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Investigating Woody-Grass Interactions in Savannas

A thesis submitted in partial satisfaction of the
requirements for the degree Master of Arts
in Geography

by

Michael Raymond Fischella

2017

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ABSTRACT OF THE THESIS

Investigating Woody-Grass Interactions in Savannas

by

Michael Raymond Fischella

Master of Arts in Geography

University of California, Los Angeles, 2017

Professor Gregory Stewart Okin, Chair

Savannas are an important environment that make up over one fifth of the planet's terrestrial area, but our current understanding of the ecohydrological mechanisms that produce this woody-grass coexistence remain limited. It has been assumed that in savannas there is no direct competition occurring belowground between woody vegetation and grasses. Although the assertion that two layers of roots are present has been questioned as a consistent representation of belowground woody-grass interactions in savannas. Thus it is necessary to repartition woody and grass roots into three-layers to provide a more consistent representation of the belowground competition observed in savannas. Then developing numerical models provides a means through which these hypotheses can be compared, and analyzed. The results show that reallocating roots into three-layers provides a far more consistent representation of belowground competition occurring between woody vegetation and grasses in savannas environments, as well as a better understanding of the ecohydrological mechanisms influencing the woody-grass distribution.

The thesis of Michael Raymond Fischella is approved.

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2017

Table of Contents

Introduction.....	1
Methods.....	5
Results.....	10
Discussion.....	13
Conclusion.....	16
Bibliography.....	18

Table of Figures

Figure 1. Mean standard deviation of vegetation in a two-layer model.....	10
Figure 2. Grass-tree ratio using a two-layer model.....	11
Figure 3. Mean standard deviation of vegetation in a three-layer model.....	11
Figure 4. Grass-tree ratio using a three-layer model.....	12
Figure 5. Comparison of grassy evapotranspiration.....	12

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Introduction

Savannas are distinct ecosystems that are home to a diverse array of species. They are typically characterized as water-limited environments that are co-dominated by both grasses (C4) and woody vegetation (C3). There has been an increasing body of research investigating the ecological phenomena observed in savannas, and the mechanisms (such as facilitation and competition) that produce the observed woody-grass coexistence (Bhattachan et al., 2012a; O'Donnell et al., 2015; Scholes and Archer, 1997). Although our understanding of savannas has improved, a gap persists regarding the epistemology of these woody-grass coexistence.

Investigating the ecohydrological mechanisms responsible for the distribution of savanna vegetation is not a new area of research, and can be traced back to the late 19th century (Eggeling, 1947; Walter, 1971). Through this culmination of research, several elements have been identified as factors influencing the woody-grass distribution. Competition between grasses and woody vegetation can directly and indirectly regulate plant recruitment (Scholes and Archer, 1997). There have also been several principal determinants influencing woody-grass interactions, which are precipitation, nutrients (N), fire, and grazing. However, the primary determinant responsible for woody-grass coexistence remain ambiguous, which makes the efficacious conservation and management of savannas challenging (Dougill and Thomas, 2004; Walter, 1971).

Therefore, it is necessary to improve our understanding of woody-grass interactions belowground, specifically competition for the available soil moisture content. It has been hypothesized that woody roots are only able to obtain water when precipitation percolates into the lower soil layer (Walter, 1971). An accurate understanding regarding the partitioning of savanna roots is necessary to investigate local and global changes in savanna vegetation. It has

been assumed that belowground biomass is relative to aboveground biomass, but recent research has shown that a “functional equilibrium” exists between aboveground and belowground biomass and is the result of an intricate process (Bhattachan et al., 2012a; Poorter and Nagel, 2000).

Savannas are found throughout the planet, but nowhere are they more widespread than on the African continent. Almost half of Africa consists of savanna environments (Scholes and Archer, 1997). The Kalahari is a region in central southern Africa that’s definition and boundaries remain relatively nebulous. Scientific literature describes the Kalahari as an aridity transect that consists of loamy sand savannas. There has been extensive research in the Kalahari, so the site provides an ideal location to use as a case study site (Thomas and Shaw, 1991). The Kalahari experiences two seasons, due in part to the Southern hemisphere’s Hadley cell (Richard and Pocard, 1998). This cell is present along the equator where warm humid air rises before it begins to cool and dry as it circulates, and eventually begins sinking around 30th southern parallel. This is a contributing factor to the precipitation gradient that occurs along the Kalahari (Tyson and Crimp, 1998). Throughout the Kalahari, precipitation events typically occur during the summer months (October-April), which is their monsoon season. Precipitation is almost completely absent throughout the Kalahari during the dry season (May-September). The Kalahari is also where Heinrich Walter conducted fieldwork that contributed to his hypothesis regarding the niche separation of woody-grass roots (Walter, 1971). It has become one of the most cited and contested theories in savanna ecohydrology, for proceeding fieldwork has been unable to corroborate the applicability of Walter’s two layer hypothesis (Walker et al., 1981; Ward et al., 2013).

Walter's two-layer hypothesis attempts to describe belowground competition in savannas, and explain the observed woody-grass coexistence (Sankaran et al., 2004). He hypothesized that woody and grass roots occupy different soil layers in savannas and are thus not in direct competition with each other for the available soil moisture (Walter, 1971). This allows woody vegetation and grasses to remain in a state of co-dominance. Walter's theory began gaining widespread acceptance as a consistent representation of woody-grass interactions belowground, and an explanation of the woody-grass codominance (Sankaran et al., 2004). Proceeding research and hypotheses have been developed based on Walter's two-layer hypothesis. Particularly when developing quantitative environmental models and investigating savanna ecohydrology (Ward et al., 2013). There has been an array of models developed to evaluate savanna ecosystems, to try and explain the ecological interactions occurring (D'Odorico et al., 2007; Okin et al., 2009; Rodriguez-Iturbe, 2000). Walter's two-layer hypothesis is a competition-based model, centered on competition between woody and grass roots for the available soil moisture. Competition based models of woody vegetation and grasses maintain this coexistence is a result of competing interactions. A model of arid savannas incorporates competition based models because resource accessibility (mean annual precipitation or nutrients) is often considered the primary determinant in regulating and sustaining woody-grass coexistence (Sankaran et al., 2004).

Previous ecohydrological savanna research has produced quantitative and qualitative data examining the mechanisms maintaining this woody-grass coexistence. The subsequent results though have been unable to provide decisive conclusions in support of Walter's two-layer hypothesis, and instead have been rather conflicting (Mordelet et al., 1997; Scheiter and Higgins, 2007). Walter's two-layer hypothesis emphasizes that water is the primary determinant controlling the distribution of woody vegetation and grasses in savannas (Walter, 1971). This

hypothesis is a highly cited study that has been integrated into theoretical savanna and ecohydrological research (Ward et al., 2013).

There is an increasing body of evidence, that has questioned the applicability of Walter's two-layer hypothesis in savanna ecohydrology. Fieldwork conducted over the last two decades has further investigated the distribution of belowground biomass in savannas as well as woody-grass coexistence (Dintwe, 2016; Goward and Prince, 1995; Mordelet et al., 1997; Scholes and Archer, 1997). The results of recent studies contradict Walter's hypothesis regarding root niche separation, and woody-grass coexistence. These studies present a much different distribution of tree root density than Walter's hypothesis suggests, and advocates Walter's hypothesis is not a consistent representation woody-grass interactions occurring in savanna environments.

Bhattachan et al. (2012) calls into question the applicability of Walter's two-layer hypothesis in savannas. The study investigated potential associations between precipitation and the rooting depth of woody vegetation. The results from this study also show that tree roots obtain the maximum density within the first 300 mm (30 cm) of soil (Bhattachan et al., 2012). The conclusions from these and additional studies have initiated a debate regarding the applicability of Walter's hypothesis as an applicable representation of woody-grass interactions in savannas. This has led some researchers to propose new hypotheses regarding woody-grass interactions in savannas. Dr. Kebonye Dintwe has proposed that redistributing woody and grass roots in savannas could produce a more consistent representation of woody-grass interactions (Dintwe et al., 2015; Dintwe and Okin, 2018).

The development of a new hypotheses is critical in order to consistently represent woody-grass interactions as well as the distribution of belowground biomass in savannas. Therefore, a three-layer hypothesis is being proposed, in which tree roots outcompete grass roots in the first

100 mm (0 mm – 100 mm), thus creating the first layer of roots. Then the preceding 300 mm (100 mm – 400 mm) of soil are dominated by grass roots, and thus delineated as the second layer of roots. The third and final layer in the three-layer hypothesis is 600 mm deep (400 mm – 1000 mm) where woody vegetation can out compete grass roots (Dintwe et al., 2015). A three-layer hypothesis presents a more realistic vertical distribution of roots as well as a more consistent representation of belowground competition (Mordelet et al., 1997; Scheiter and Higgins, 2007). However, this model is not intended to provide an accurate representation of the intricate processes that influence these dynamics, but rather provide a better understanding of woody-grass interactions in savannas. Developing a numerical model based on this three-layer hypothesis would help identify which model provides a more consistent representation of these ecohydrological processes observed in savannas.

There have been various analytical models developed to simulate belowground competition in savannas (D’Odorico et al., 2009; Porporato et al., 2003; Rodriguez-Iturbe et al., 1999a). However, these models are investigating different questions regarding savanna vegetation and ecohydrology, so it is necessary to develop a new model. These models as well as other ecohydrological models, assume that savannas consist of two layers belowground and that grass roots dominate the top soil (0 mm – 300 mm) and tree roots out compete grasses in the sub soil (300 mm – 1000 mm), which is a result of Walter’s two-layer hypothesis. The development of a numerical soil moisture model based on this three-layer hypothesis will provide a far more consistent and realistic representation of these woody-grass interactions than previous models.

Methods

There are two models used in this study that are patterned after the one-dimensional soil moisture model developed by Yu and D’Odorico (2014). In the original model, there are two soil

layers, but the model has also been adapted to include three-layers for this study. In both models the precipitation is modeled as a Poisson process. Evapotranspiration from each layer is a function of soil moisture and serves as a proxy through which it is possible to investigate vegetative growth (Williams et al., 2010). In the two-layer model, the evapotranspiration from the top layer is assigned to grasses and evapotranspiration from the bottom layer represents woody vegetation. In the three-layer model, woody vegetation is assigned to the first and third layers, and grasses are allotted the evapotranspiration from the second layer. To represent various savanna environments there were several precipitation points used to produce a precipitation gradient.

Throughout both models the first-layer of soil moisture is simulated as

$$(1) \quad nZ_i \frac{dS_i}{dt} = P - ET_i - D_i,$$

where n (dimensionless) is soil porosity, Z_i (mm) layer depth, S_i (unitless) soil moisture content, t (d^{-1}) is time, P ($mm\ d^{-1}$) precipitation, ET_i ($mm\ d^{-1}$) is evapotranspiration, and D_i ($mm\ d^{-1}$) is the drainage rate. The subsequent layers in the two and three-layer models are represented as

$$(2) \quad nZ_i \frac{dS_i}{dt} = D_{i-1} - ET_i - D_i.$$

Precipitation

The model simulates precipitation as a Poisson process stochastically. A Poisson process parameterizes events, in this case precipitation, based on two variables, the depth of precipitation events as well as the interval between these events (Rodríguez-Iturbe et al., 1999b). It is assumed that the two variables representing precipitation intensity and the duration between precipitation events are temporally independent of each other (Milly, 1993). This model has been adapted from previous studies that have employed a Poisson process to simulate precipitation annually with a daily level of aggregation (Rodríguez-Iturbe and Porporato, 2007;

Yu and D’Odorico, 2014). The first parameter is the duration between precipitation events and is determined by

$$(3) \quad P_L = \frac{-1}{\lambda \ln(1-x_L)},$$

where λ is the reciprocal of the average duration of precipitation events, and x_L is drawn from a random uniform distribution on the interval [0,1]. The second parameter of the precipitation function produces the average depth of the individual precipitation events, and is expressed as

$$(4) \quad P_D = \frac{-1}{C \ln(1-x_D)},$$

where C is the average intensity of precipitation events reciprocal, x_D is from a random uniform distribution on the interval;[0,1]. This precipitation function is capable of producing precipitation events over a specific time interval. For this study it is set to produce precipitation events ranging from 150 mm – 800 mm MAP.

Evapotranspiration

Evapotranspiration is a process that influences the soil moisture rate as well as providing a means through which plant water stress and vegetative growth can be simulated as well as quantitatively investigated (Laio et al., 2001). The maximum amount of evapotranspiration that can occur in a single day is set at 5 mm d⁻¹ (ET_{max}) and can be apportioned as

$$(1) \quad ET_{gmax} + ET_{wmax} = ET_{max},$$

where ET_{wmax} is the maximum daily potential evapotranspiration of woody vegetation and ET_{gmax} is the daily potential evapotranspiration of grassy vegetation.

In the two-layer model the evapotranspiration rate is not apportioned any further, since there is only one layer of grasses and woody vegetation. The first layer’s maximum rate of evapotranspiration is determined by

$$(2) \quad ET_{1max} = ET_{gmax},$$

where ET_{gmax} is equal to ET_{1max} the first layer's maximum daily rate of evapotranspiration (mm d^{-1}). In the second-layer the maximum rate of daily evapotranspiration rate is determined by

$$(3) \quad ET_{2max} = ET_{wmax},$$

where ET_{2max} the second layer's maximum rate of evapotranspiration (mm d^{-1}) is set to equal ET_{wmax} . In the three-layer model, woody roots are partitioned into two separate layers' as

$$(1) \quad ET_{1wmax} + ET_{3wmax} = ET_{wmax},$$

where ET_{1wmax} is the first layer's maximum rate of evapotranspiration and ET_{3wmax} is the third layer's. There is also evapotranspiration occurring because of grasses, but there is only one-layer of grassy vegetation so

$$(2) \quad ET_{gmax} = ET_{2gmax},$$

where ET_{gmax} equals ET_{2gmax} the second-layer's rate of evapotranspiration.

The evapotranspiration that occurs throughout the soil layers in either of these models can be determined by

$$(3) \quad ET_i = \frac{ET_{imax} \times r_i \times f(S_i)}{(nZ_i)},$$

where ET_{imax} the maximum daily rate of evapotranspiration, r_i the layer's root density, and $f(S_i)$ the soil moisture content of layer i . The function $f(S_i)$ is incorporated in both models as

$$(4) \quad (S_i) \begin{cases} 0, & S_i < S_w, \\ \frac{S_i - S_w}{S^* - S_w}, & S_i < S^*, \\ 1, & S_i \geq S^*, \end{cases} ,$$

where S_i is the respective layer's soil moisture content, S_w is the wilting point, and S^* is the value below which evapotranspiration is limited by soil moisture (Bhattachan et al., 2012; Rodriguez-Iturbe, 2000). It is assumed in these models that the soil moisture content of any layer cannot decrease below the wilting point.

Root Density

It is necessary to determine the root density of grasses and woody vegetation in the two-layer model by

$$(5) \quad r_{1g} \cdot z_1 = r_{2t} \cdot z_2,$$

where r_{1g} is the first layer's root density, and r_{2t} is the second layer's root density. It is assumed that grass root density equals 1, therefore tree root density is assumed to equal $\frac{3}{7}$. In the three-layer model grass root density is assumed to be consistent with grass root density in the two-layer model

$$(6) \quad r_{1g} \cdot z_1 = r_{2g} \cdot z_2,$$

where r_{2g} the three-layer models' grass root density. In the three-layer model woody roots are apportioned into layer's one and three

$$(7) \quad r_{2t} \cdot z_2 = (r_{1t} \cdot z_1) + (r_{3t} \cdot z_3),$$

where r_{1t} is the first layer's tree root density, and r_{3t} is the third layer's tree root density. In the three-layer model the first and third layer's root density are set to be

$$(8) \quad r_{1t} \cdot z_1 = r_{3t} \cdot z_3,$$

where half of the root density is found in the top 400 mm and the other half below 400 mm based on (Bhattachan et al., 2012a; D'Odorico et al., 2007). It is necessary to identify the root density of the third and first layer through

$$(9) \quad r_{it} = \frac{r_{2t} \cdot z_2}{2z_i},$$

where the layer's depth is used to determine the root density.

Drainage

The drainage of each layer begins once that layer's soil moisture content exceeds the field capacity, and will exponentially decline as soil moisture content decreases. It is assumed that the drainage rate is driven exclusively because of gravity. The drainage rate in these models' are

$$(10) \quad D_i = \frac{\frac{K_s}{\exp[\beta(1-S_{fc})-1]} [\exp[\beta(S_i-S_{fc})-1]]}{nZ_i},$$

where K_s is soil hydraulic conductivity, β is a coefficient, and S_{fc} is field capacity. The field capacity throughout the layers' remains constant and is set to 0.35 as well as the soil's porosity which is set to 0.42. The soil profile used in this study is classified as a loamy sand. Thus, K_s is parameterized with a value of $50 \cdot 24$ based on Yu and D'Odorico (2014a).

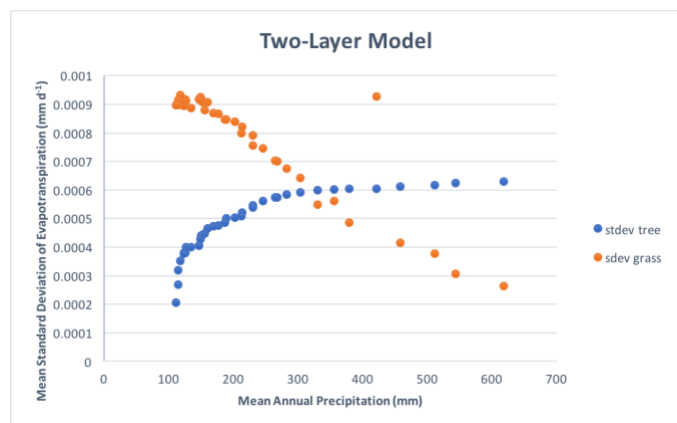
Parameterization

The models used in this study were run for a set of precipitation parameters, and precipitation events are set to occur throughout the first quarter the year. This set of precipitation parameters produces a precipitation gradient that produces between 150mm-800mm annually. Then along each set of precipitation parameters each model is run 10,000 times. Therefore, the models' average these values (such as mean total precipitation, mean soil moisture rate 1, etc...), at each precipitation depth interval. This provides a far more consistent analysis of the results from both models.

Results

In the two-layer model the mean standard deviation of woody evapotranspiration reaches its maxima during mesic precipitation parameters (>600mm MAP). The mean standard deviation

Figure 1. Mean standard deviation of vegetation in a two-layer model



of woody evapotranspiration's reaches its minima under the most arid precipitation parameters (<200 mm MAP) (Figure 1). Contrastingly, the mean standard deviation of grassy evapotranspiration reaches its maxima during the most arid periods (<200mm MAP), and begins to decline as

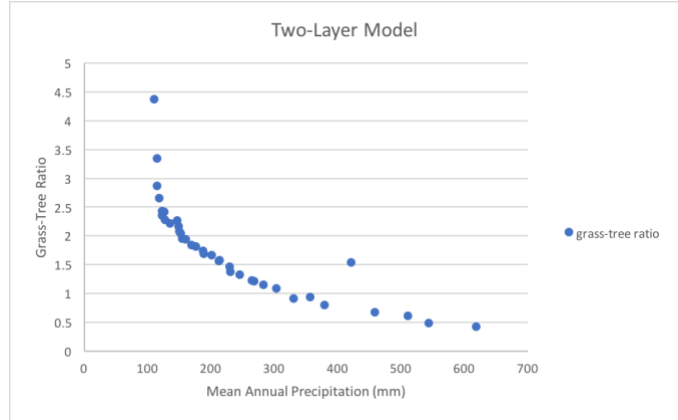


Figure 2. Grass-tree ratio using a two-layer model MAP

increases (Figure 1). There is an upturn in the mean standard deviation of woody evapotranspiration in intermediate MAP simulations (~400-500 mm MAP), while the mean

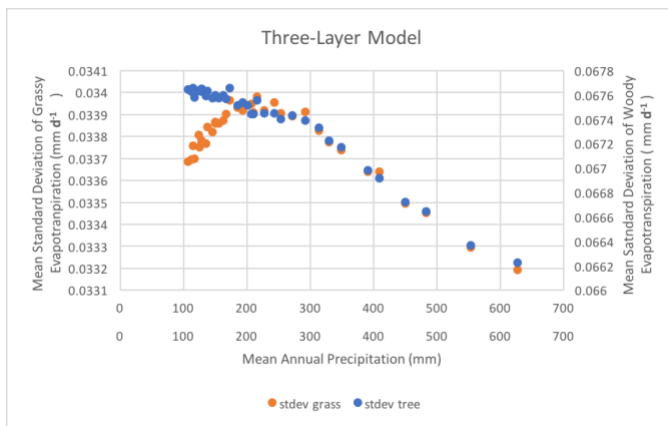


Figure 3. Mean standard deviation of vegetation in a three-layer model

standard deviation of grassy evapotranspiration is observed declining under intermediate MAP. As precipitation increases so does the mean standard deviation of evapotranspiration, but there is an increase in the rate of

evapotranspiration rate although it is not linear. Overall the mean standard deviation of grass declines with MAP except for one atypical event where the mean standard deviation of grass is exceptionally high. In the two-layer model the grass-woody vegetation ratio peaks in arid conditions before it begins declining as MAP increases (Figure 2).

The mean standard deviation of grass and woody evapotranspiration rates in the three-layer model are based on edaphic parameters and MAP. In grasses the mean standard deviation of evapotranspiration is observed peaking during intermediate MAP simulations. Subsequently

the mean standard deviation of woody evapotranspiration peaks (~0.034 mm d⁻¹) in the most arid simulations, but the peak in the mean standard deviation of grass occurs (~0.034) under intermediate MAP simulations (Figure 3). The results regarding the mean standard deviation of

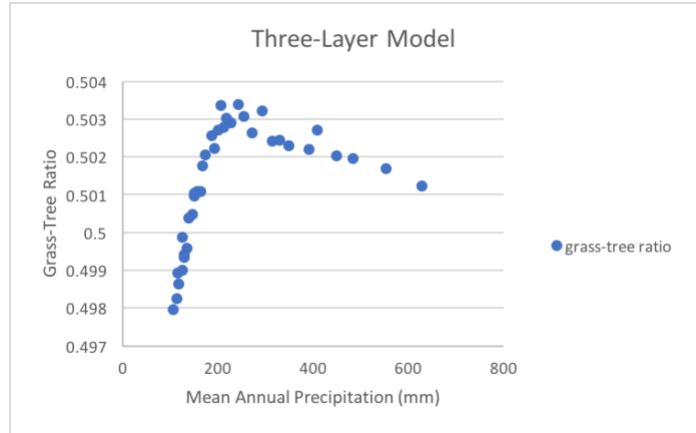


Figure 4. Grass-tree ratio using a three-layer model

woody evapotranspiration suggests that it thrives under more extreme changes in MAP. In the three-layer model the grass-woody vegetation ratio increases rather linearly until it reaches

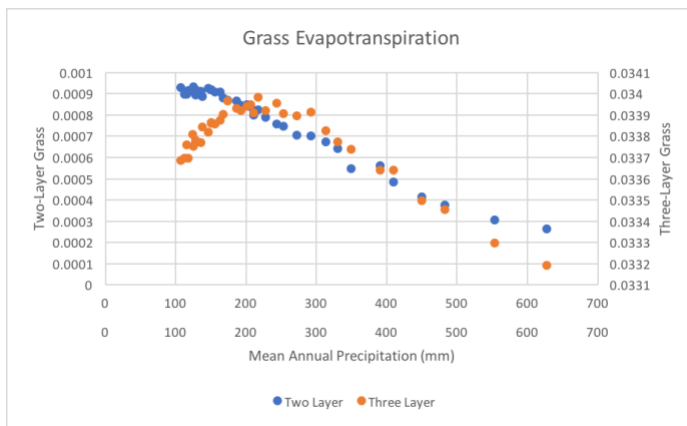


Figure 5. Comparison of grassy evapotranspiration

intermediate MAP before it begins declining as MAP continues increasing (Figure 4).

In both models, there is a change in the mean standard deviation of evapotranspiration relative to

precipitation. The peaks in mean standard

deviation of evapotranspiration vary significantly based on which model has been applied. The mean standard deviation of grassy and woody evapotranspiration increases once the soil's moisture content begins increasing until intermediate MAP, when the three-layer model is used. Although when the two-layer model is applied there is an observed decrease in the ratio of grass-woody vegetation (Figure 4).

A comparison of the mean standard deviation of grassy evapotranspiration in the two and three-layer models shows distinct patterns (Figure 5). Using the two-layer model results in a

peak in the mean standard deviation of grassy evapotranspiration when the least amount of MAP is received. In the three-layer model the peak in the mean standard deviation of grassy evapotranspiration occurs under intermediate MAP generations (Figure 5). Although as MAP continues increasing then the mean standard deviation of evapotranspiration starts declining. The results from these two models provide the ratio of grassy mean standard deviation to woody mean standard deviation, and provide important new insight into the woody-grass interactions occurring in savanna environments.

Discussion

There has been a considerable amount of interest in woody-grass interactions as well as belowground competition in dryland ecohydrology. The results provide a unique opportunity to investigate woody-grass belowground competition quantitatively in savannas. Research over the last twenty years' is focused on better understanding the role of the ecohydrological mechanisms contributing to the tree-grass coexistence observed in savannas. Previous studies have shown that a positive feedback exists between the soil moisture content and the overall rate of evapotranspiration (Obakeng, 2007; Porporato et al., 2003). This study has shown a positive relationship exists between the rate of grassy evapotranspiration and intermediate precipitation, which is a conclusion that is supported by previous studies (Mordelet et al., 1997; Scanlon et al., 2002; Scheiter and Higgins, 2007). These results also suggest that water is the primary determinant in water-limited environments regarding vegetative productivity. The bounds set for this precipitation simulation, produces a precipitation gradient that can simulate the MAP observed along the KT. Precipitation events predominantly begin occurring in October and continue through April along the KT. These precipitation events occur during the summer

months, and is why the region is characterized with wet (Oct- Apr) and dry (May- Sept) seasons (Bateman et al., 2003; Caylor and Shugart, 2004).

Two-Layer Model

The peak in the mean standard deviation of grassy evapotranspiration occurs when MAP is approximately 200 mm (Figure 3), and decreases as MAP increases along the gradient (Figure 3), but this decline in the mean standard deviation of grassy evapotranspiration is not reflected in the environment (Dintwe et al., 2015; Mordélet et al., 1997; Scheiter and Higgins, 2007). Several studies have questioned the applicability of Walter's hypothesis as a consistent representation of woody-grass interactions occurring in savannas (Sankaran et al., 2004; Scholes and Archer, 1997; Ward et al., 2013). These results suggest that savannas are inherently unstable environments that are in transition, which has been discussed (Scholes and Archer, 1997; Walker et al., 1981). Recent research has shown that savannas are in fact a relatively stable environment ecologically than previous hypothesized (D'Odorico et al., 2009; Okin et al., 2009). In particular, research is suggesting that direct competition occurs between trees and grasses for available belowground resources in savannas (Dintwe et al., 2015; Mordélet et al., 1997; Scheiter and Higgins, 2007). Walter's two-layer hypothesis has been unable to account for the observed peak in grassy vegetation under intermediate MAP (Caylor et al., 2003; Scanlon et al., 2002). This shortcoming drastically underestimates the direct competition occurring between woody vegetation and grasses.

Three-Layer Model

This model produces a peak in mean standard deviation of grassy evapotranspiration that varies from Walter's two-layer hypothesis, which occurs under intermediate MAP (Figure 3). The three-layer soil model appears to provide a far more consistent simulation of the observed

woody-grass interactions occurring in savannas than previous studies (Walter, 1971; Ward et al., 2013). These results are providing a new perspective through which woody-grass interactions in savannas can be investigated. The model shows an overall increase in the mean standard deviation of woody vegetation's rate of evapotranspiration at the lower (~200 mm) bound of the precipitation gradient (Figure 2). This produced an overall decline in grassy evapotranspiration as MAP variability increased (Figure 3). A decline in grass cover is especially problematic for it is typically an irreversible transition in which the environment becomes locked in a state dominated by woody vegetation (Okin et al., 2009).

This model is also potentially useful in investigating the influence of changing soil moisture dynamics on woody-grass interactions. The objective is to show some of the possible dynamic interactions occurring between vegetation, and soil moisture content in savannas. In previous studies that have investigated savanna soil moisture content there is a consensus that a positive feedback exists between soil moisture content and vegetation (Caylor et al., 2003; D'Odorico et al., 2007). It is apparent that with the three-layer model an overall increase in the mean standard deviation of grassy evapotranspiration occurring. These results further support the hypothesis that there is a positive feedback between vegetation and soil moisture content. The increase in overall evapotranspiration as MAP increases along the KT further supports the conclusions of previous research (Bhattachan et al., 2012; Dintwe et al., 2015). Inversely the results also concur with what the stress-gradient hypothesis predicts, but not directly (Figure 2). The stress-gradient hypothesis predicts that a shift will occur from competition in mesic savannas, and as precipitation decreases a transition to facilitation in arid savannas (Dohn et al., 2013). As precipitation decreases along the KT so does the overall rate of evapotranspiration. This can be interpreted as an overall decrease in direct competition occurring between trees and

grasses as savannas increase in aridity, for as evapotranspiration decreases so does vegetative activity. The results from this study provide a much more in depth understanding regarding the influence of climate and soil on the distribution of vegetation in savannas.

Conclusion

This model provides a new perspective through which savanna ecohydrology and woody-grass distribution can be investigated. There is an increasing body of research suggesting Walter's two-layer hypothesis does not provide a consistent distribution of woody-grass roots (Ward et al., 2013). There have been many analytical and numerical models that use Walter's two-layer hypothesis as the conceptual foundation (Lehmann et al., 2009; Ward et al., 2013; Yu and D'Odorico, 2014). The results show redistributing woody and grass roots into three-layers, provides a far more consistent representation of woody-grass interactions in savannas. This affirms the need to continue investigating the ecohydrological mechanisms responsible for the woody-grass distribution, as well as developing more accurate models of belowground competition (Dintwe et al., 2015; Dintwe and Okin, 2018). Resulting in a fundamental change in analytically and numerically modeling savanna ecohydrology. There remain many questions regarding woody-grass interactions in savannas and the eco-mechanisms responsible for their coexistence. How would dynamic roots respond to changes in MAP, and how would this influence these woody-grass interactions? This study has helped improve upon current knowledge regarding the influence that MAP has on the woody-grass distribution in savannas. These results support the theory that roots remain as shallow as necessary for evapotranspiration to happen, and that if roots are too deep evapotranspiration is unable to take place (Bhattachan et al., 2012). This study shows that woody vegetation has an extended growing season due to the distribution of roots vertically. Although savannas have been studied extensively for over a

century there remain many unanswered questions. Particularly regarding the eco-mechanisms responsible for the distribution of vegetation. This study helps provide a more refined and accurate depiction of woody-grass interactions as well as savanna ecohydrology. Further research is necessary to build upon current theories and provide a more complete picture of the ecohydrological mechanisms responsible for the distribution of savanna vegetation.

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