., 2005). We refer to this as the 'Sankaran curve'. We propose that (1) grasses outcompete trees for soil moisture in upper soil layers under a wide range of conditions, but trees persist and survive by accessing moisture in deeper layers. Trees might eventually outcompete grasses, but (2) below the precipitation threshold, hydrology constrains maximum leaf area index and therefore competitive exclusion driven by light limitation. (3) Both below and above this threshold, intense grass–tree competition slows tree growth and amplifies opportunities for fire- and herbivory-mediated demographic bottlenecks to occur. In addition, we suggest that soil texture affects the location of the WC upper boundary and/or MAP threshold.

from forming a closed canopy. Such a resource-based mechanism is absent in disturbance-based models, which predict eventual tree dominance in the absence of disturbance even in dry savannas (Jeltsch *et al.*, 1996; Higgins *et al.*, 2000; D'Odorico *et al.*, 2006; Beckage *et al.*, 2009). For these models to be able to explain the Sankaran curve, either disturbance rates or tree/grass demographic rates would need to vary systematically with MAP to limit trees to an upper boundary below 100% cover. We are not aware of a disturbance-based model that explains such an upper boundary.

We propose instead that the Sankaran curve is simply the outcome of water limitation of leaf area and therefore of tree capacity for shading the understory. As MAP increases, deep infiltration (Holdo, 2013) and the amount of water taken up through tree root systems also increase. This is mirrored by a commensurate allocation to leaf area to maintain a balanced soil–plant atmosphere transpiration pipeline, but neither trees nor grasses can exceed an investment in leaf area that exceeds their soil water uptake capacity (Fig. 1). As a result, both tree and grass leaf area indexes (LAIs) should be constrained by transpirational supply (soil moisture) and demand (driven by light and vapor pressure deficit (VPD)) and therefore MAP. This is a relationship that has been shown both empirically (Caylor *et al.*, 2005) and theoretically (Yang *et al.*, 2018). Tree and grass biomass (and LAI) follow similar positive relationships with MAP but with different intercepts and slopes (Caylor *et al.*, 2005). A key difference between trees and grasses is simply that, although tree LAI may be lower than grass LAI for a given MAP, tree investment in structural tissue puts tree leaves above the grass canopy. Light interception and therefore limitation (primarily in grasses) is strongly related to LAI (Xu *et al.*, 2015). At low maximum LAI, shading effects by trees may lower grass transpiration (Xu *et al.*, 2015) without diminishing photosynthetically active radiation (PAR) below the point where grass respiration exceeds photosynthesis (and grasses are competitively excluded). In fact, small amounts of shading by trees may limit moisture stress in grasses and even lead to facilitation. As MAP increases beyond a threshold, tree LAI will eventually lead to grass exclusion *via* light limitation. This shift from facilitation to competition would be consistent with observations of positive-to-negative effects of trees on grasses as trees grow in size (Scholes & Archer, 1997). Under high tree LAI, disturbance would be required to maintain the savanna state (Sankaran *et al.*, 2005; Staver *et al.*, 2011). This is consistent with the description of savannas as 'equilibrium' and 'disequilibrium' systems below and above a MAP threshold, respectively (Sankaran *et al.*, 2005). A key argument we make here is that the Sankaran 'tree cover' curve is a manifestation of the general positive relationship between maximum LAI and MAP that occurs in both trees and grasses (Caylor *et al.*, 2005), but the tree fraction of LAI translates into a clearer MAP–cover relationship than the grass fraction. A corollary of this argument is that MAP should impose an upper limit on the ability of the woody component to encroach into and permanently exclude grasses from dry savannas. At the same time, it implies that the upper boundary of tree cover is not fixed by rainfall but by a combination of rainfall limitations on plant LAI and grass biomass. In other words, overgrazing or other processes limiting grasses should allow tree LAI to expand to a new upper limit imposed by MAP.

The relationship between LAI and MAP should be expected to be influenced by any factors that impact the ability of plants to move water from soil to atmosphere. On sandy soils, a greater amount of deep infiltration occurs, allowing trees to form closed canopies below the 650 mm threshold. On clay soils, the higher uptake capacity of grasses and the more limited opportunities for rooting separation and niche partitioning (given that saturated conductivities are lower) suggest that tree–grass competition is more intense (Holdo, 2013; Case *et al.*, 2020), and transpiration will be lower for a given volumetric water content. The resulting LAI distribution favors grasses, perhaps explaining the lower amount of tree cover in these systems. The Sankaran threshold is therefore probably higher under these conditions (Fig. 1). In these systems, trees need to compete more intensely with grasses, having lower points of stomatal closure and smaller leaves to maintain transpiration under a wider range of atmospheric conditions (Scholes & Walker, 1993). This might also explain why clay-dominated savannas are characterized by fine-leafed species (Scholes & Walker, 1993).

Overall, hydrology and light availability both play a role in the tree–grass coexistence problem, as proposed by Scheiter & Higgins (2007). An important caveat is that allocation to shoots (and therefore shading) is strongly constrained by root mass and competitive interactions. These constraints can only be accounted for by explicitly modeling resource dynamics.

VI. Role of disturbance and bottlenecks

Walker & Noy-Meir (1982) argued that resource limitation plays the dominant role in explaining tree–grass coexistence, with fire and herbivores being 'modifying' factors. Current evidence supports this interpretation in dry savannas but not in wet savannas, as suggested by Sankaran *et al.* (2005). Still, the disturbance/demographic bottleneck paradigm is key to understanding tree : grass ratios in savannas, if less so for explaining tree–grass coexistence.

As previously discussed here and identified by Higgins *et al.* (2000), tree–grass ratios are highly sensitive to tree growth rates. By limiting tree growth, grasses expose trees to windows of vulnerability (Holdo *et al.*, 2022), where they can be damaged and topkilled and kept in a disturbance or herbivory 'trap' below the Sankaran curve (Bond & van Wilgen, 1996; Staver & Bond, 2014), not only in mesic savannas but potentially across the full MAP range (Fig. 1). The storage effect identified by Higgins *et al.* (2000) also plays a key role in shaping vegetation structure. Grasses propagate readily, either sexually or vegetatively, and form a relatively continuous canopy across a wide precipitation range. Across this range, newly established trees need to emerge through the grass rooting zone and the grass canopy, with the result that true tree seedlings occur at very low densities and establishment events are rare (Wakeling *et al.*, 2015). This concentrates the maximum LAI that trees can attain into a discrete number of individuals, translating the upper tree LAI limit into a tree cover limit. Tree resprouting and longevity are also key aspects of the storage effect, which buffers the unrealistically fast dynamics of establishment/death that are required to achieve coexistence in other models. In the Higgins *et al.* (2000) model, trees can persist in the grass canopy following topkill and contribute to tree expansion under suitable conditions. The vast majority of 'seedlings' found in savannas tend to be resprouts rather than true seedlings (Boaler & Sciwale, 1966; Higgins *et al.*, 2000), and this relegates the role of seed dispersal and sexual reproduction in savanna dynamics. A model that accounts for both resprouting and intense asymmetric grass–tree competition can explain the rapid woody encroachment of overgrazed landscapes.

More importantly, the demographic aspect of the tree life cycle (i.e. based on individuals rather than a tree biomass compartment) introduced by Higgins *et al.* (2000) is an essential ingredient of a tree–grass dynamics model. Most resource-based models are compartment models and ignore the differences between biomass and individual living organisms. In these models, plant biomass increases or decays based on the difference between transpiration times water use efficiency and respiratory costs (Holdo, 2013; Xu *et al.*, 2015). Trees and grasses can theoretically persist as long as their biomass does not decline to zero. The demographic framework, in contrast, tracks living individuals rather than biomass and therefore potentially allows for more realistic size-dependent tree die-offs during periods of hydraulic stress (Fensham *et al.*, 2009; Tai *et al.*, 2017; Case *et al.*, 2019). Such sudden losses may be a key ingredient of the coexistence problem. It is important, although, that demographic rates in these models are explicitly associated with resource availability and other environmental variables.

VII. A synthetic model of tree–grass coexistence and savanna vegetation structure: key ingredients

A large number of models have been proposed that can successfully predict tree–grass coexistence (Table 1). These models run the gamut of coexistence mechanisms supported by ecological theory. Proof of coexistence, however, is a weak test of model adequacy. Beyond coexistence, we must identify the underlying mechanisms driving tree–grass systems. As has been illustrated throughout this review, the existing models of tree : grass coexistence each bring ecological relevance and useful components to address this question. Ultimately, we believe that a definitive model of coexistence (and tree–grass dynamics) can be best represented by fusing elements of existing resource-based models (Holdo, 2013; Xu *et al.*, 2015; Yu & D'Odorico, 2015) with key aspects of the disturbance model outlined in Higgins *et al.* (2000) (Fig. 2). The basic resource model contains two or more soil layers, with topsoil dynamics affected by precipitation, evaporation, water uptake (= transpiration), and drainage to the subsoil layer(s). The depth axis could also be treated continuously, as in Richard's equation (e.g. Guswa *et al.*, 2002), although this treatment would make the model more challenging to solve numerically. Subsoil dynamics are driven by drainage from the topsoil layer, transpiration, and drainage to deeper layers (Fig. 2a). Uptake is driven by available soil moisture, tree and grass biomass and functional rooting depth, plant transport capacity (conductance), drought tolerance, and atmospheric demand (radiation and VPD, Fig. 2a). Several existing models capture these processes, with the Yu & D'Odorico (2015) and Xu *et al.* (2015) models being the most comprehensive in terms of modeling the shading effects of trees on grasses. The Yu & D'Odorico (2015) model, however, maintains the assumption of 'exclusive use' for subsoil layers, which can be relaxed as shown by Holdo (2013), in agreement with empirical findings (Case *et al.*, 2020).

We propose that soil moisture in each layer, as well as a grass compartment, can be effectively modeled through a set of differential equations. Trees, however, are best modeled using the

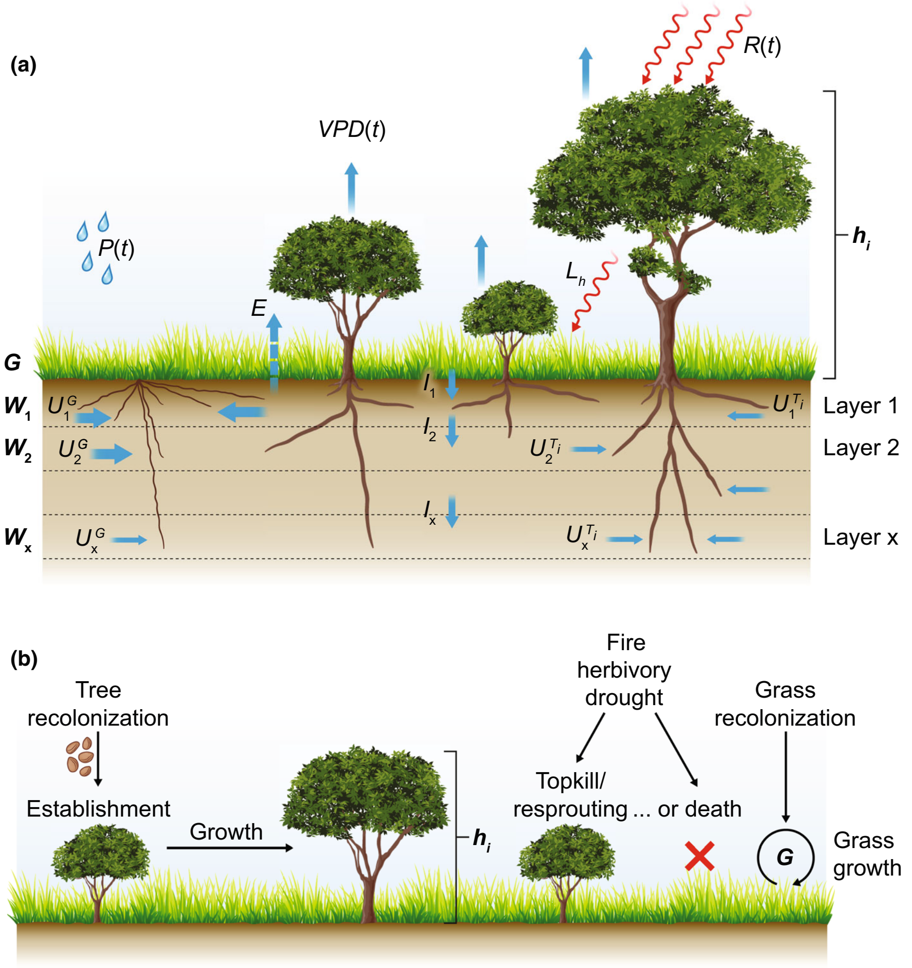

Fig. 2 Essential elements of proposed synthetic tree–grass dynamics models incorporating key biophysical and demographic elements. (a) Components of a compartment model showing state variables (in bold) and water pathways (blue arrows) through multiple soil layers and plant (grass and trees) compartments: infiltration into (I_x) and drainage out of (I_{x+1}) a given soil layer x; evaporation (E) from upper soil layer(s) and uptake (and eventual transpiration) into grass (U_x^G) and tree ($U_x^{T_i}$) roots in soil layer x. The total uptake from a given layer x is equal to $A = U_x^G + \sum_i U_x^{T_i}$, which sums the grass uptake (as a single compartment) and cumulative tree uptake across individual trees i, which have height (h) as a state variable. Uptake from a given layer is determined by soil moisture availability (W_x) in that layer (as well as other soil-related factors such as texture), root mass allocated to the layer, plant conductance (itself a function of water supply and demand), and atmospheric demand, which is driven by the light regime (L) and vapor pressure deficit (VPD). Incoming radiation (R), VPD, and precipitation (P, which drives infiltration into soil layer 1) are forcing functions of time. The light regime at a given height h is determined by the leaf area index above h. (b) Components of a demographic model, showing the key demographic processes affecting grasses and trees. We treat grasses as a single compartment, given the lesser importance of size structure for this functional type and the ready ability of grasses to spread vegetatively and colonize the available space. Changes in grass biomass (***G***) are given by the balance of total water uptake times water use efficiency (WUE) minus respiratory costs and losses from fire and herbivory. If grass biomass reaches 0 and cannot reinvade, it is assumed to be competitively excluded from the system. We treat trees as individuals in an individual-based model (IBM). In the simplest case, this model is not spatially explicit, and there is a single state variable, height (h). Like grasses, trees grow when summed uptake across all soil layers times WUE exceeds respiratory losses. Seeds (either endogenous or exogenous in origin) germinate and establish probabilistically as a function of W_1, G, and $L_{h=0}$. Trees can revert to smaller sizes as a result of fire or herbivory, and some will probabilistically undergo topkill (i.e. h is reset to 0) or death (and be removed from the system). When death exceeds establishment, trees will eventually be removed. If trees fail to recolonize, they are competitively excluded.

Higgins *et al.* (2000) framework. To effectively capture the demographic bottlenecks that are a key feature of tree dynamics, disaggregation is required across a range of possible tree sizes (Fig. 2b). Higgins *et al.* (2000) use a spatially explicit individual-based model (IBM) to simulate savanna trees. Here, we propose minimizing the importance of space but keeping the IBM as a simple means of treating size (mainly height) as a continuous variable for characterizing trees. Trees exploit available soil moisture and impose shading on smaller size classes purely based on size. We assume that newly germinated seedlings initially have rooting niches that overlap with grasses, (Fig. 2a), but shortly thereafter, larger size classes develop a higher water uptake capacity from deeper soil layers than grasses (Kulmatiski & Beard, 2013a). Transpiration is partitioned across individual trees and the grass compartment on the basis of demand (dictated by VPD, modified by shading) and soil moisture availability. Grass growth and individual tree growth are then modeled by translating transpiration into new biomass through whole-plant water use efficiency.

Table 2 Minimum data requirements and current data availability for a proposed synthetic tree–grass savanna dynamics model (W, soil moisture content; VPD, vapor pressure deficit; L = light; F = fire frequency/intensity; H, herbivory frequency/intensity; h, individual tree height).

Data requirement	General approach	Data availability
Functional rooting depth	Stable isotope or tracer approaches	High
Soil moisture dynamics as f (texture)	Direct parameter estimation or parameterization based on soil physics	Very high
Tree recruitment from seed as $f(W, G)$	Seed addition experiments across soil moisture gradients	Low
Whole-plant transpiration as $f(\Psi, \text{VPD}, \text{L})$	Direct glasshouse/field experiments with potted plants	Low
Whole-plant WUE as $f(W, \text{VPD}, \text{L})$	Direct glasshouse/field experiments with potted plants	Low
Onset of dormancy as $f(\int W)$[1]	Field/glasshouse dry-down experiments	Low
Death as $f(\int W)$	Field/glasshouse drought experiments, observational data during drought	Low
Topkill/death as $f(F, H, h)$	Field observational/experimental data	Very high

[1] $\int W$, soil moisture content integrated over the course of the growing season.

In the simplest case, grazing, browsing, and fire can be assumed to occur as external drivers, following van Langevelde *et al.* (2003). This assumption can also be relaxed, allowing vegetation feedbacks on herbivores (Holdo *et al.*, 2013) and/or fire frequency (Beckage *et al.*, 2011; Schertzer *et al.*, 2015). Grazing reduces grass biomass and therefore moderates both fire effects on trees (Staver *et al.*, 2021; Donaldson *et al.*, 2022) and the intensity of tree–grass competition (Donaldson *et al.*, 2022). Fire occurs as a stochastic process (D'Odorico *et al.*, 2006), with intensity being a function of grass biomass (Higgins *et al.*, 2000; van Langevelde *et al.*, 2003). Tree biomass loss and topkill occur as a result of fire and browsing, both of which are treated stochastically, as well as drought, which can be modeled as an extended interval with a high atmospheric soil pressure differential (low soil moisture potential coupled with high VPD). Whole-tree mortality occurs either due to background mortality or as a consequence of topkill. All of these processes are size dependent. Surviving top-killed trees revert to the sapling stage, with rooting distributions comparable to those of established trees (unlike true seedlings). Finally, we assume, like (Higgins *et al.*, 2000), that recruitment of true seedlings is rare and strongly impacted by soil moisture availability (driven by grass and rainfall) and VPD. Competitive exclusion occurs when either trees or grasses fail to recolonize the system following local extinction (Fig. 2b).

VIII. Remaining questions and knowledge gaps

Despite significant empirical and theoretical progress in our understanding of tree–grass coexistence and dynamics, data and knowledge gaps remain. The tree–grass debate has tended to ignore potentially important players, both aboveground and belowground. Aboveground, there are other important plant functional types, such as C_3 forbs (Siebert & Dreber, 2019) and lianas (Coverdale *et al.*, 2021), which can comprise a significant fraction of plant biomass and have been shown to affect savanna vegetation structure (Coverdale *et al.*, 2021). Belowground, there has been a strong emphasis on the role of water in the coexistence debate, but less is known about the role that plant–soil feedbacks and soil microbes play in facilitating coexistence. For example, in North American grasslands, soil microbial communities have been shown to be associated with the stability of the plant community, and it remains unclear if microbes are responding to or driving these dynamics (Chung *et al.*, 2019). Beyond these broader considerations, we still lack key datasets. Great progress has been made over the past two decades in several areas, especially in our understanding of functional rooting patterns, but we still require datasets that allow us to link resources with demographic rates, particularly differences in tree vs grass rates of mortality and recruitment from seed as a function of moisture stress (Table 2).

IX. Conclusion: is the savanna problem essentially solved?

We argue that new empirical evidence and theoretical insights can allow us to conclude that the problem of tree–grass coexistence is essentially solved, and acknowledging this can help us move toward a unified, ecologically relevant model of savanna dynamics. The key building blocks required for a definitive model are well established and simply need to be combined. In this review, we provide three important insights that need explicit consideration for model revision (Fig. 1). First, niche partitioning as a function of soil depth is an essential component of the tree–grass coexistence problem. Recent work shows that the extent of differences in functional water uptake among tree–grass populations is sufficient to allow coexistence while simultaneously leading to an intense competition between the two functional types. Our review of available evidence suggests that rooting differences are necessary to prevent grasses from excluding trees when water is a limiting resource. By being deeper-rooted and having greater functional uptake plasticity (Nippert & Knapp, 2007b; Kulmatiski & Beard, 2013a), trees survive and escape competitive exclusion by grasses. This is because grasses are always competitively dominant to trees for water in the upper soil layers. In short, Walter was essentially correct: niche partitioning is key to tree : grass coexistence, and the basis of this partitioning is captured by functional rather than structural differences in water uptake (Nippert & Holdo, 2015; Kulmatiski & Beard, 2022). Second, we emphasize the contrasting role of light in arid/semi-arid (where 'low-LAI' shading may alleviate moisture stress and result in facilitation) vs mesic (where 'high-LAI' shading can lead to competitive exclusion *via* light limitation) systems and the important coupling of shading effects with water availability through the limitation imposed by the transpiration pipeline on

LAI. Trees are unable to develop enough leaf area to exclude grasses when the supply of water keeps the leaf area below a certain threshold. Third, tree–grass rooting overlap and grass dominance in shallow soil layers lead to strong negative effects of grasses on tree growth rates, exposing trees to damage and topkill to a far greater extent than existing in a grass-free environment. Finally, in agreement with Sankaran *et al.* (2004), we argue that a limitation of many resource-focused models is a failure to account for the importance of treating trees as discrete individuals whose role in the system is strongly size dependent (Table 1). This disaggregation need not extend to grasses, leading to a hybrid model as the most efficient approach (Fig. 2b). Overall, our proposed framework unifies compartment models focused on resources with individual-based models focused on disturbances. Resolution and aggregation of the valuable components of resource-based and disturbance-based models can effectively capture tree–grass dynamics across a wide range of environmental conditions and provides a mechanistic framework for predicting savanna cover in the future.

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Competing interests

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Relationship between rainfall intensity and mean annual precipitation in African savannas.