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Tree-grass co-existence in savanna: Interactions of rain and fire

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Abstract

The mechanisms permitting the co-existence of tree and grass in savannas have been a source of contention for many years. The two main classes of explanations involve either competition for resources, or differential sensitivity to disturbances. Published models focus principally on one or the other of these mechanisms. Here we introduce a simple ecohydrologic model of savanna vegetation involving *both* competition for water, and differential sensitivity of trees and grasses to fire disturbances. We show how the co-existence of trees and grasses in savannas can be simultaneously controlled by rainfall and fire, and how the relative importance of the two factors distinguishes between *dry* and *moist* savannas. The stability map allows to predict the changes in vegetation structure along gradients of rainfall and fire disturbances realistically, and to clarify the distinction between *climate-* and *disturbance-dependent* ecosystems.

Keywords: savanna, tree-grass co-existence, fire, rainfall, soil water

INTRODUCTION

The term *savanna* describes ecosystems characterized by the co-dominance of trees and grasses. The proportions of tree and grass can vary greatly. Savannas occur in areas with annual rainfall from 300 to 1800 mm, and are commonly split into *dry* and *moist* forms (semi-arid and wet, nutrient-rich and nutrient-poor, fine-leafed and broad-leafed are all synonyms for this division). In *dry* savannas, the grass primary production is a strongly increasing function of annual rainfall, while in *moist* savannas the relation is weak or absent. The transition between *dry* and *moist* savannas can be located around 500–700 mm of annual rainfall (e.g., Scholes and Walker, 1993, Sankaran et al., 2005).

What is special about the savanna environment that allows trees and grasses to coexist, as opposed to the general pattern in other areas of the world where either one or the other functional type is dominant?

This has been referred to as the '*savanna question'* (Sarmiento, 1984). The question has attracted the interest of many scientists in the last forty years: Walter (1971), Walker and Noy-Meir (1982), Scholes and Walker (1993), Scholes and Archer (1997), Sankaran et al. (2004), Sankaran et al. (2005), D'Odorico et al. (2006), Scheiter and Higgins (2007), Lüttge (2008), Hanan et al. (2008), and Leibold (2008), among others.

According to rangeland ecology literature (e.g.,Westoby, 1989 and Briske et al., 2003), savannas can be viewed in light of range succession or state-and-transition models. In range succession models, savannas are a point in a continuous spectrum whose extremes are grassland and forest. Disturbances like fire or herbivores just modify the tree-grass ratio

along this spectrum with reversible transformations. In state-and-transition models multiple stable states are possible, and the rangeland dynamics is explained through transitions (reversible or irreversible and abrupt) due to disturbances between steady states. The existence of multiple stable states has been pointed out by Dublin (1995), van de Koppel et al. (1997), Anderies et al. (2002), van Langevelde et al. (2003), D'Odorico et al. (2006), Hanan et al. (2008), Okin et al. (2009), Baudena et al. (2010).

According to savannas ecology literature (e.g., Sankaran et al., 2004), the 'savanna question' is addressed within paradigms of equilibrium and disequilibrium. The former interprets the savanna as a long term stable state due to internal factors, being disturbances modifiers of the tree-grass ratio. According to the latter, savanna is an unstable state and its existence is due to disturbances which maintain the tree-grass mixture, preventing the achievement of the complete dominance of trees or grasses.

Within the equilibrium paradigm, the tree-grass co-existence has been explained through competition based mechanisms (e.g., root niche separation and balanced competition), while demographic bottleneck mechanisms are related to the disequilibrium paradigm (see Sankaran et al., 2004).

The archetypal competition-based model of tree-grass co-existence in savannas is based on the 'Walter hypothesis' (Walter, 1971), which assumes soil water to be the limiting resource, with grasses as the superior competitor, but having roots restricted to the topsoil layer whereas trees roots both in the topsoil and subsoil. The niche separation avoids the tree-grass competition and allows the stable co-existence. The absence of niche separation in fact would lead to one species equilibrium. Models based on the 'Walter hypothesis'

have been widely applied in literature (Walker et al., 1981, Walker and Noy-Meir, 1982, Eagleson and Segarra, 1985, van Langevelde et al., 2003).

Some experiments and observations have supported 'Walter hypothesis' (Knoop and Walker, 1985, Sala et al., 1989, Pelaez et al., 1994) but many others have cast doubts on the existence of vertical rooting niche separation (Scholes and Walker, 1993, Belsky, 1990, Le Roux et al., 1995, Mordelet et al., 1997, Smit and Rethman, 2000, Hipondoka et al., 2003).

In 'balanced competition' models, the superior competitor limits its own abundance and the inferior competitor can grow; in other terms the intra-specific competition of the superior competitor is stronger than the inter-specific competition (Amarasekare et al., 2003). For example, the water scarcity can limit the abundance of trees in savannas.

In the past two decades, the disequilibrium paradigm has gained favor over the equilibrium one (Higgins et al., 2000, Jeltsch et al., 2000, van Langevelde et al., 2003, D'Odorico et al., 2006, Gardner, 2006, and Hanan et al., 2008). The near-universal finding that tree cover increased when fires are excluded from savannas (Trapnell, 1959, Shackleton and Scholes, 2000) and that elephants (see the several studies reviewed in Kerley et al., 2008), giraffe (Pellew, 1983) and other herbivores can substantially modify savanna structure, lend evidence to this school of thought.

Fire is an intrinsic characteristic of many savanna ecosystem allowing tree-grass co-existence: trees at the seedling stage can be easily attachable by flames, thus fire acts as bottleneck in trees demography preventing the canopy closure. Fire has been explicitly included in many savanna models (Hochberg et al., 1994, Anderies et al., 2002, van Langevelde et al., 2003, D'Odorico et al., 2006, Beckage et al., 2009) and has often been

described as dependent on the availability of fuel load, that in arid ecosystem is given by dead grass. Hanan et al. (2008) and Baudena et al. (2010) have considered explicitly the demography of trees underlining the asymmetry of the fire effects between saplings and adult trees. This asymmetry can allow the survivorship of trees population at low densities thanks to mechanisms of 'storage effect' that compensate the loss of young trees due to demographic bottlenecks with the very low mortality of adult trees (Warner and Chesson, 1985). In addition, various studies focused on fire as cause of bistability in rangelands (Anderies et al., 2002, van Langevelde et al., 2003, Okin et al., 2009).

Simple (non-spatial) models of savanna dynamics, available in literature, focus the attention principally on one mechanism at a time. Competition mechanisms are considered by Walker et al. (1981), Walker and Noy-Meir (1982), Eagleson and Segarra (1985), Fernandez-Illescas and Rodriguez-Iturbe (2004), Baudena et al. (2010), while disturbances-driven mechanisms are used by Casagrandi and Rinaldi (1999), D'Odorico et al. (2006), Hanan et al. (2008), Beckage et al. (2009).

Sankaran et al. (2004) point out the necessity to take into account both disturbances and the competition for resources, simultaneously in order to capture their relative importance in shaping the different types of savannas.

Based on data from 854 sites in Africa, Sankaran et al. (2005) identify a distinction between savannas receiving less that ~650–700 mm of annual rainfall (*dry savannas*) and those receiving more (*moist savannas*). The former are stable, and disturbances modify the woody cover, but are not necessary for tree-grass coexistence; the latter are unstable and maintained by disturbances, in this case they are essential for the maintenance of a savanna.

van Langevelde et al. (2003) represent the savanna vegetation through a simple model of two equations (one for tree and one for grass) considering the joint role of water (through the root niche separation mechanism) and disturbances (fire and herbivores) that remove grasses and trees. In arid and semiarid ecosystems the dynamics of soil water is closely linked to the the dynamics of vegetation (Scholes and Walker, 1993, Rodriguez-Iturbe and Porporato, 2004), thus in our approach, we will consider explicitly the soil water in the root zone as a state variable.

Here, we address the 'savanna question' including in an ecohydrologic model balanced competition and bottleneck mechanisms. We propose a space implicit model of tree-grass dynamics competiting for soil water and perturbated by fire. In the *Materials and Methods* section, the savanna is described through a set of three differential equations including the dynamics of trees, grasses, and soil water, fed by rainfall, and disturbed by fire. The variability of the model's parameters is investigated and the stability analysis is presented. In the *Results* section, changes of vegetation structure along gradients of rainfall and fire frequency are predicted using the stability map in the rainfall-fire frequency space. The role of rainfall and fire frequency in maintaining dry and moist savannas is illustrated.

MATERIALS AND METHODS

Tree-grass dynamics

Let us consider the space implicit model introduced by Tilman (1994) to represent the

temporal dynamics of tree and grass

$$\begin{cases} \dfrac{dT}{dt} = & c_T T(1-T) - \delta_T T \\ \dfrac{dG}{dt} = & c_G G(1-G-T) - c_T TG - \delta_G G \end{cases} \quad (1)$$

where T and G are the fractions of area, occupied respectively by tree and grass. T and G are dimensionless, and range in the closed interval [0, 1]: $T = 0$ means that trees are not present in the area, $T = 1$ means that the area is fully covered by trees, and similarly for grasses. In addition, the values of T and G must satisfy also the condition $0 \leq T+G \leq 1$. c_T and c_G are the colonization rates, whereas δ_T and δ_G are the 'offtake' rates for trees and grasses respectively. c_T, c_G, δ_T, δ_G are all positive and carry dimension [1/t], where t is the time. In Eq. (1), trees are the *superior competitor*, while grasses are the *inferior competitor*. Tree can displace grass (the term - $c_T TG$), and colonize places where trees are absent (the term (1-T)), while grass can colonize places where both trees and grass are absent (the term (1-G-T)). See Tilman (1994) for further details.

Fire forcings and tree-grass dynamics

There is much evidence that fire influences the balance between tree and grass in savannas (e.g., Scholes and Walker, 1993). The occurrence and spread of fires depends on the presence of sufficient mass of dry plant material to provide a near-continuous fuel load. The fuel for savannas fires is mostly provided by dead grass: the fire may only burn

following years of adequate rainfall and low herbivory, when sufficient grass biomass has accumulated (Bond and van Wilgen, 1996).

The fire acts differently on grass and tree. Fire occurs mainly in the dry season, when the perennial grasses are dormant. It consumes grass leaves as fuel, but does not generally kill the dormant grass buds at/or below the soil surface. The fire also consumes tree leaf litter, but if grass is completely absent it is very difficult for fire to propagate. The living tree biomass is seldom ignited, but dead wood and leaf litter may be, and the aboveground live tree biomass can be killed by exposure to fire. Small trees are the most vulnerable, since they may be entirely within the flame zone. Mature trees are little affected, since their bark protects the main stem and their buds (dormant in the fire season) are held above the flame zone.

To take into account explicitly the fire forcing in our model system, Eq. (1), the removal term for grass, $-\delta_G G$, is split in two: $-fG$ describing the consumption of grass by fires, and $-\delta_{GO} G$ representing the grass reduction due to the other causes such as mortality and herbivores, similarly to van Langevelde et al. (2003); while in the equation for trees the reduction at aboveground cover due to fire ($-\delta_F fGT$) is determined by the amount of grass fuel load (fG), the tree abundance itself (T) and the trees vulnerability to fire δ_F, similarly to van Langevelde et al. (2003).

The system presented in Eq. (1) becomes:

$$\begin{cases} \dfrac{dT}{dt} = c_T T(1-T) - \delta_T T - \delta_F fGT \\ \dfrac{dG}{dt} = c_G G(1-T-G) - c_T TG - \delta_{GO} G - fG \end{cases}. \qquad (2)$$

In Eq. (2), the coefficient f [1/t] can be viewed as proxied by the fire frequency, while the coefficient δ_F [–] is a function of both the frequency and intensity of fire, where grass fuel load is a proxy for fire intensity. In Eq. (2) no differentiation is made between juvenile and adult trees. However, the value of the parameter δ_F can provide information about the mean age of trees. High values of δ_F represent sites where trees are young, and vulnerable to fire, while low values of δ_F represent sites where trees are adult and little affected by fire.

Rainfall forcing, soil water and tree-grass dynamics

Soil water is a direct link between the hydrologic cycle and the ecological system. In arid and semi-arid environments, the water present in the rooting zone is the primary determinant of vegetation composition, structure and function. Root zone water content is highly variable in time. In contrast to the 'Walter hypothesis' (Walter, 1971), where grasses have access only to the topsoil layer, and trees extend their roots both in topsoil and subsoil layers for water uptake, here we assume that the depth at which trees and grasses extract water is the same.

We further assume that the water table is so deep that it does not affect the water dynamics in the root zone. Let z [ℓ] indicate the root zone depth, n is the porosity (fractional pore volume [–]), w [ℓ^3] the control volume which is assumed having unit area and depth z, $w = 1 \times z$, and w_p [ℓ^3] the pore space in the volume w, $w_p = 1 \times z \times n = 1 \times w_1$, indicating with $w_1 = z \times n$.

Let S be the degree of saturation of the profile available water capacity, defined as the

water volume present in the root zone relative to the maximum volume of water that can be held in this zone (the pore space in the volume w). The dynamics of S is described by the following mass balance equation in the control volume w:

$$\frac{dS}{dt} = \frac{p}{w_1}(1-S) - \varepsilon S(1-T-G) - \tau_T ST - \tau_G SG. \quad (3)$$

S is dimensionless assuming values in the closed interval [0, 1], in particular $S = 0$ corresponds to completely dry soil, and $S = 1$ to completely saturated soil. The condition $S = 1$ rarely happens in semiarid and arid savannas, particularly if the balance is investigated at seasonal or annual time scales.

The term p/w_1, $[1/t]$, is the rainfall rate (over the unit area) $p \geq 0$ $[\ell/t]$ normalized by w_1 $[\ell]$. Here we assume that the soil surface is more-or-less horizontal, and that all the rainfall infiltrates in the soil. The term $(p/w_1)S$ is the deep percolation, i.e., the amount of rainfall exceeding the root zone capacity percolating beyond the root zone depth.

Note that in literature, the deep percolation is represented through a non-linear function of S (e.g., Rodriguez-Iturbe and Porporato, 2004). However, since the deep percolation is not a prominent feature of the hydrology of semi-arid systems (often less than 1% of the budget drains to the water table, e.g., Scholes and Walker, 1993, and references therein), we have made the linear assumption to keep the model tractable as first approximation.

The term $\varepsilon S(1-T-G)$ is the evaporation from bare soil. It depends on the fraction of bare soil, $(1-T-G)$, and the available soil moisture S. The term $\tau_T ST$ is the water uptake by

tree and $\tau_G SG$ the water uptake by grass. In Eq. (3), the parameters ε, τ_T, τ_G, normalized by w_1, are: maximum evaporation rate from the bare soil, water uptake rate by trees, and water uptake rate by grass respectively. The parameters ε, τ_T , τ_G are all positive, and carry dimension [1/*t*].

Model of savanna dynamics

The dynamics of trees and grass are linked to the dynamics of soil water. Thus in Eq. (2), the colonization rates, of tree, c_T, and grass, c_G, are not constant, but functions of the soil moisture in the root zone. For simplicity, we assume a linear dependence of c_T and c_G on S, i.e., $c_T = \gamma_T S$ and $c_G = \gamma_G S$, where γ_T, and γ_G are the maximum colonization rates, carrying the dimension [1/*t*].

Thus the coupled dynamics of tree, grass, and soil moisture in the presence of fire are described by a system of three differential equations:

$$\begin{cases} \dfrac{dS}{dt} = & \dfrac{p}{w_1}(1-S) - \varepsilon S(1-T-G) - \tau_T ST - \tau_G SG \\ \dfrac{dT}{dt} = & \gamma_T ST(1-T) - \delta_T T - \delta_F fGT \\ \dfrac{dG}{dt} = & \gamma_G SG(1-T-G) - \gamma_T STG - \delta_{GO} G - fG \end{cases} . \qquad (4)$$

Equation (4) is *a minimal ecohydrologic model* of savanna, characterized by 10 parameters: z, n ($w_1 = z \times n$), ε, τ_T , τ_G, γ_T, γ_G, δ_T, δ_{GO}, δ_F. The annual rainfall, p, and the fire frequency, f, are environmental forcings treated here as constants. In reality, they are stochastic variables as assumed by Fernandez-Illescas and Rodriguez-Iturbe (2004) in the case of

rainfall forcing and by D'Odorico et al. (2006) and Hanan et al. (2008) in the case of fire disturbances.

Their stochastic behavior can be considered through the statistical dynamical approach outlined by De Michele et al. (2007). The analytical results obtained here do not depend on rainfall and fire stochasticity, so our mathematical treatment is kept as simple as possible.

The model proposed in Eq. (4) is an extension of the model proposed by De Michele et al. (2007), and Vezzoli et al. (2008) for the coupled dynamics of soil moisture and one plant functional group in arid and semiarid ecosystems. The groups of parameters represented by the ratios $\lambda_T = \delta_T/\gamma_T$ and $\lambda_T = (\delta_{GO}+f)/\gamma_G$ are of particular interest in the next.

Values of the parameters

The values of the parameters in Eq. (4) are determined as follows. The depth of the root zone z is in the range 0.1 – 1 m, while the porosity n in the range 0.05 – 0.55, Scholes and Walker (1993). The colonization and loss rates are obtained by consideration of the time scales necessary to attain the steady state. For the loss rates we consider one plant functional group at a time, in absence of fire and soil water. Under these conditions, the vegetation declines to zero exponentially, i.e. $\propto exp(-\delta t)$. Making hypotheses about the time needed for each functional type to go close to extinction starting from its maximum value, we can estimate the mortality rate δ. Savanna trees have a lifespan in the order of $\approx$10 – 100 years, consequently $\delta_T \approx 0.03 - 0.3$ y^{-1} (e.g., a value of 0.0255 is used in Bampfylde et al., 2005). Grass tillers, on the other hand, live for 1 – 3 years, consequently

$\delta_{GO} \approx 1 - 3\ y^{-1}$. For the colonization rates, once we have fixed a value for the loss rates, we estimate the time interval necessary to the vegetation to attain its steady state, with unlimited resources ($S = 1$) and in the absence of competitors. We assume for trees that this takes 5 – 100 years, consequently $\gamma_T \approx 0.15 - 2.5\ y^{-1}$; and for grass, 20 – 180 days and consequently $\gamma_G \approx 20 - 200\ y^{-1}$. The parameter ε is determined assuming complete bare soil condition (i.e., $T = 0$, $G = 0$) and absence of rainfall ($p = 0$). In these conditions $S \rightarrow 0$ with an exponential function $S(t) = exp(-\varepsilon t)$, thus using a desiccation time (i.e., the time to go from $S = 1$ to $S = 0$) of 35 – 50 days (Wythers et al., 1999), $\varepsilon \approx 20 - 30\ y^{-1}$. The values of the uptake parameters, τ_G and τ_T, are determined fitting Eq. (4), at the steady state to the upper bound of the woody cover data collected by Sankaran et al. (2007), having fixed $z = 1$ m, $n = 0.345$, $\varepsilon = 20\ y^{-1}$, $\gamma_T = 2\ y^{-1}$, $\gamma_G = 180\ y^{-1}$, $\delta_T = 0.04\ y^{-1}$, $\delta_{GO} = 2.8\ y^{-1}$ and assuming $f = 0$. Figure (1) gives a comparison among the experimental data collected by Sankaran et al. (2007), the maximum tree cover obtained using a 99th quantile piece-wise linear regression by Sankaran et al. (2005), and the tree coverage calculated using Eq. (4) at the steady state. A range of $1 - 50\ y^{-1}$ is obtained for τ_G and τ_T, we will use $\tau_T = 30\ y^{-1}$, $\tau_G = 10\ y^{-1}$. The parameter δ_F varies from 0.02 if trees are very fire resistant to 0.6 if trees are easily killed by fire, in according to Casagrandi and Rinaldi (1999). We consider the annual rainfall in the range $p \approx 0 - 1800$ mm y^{-1}. According to Belsky (1994), in Africa, the fire occurrence in moist savannas is one every 1 – 2 years, while in dry savanna it is one every 3 to 10 years. For Brazilian cerrados and the wetter regions of Africa (the most frequently burnt ecosystems in the world) Bond and Keeley (2005) report values of the fire frequency that reaches a maximum of $2\ y^{-1}$. Here, we consider $f \approx 0 - 1.2\ y^{-1}$. Table 1 reports the range for the parameters and environmental forcings involved in Eq. (4).

Steady states

Equation (4) admits five steady state solutions, i.e., $dS/dt = dT/dt = dG/dt = 0$, but only four satisfy the conditions $0 \leq T \leq 1$, $0 \leq G \leq 1$, and $0 \leq T+G \leq 1$. Of these, the first solution is characterized by the absence of vegetation, which we will refer to as *unvegetated* i.e., $T = 0$, $G = 0$. The second solution has grass only, i.e., (desert) *grassland*, $T = 0$, $G > 0$. Solution three has trees only i.e., *forest*, $T > 0$, $G = 0$. The fourth solution has a co-existence of tree and grass, i.e., *savanna*, $T > 0$, $G > 0$. Table 2 reports the analytical expressions for the four stable states. For simplicity the equilibrium of tree-grass co-existence is given in the implicit form.

Stability analysis

Conditions for the spreading of a single functional type

The conditions for the spreading of a single functional type are determined by considering one functional type at a time. The type can have a positive stable equilibrium if its colonization rate is greater than its mortality rate. In Eq. (4) this is satisfied by the condition $S > \lambda_T$ for trees, and to $S > \lambda_G$ for grass, where S is the soil moisture at the equilibrium. Note that if $\lambda_G > 1$, then the conditions for the grass spreading can never be met because S takes values in the closed interval [0, 1]. Similarly, if $\lambda_T > 1$ then the condition for the tree spreading can never be satisfied.

Stability map

A stability analysis of the system described in Eq. (4) is performed in the space of parameters $p - f$, i.e., the environmental space defined by rainfall and fire.

The other parameters are assumed to be: $z = 1$ m, $n = 0.345$, $\varepsilon = 20\ y^{-1}$, $\tau_T = 30\ y^{-1}$, $\tau_G = 10\ y^{-1}$, $\gamma_T = 2\ y^{-1}$, $\gamma_G = 180\ y^{-1}$, $\delta_T = 0.04\ y^{-1}$, $\delta_{GO} = 2.8\ y^{-1}$, $\delta_F = 0.35$.

Within the ecologically-feasible domain, i.e., positive values of the environmental forcings and state variables, the system has 7 different regions of stability and bistability, see Fig. (2). Region 1 is *unvegetated*: the rainfall, $p \leq 100$ mm y^{-1}, is not sufficient to support either grasses or trees. In region 2, the stable equilibrium is (desert) *grassland: p* is sufficient for the existence of grasses, but not trees. In region 3, rainfall allows the occurrence of both trees and grasses, and the stable equilibrium is thus *savanna.* For high rainfall values ($p \geq 1100$ mm y^{-1}), within region 3, the equilibrium values of tree canopy cover are $T \geq 0.8$, in other words, although grass is present, this vegetation is a *forest*, closed woodland or thicker, Scholes (1997). In Fig. (2) the region 3 has been divided into two subregions (3a) and (3b) by the isoline $T = 0.8$ (grey line), corresponding to the cover fraction corresponding to the canopy closure, above which virtually no grass would be present because of shading.

In region 4, the stable equilibrium is *forest*, as well as in region 5. In region 4 grass cannot grow because the mortality due to fire is too high (i.e., very high fire frequencies can only be tolerated if the rainfall is also high). In region 5, the fire is not sufficient to prevent the closure of the tree canopy – a condition that is widely encountered. In both regions 4 and 5, the direct effect of fire on grass is greater than the indirect effect on trees. Regions 6 and 7 are characterized by *bistability*. In region 6, the stable equilibria are *grassland* and *forest*,

while in region 7 are *savanna* and *forest*.

The bistability between savanna and forest has been found also by da Silveira Lobo Sternberg (2001). The equilibrium state of the system in the bistability regions depends on the initial condition and on the history of disturbances (Solbrig et al., 1996).

The bistability in regions 6 and 7 is associated to the high fire frequency. Depending on initial condition, two scenarios are possible: 1) fire completely removes grasses leaving only trees (forest), 2) fire is enough to completely remove trees (region 6), or to limit their abundance (region 7), but some grass is left.

Note that the boundaries of the regions are parameter-dependent.

RESULTS

In this Section we discuss the stability map in detail showing the changes in vegetation that it predicts along gradients of rainfall and fire. Moving up a rainfall gradient, $50 \leq p \leq 1800$ mm y^{-1}, at two different levels of disturbance: one characterized by fires once every five years, $f = 0.2$ y^{-1}, transect A-B in Fig. (2); and the other by annual fires, $f = 1$ y^{-1}, transect C-D in Fig. (2); Fig. (3) shows the values of T and G along the transects. Thereafter we consider the fire gradient, $0.2 \leq f \leq 1$ y^{-1}, at a value of annual rainfall $p = 650$ mm y^{-1}, transect P-Q in Fig. (4), at two different levels of trees fire vulnerability, i.e., $\delta_F = 0.05$ and $\delta_F = 0.35$.

Vegetation changes along a rainfall gradient with infrequent fires

The transect $50 \leq p \leq 1800$ mm y^{-1} at $f = 0.2$ y^{-1} is characterized by a continuous change of vegetation, without abrupt transitions, from unvegetated, to (desert) grassland, to savanna,

to forest.

This sequence has been described as the *sub-tropical succession* according to Shmida and Burgess (1988). In Fig. (3) note that the boundary between *grassland* and *savanna* is located at different values of annual rainfall (p) depending on the fire frequencies (f). If $f \to 0$ y^{-1} the region of grassland between *unvegetated* and *savanna* is small. In Fig. (2), the transect A-B is representative of fire conditions with $0 \leq f \leq 0.6$ y^{-1}. In absence of fire disturbance ($f = 0$ y^{-1}), the same vegetation sequence is observed with the only difference being the tree coverage at a given rainfall, see Fig.s (3a, b). This means that the fire influences the tree-grass ratio in region 3, and the grass coverage in region 2, while the rainfall availability determines the type of vegetation. Regions 2 and 3 could be designated *climate-dependent ecosystems*, following the nomenclature suggested by Bond et al. (2003).

For values of annual rainfall in the range $100 \leq p \leq 600$ mm y^{-1} the co-existence of tree and grass is permitted by the limited amount of water resource, while the fire influences the tree-grass ratio only. The water scarcity limits the density of the superior competitor, allowing the co-existence through mechanisms of balanced competition.

Along the rainfall gradient the savanna equilibrium varies continuously without abrupt or irreversible transition. This behavior is coherent with the equilibrium paradigm and the range succession models philosophy. In this case, savannas can be considered as broad ecotones between grasslands and closed woodlands as noticed in Walter (1971). This type of savanna is commonly called *dry savanna*, (Sankaran et al., 2005).

Vegetation changes along a rainfall gradient with frequent fires

The transect C-D for high fire frequency ($f = 1\ y^{-1}$) intersects regions of bistability: this implies that the vegetation model exhibits an hysteresis cycle (i.e., abrupt changes) in terms of both tree and grass.

Figures (3c, d) give the values of T and G along the transect C-D. Starting from point E in Fig.s (3c, d), where the vegetation is *grassland*, and increasing the annual rainfall, point F is reached, where trees can colonize grass patches and bare soil, and the co-existence of tree and grass is possible, i.e., a *savanna* equilibrium (pathway F→ G → H). Further increasing the rainfall leads to an abrupt transition from *savanna* to *forest* (pathway H → I): grass goes to zero and trees increase sharply in coverage. With further increases in P, the system remains in the *forest* state (pathway I → D). In reverse, if the annual rainfall decreases (pathway D → I → L → M → N) the system remains as *forest* until the *unvegetated* state is attained. The existence of a 'catastrophic' transition from *savanna* to *forest* is in agreement with Sankaran et al. (2005), who observe that when fire is essential to maintaining the savanna, then an abrupt, rather that gradual, increase in the maximum value of woody coverage is expected. From Fig.s (3c, d), if the system is at forest equilibrium (e.g., point M or L), an intensive tree harvesting (i.e., deforestation or high browsing pressure for instance by elephants) can provoke a rapid transition to grassland (M → E) or savanna state (L → G). The forest ecosystem can be recovered only by replanting or by an increase of the annual rainfall over the catastrophic transition (H → I). Abrupt transitions in space from forest to savanna or grassland lead to patchy landscapes – a widely observed phenomenon at high values of annual rainfall (e.g., Murphy and Lugo, 1986).

In Fig. (2), the transect C-D is representative of high fire conditions with $0.7 \le f \le 1.2\ y^{-1}$. Comparing the transect C-D with the transect at $f = 0\ y^{-1}$ and $50 \le p \le 1800$ mm y^{-1} (i.e., absence of fire disturbance), it is possible to observe a different

vegetation sequence. Thus fire determines the type of vegetation in this case and regions 4, 5, 6, 7 could be classified as *fire-dependent ecosystems*, according to Bond et al. (2003). The alternation of stable states along the rainfall gradient and the presence of abrupt transitions are coherent with the disequilibrium paradigm and the state-and-transitions models philosophy. Fire-dependent savannas exist because of fires causing bottlenecks in tree demography preventing the canopy closure. Moreover, the persistence of grass in fire-dependent ecosystem is strengthened by the positive feedback between grasses and fire: more grasses means more fuel load, more fire implies less trees, and consequently more space available to grasses and, thence, an increase in fire fuel load; in case of grasses extinction, trees grow undisturbed due to the absence of grass and, thence, of fire.

The grassland in region 6 can be denoted as *false grassland* according to Acocks (1953) and Bond et al. (2003), because in absence of fire the vegetation should be more wooded. For high values of annual rainfall, $p \geq 1100$ mm y^{-1}, the co-existence of tree and grass is permitted only by the high levels of fire disturbance. This type of savannas, *disturbance-driven*, is often called *moist savanna*.

Vegetation changes along gradients of fire frequency

Here a fire gradient, $0.2 \leq f \leq 1$ y^{-1} at a value of annual rainfall $p = 650$ mm y^{-1} is considered. Figure (4) gives the bifurcation diagram for two different values of the fire sensitivity parameter δ_F: 0.05 and 0.35. The first value is representative of fire resistant trees, panel (a), while the second value represents fire-vulnerable trees, panel (b). The

stability map in Fig. (4) can refer to plant communities with different fire vulnerabilities of trees, but also to different life stages of trees at a single site, e.g., panel (a) for adult trees, and panel (b) for juvenile trees. In both panels of Fig. (4), starting from point P of savanna equilibrium, and increasing the fire disturbance in the range $0.2 \leq f \leq 0.8$ y^{-1}, savannas persist. A further increase of the fire disturbance, $f > 0.8$ y^{-1}, leads to a transition from savanna to forest in panel (a), a counter-intuitive result. In practice, fires so frequent cannot be sustained at this rainfall level, especially in presence of trees. In panel (b), with $0.8 \leq f \leq 1$ y^{-1}, the system comes into regions 6 and 7 of bistability. Tolerance to the fire, especially in the juvenile life stages, has been noted by Bond et al. (2003) as a key requirement for savanna trees. In panel (b), the system can stay in savanna (when the system is in region 7) and then pass into grassland (when the system is in region 6). This is in agreement with the school of thought according to which: fire might be, in the long term, the only management tool to maintain healthy grass populations (e.g., Zimmermann et al., 2009 and reference therein). If the increase of fire is not gradual, abrupt transitions from savanna to grassland or from savanna to forest are feasible.

CONCLUSIONS

We present a simple ecohydrologic model of savanna vegetation, described through a set of three differential equations. The space implicit model includes the dynamics of tree, grass, and soil water as forced by rainfall and fire. This analytical (as opposed to numerical simulation) model is unusual in that it combines both competition- and disturbance-based mechanisms, and shows that they occupy a continuum rather than being alternative

descriptions of savanna dynamics.

The stability map in the parameters space of rainfall and fire synthesizes the conditions for the different types of vegetation: *unvegetated,* (*desert*) *grassland*, *savanna*, and *forest*. It helps to 1) clarify that the co-existence of tree and grass is due to the simultaneous influence of rainfall and fire, and 2) distinguish the two main types of savanna. For $100 \leq p \leq 600$ mm y^{-1} the *dry* savanna co-existence is permitted by the balanced competition for limited rainfall and fire influences only the tree-grass ratio. The system would still be a savanna, even in the absence of fire. For rainfall above 1100 mm y^{-1} the *moist* savanna co-existence can only occur in the presence of a high level of fire disturbance, because the ecosystem would be a forest in the absence of fire. In the intermediate range, $600 \leq p \leq 1100$ mm y^{-1}, savanna is the result of the co-occurence of water limitation and fire. The stability map shows how *dry savannas* are stable equilibria, while *moist savannas* are a bi-stable condition with forest. The stability map allows also to predict the vegetation structure changes that occur along gradients of rainfall and fire frequency, and to clarify the distinction between *climate-dependent ecosystems* and *fire-dependent ecosystems*.

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TABLES

Table 1 Range for parameters and environmental forcings of the model in Eq. (4).

Symbol	Unit	Range
z	m	0.1 – 1
n	–	0.05 – 0.55
ε	y^{-1}	20 – 30
τ_T	y^{-1}	1 – 50
τ_G	y^{-1}	1 – 50
γ_T	y^{-1}	0.15 – 2.5
γ_G	y^{-1}	20 – 200
δ_T	y^{-1}	0.03 – 0.3
δ_{GO}	y^{-1}	1 – 3
δ_F	–	0.02 – 0.6
p	mm y^{-1}	0 – 1800
f	y^{-1}	0 – 1.2

Table 2 Steady states of the model in Eq. (4).

	Steady state			
Variable	*Unvegetated*	*Grassland*	*Forest*	*Savanna*
S	$\frac{p/w_1}{(p/w_1)+\varepsilon}$	$\frac{(p/w_1)-(\varepsilon-\tau_G)(\delta_{GO}+f)/\gamma_G}{(p/w_1)+\tau_G}$	$\frac{(p/w_1)-(\varepsilon-\tau_T)\delta_T/\gamma_T}{(p/w_1)+\tau_T}$	$\frac{(p/w_1)}{(p/w_1)+\varepsilon(1-T-G)+\tau_T T+\tau_G G}$
T	0	0	$1-\frac{\delta_T}{\gamma_T S}$	$1-\frac{\delta_T}{\gamma_T S}-\frac{\delta_{GO}+f}{\gamma_G S}$
G	0	$1-\frac{\delta_{GO}+f}{\gamma_G S}$	0	$1-\frac{\delta_{GO}+f}{\gamma_G S}-T\left(1+\frac{\gamma_T}{\gamma_G}\right)$

FIGURES

AF_DMC_VR_DD_SRJ_Figure_1.eps

Figure 1 Patterns of tree cover in relation to annual rainfall. Points represents observations collected by Sankaran et al. (2007). The dashed line represents the maximum tree cover obtained using a 99th quantile piece-wise linear regression by Sankaran et al. (2005). The continuous line is the tree coverage calculated using Eq. (4) at the steady state, with the parameter values set at $z = 1$ m, $n = 0.345$, $\varepsilon = 20\ y^{-1}$, $\tau_T = 30\ y^{-1}$, $\tau_G = 10\ y^{-1}$, $\gamma_T = 2\ y^{-1}$, $\gamma_G = 180\ y^{-1}$, $\delta_T = 0.04\ y^{-1}$, $\delta_{GO} = 2.8\ y^{-1}$, $\delta_F = 0.35$, $f = 0$.

AF_DMC_VR_DD_SRJ_Figure_2.eps

Figure 2 Stability map. Free parameters are p and f, whereas the values for the other parameters are: z = 1 m, n = 0.345, $\varepsilon = 20\ y^{-1}$, $\tau_T = 30\ y^{-1}$, $\tau_G = 10\ y^{-1}$, $\gamma_T = 2\ y^{-1}$, $\gamma_G = 180\ y^{-1}$, $\delta_T = 0.04\ y^{-1}$, $\delta_{GO} = 2.8\ y^{-1}$, $\delta_F = 0.35$. Region (1): unvegetated. Region (2): (desert) grassland. Region (3): savanna, this is divided into region (3a) where $T < 0.8$, and (3b) where $T \geq 0.8$, (i.e., a forest, if our model considered competition for light as well as water) the grey line is the isoline $T = 0.8$. Region (4): forest. Region (5): forest. Region (6): bistability grassland–forest. Region (7): bistability savanna–forest. The transects A-B and C-D are rainfall gradients, in low and high fire conditions respectively.

AF_DMC_VR_DD_SRJ_Figure_3a.eps
(a)

AF_DMC_VR_DD_SRJ_Figure_3b.eps
(b)

AF_DMC_VR_DD_SRJ_Figure_3c.eps
(c)

AF_DMC_VR_DD_SRJ_Figure_3d.eps
(d)

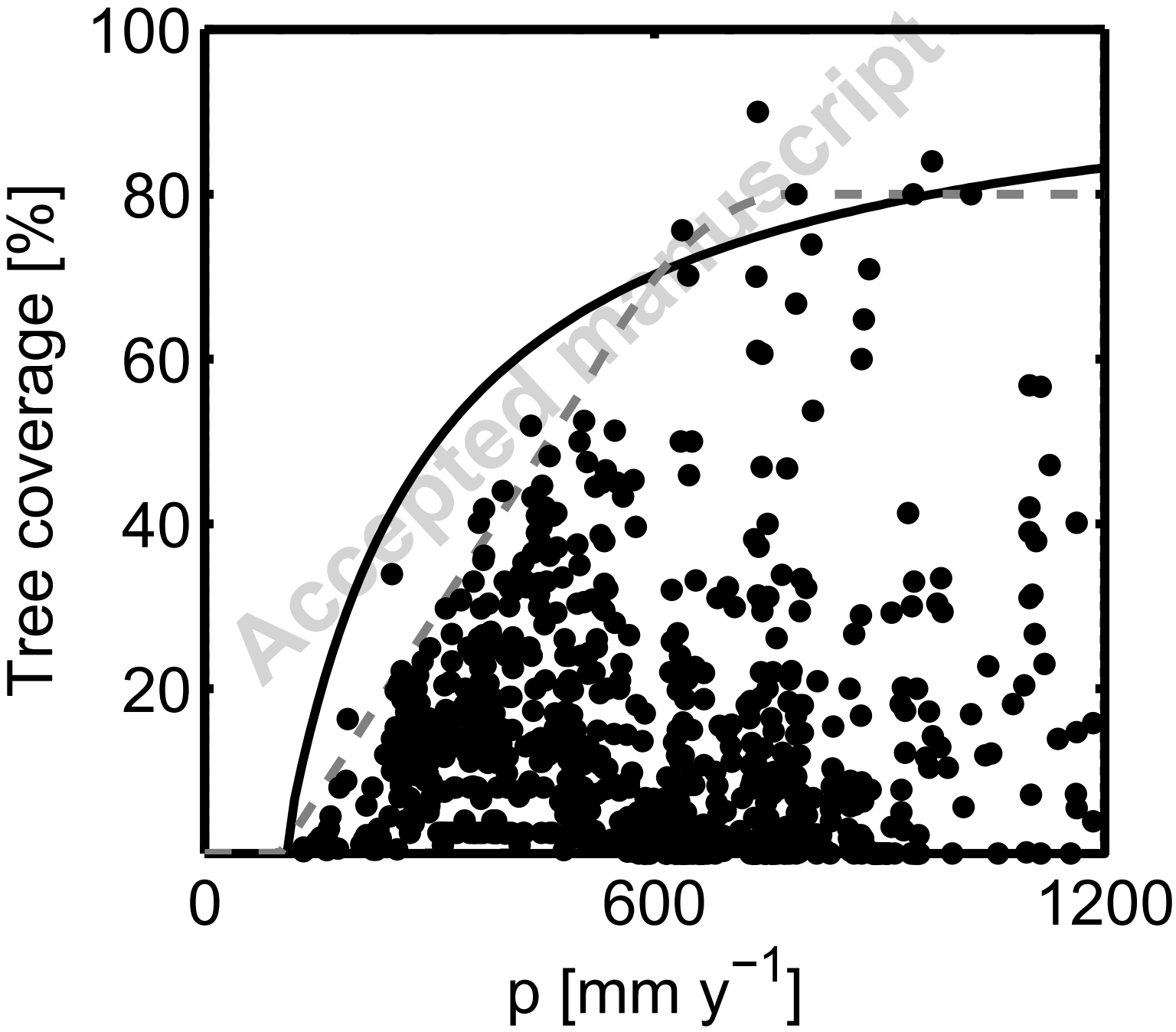
Figure 3 Changes in vegetation stable states over rainfall gradients in low and high fire conditions. Panels (a) and (b) show *T* and *G*, respectively, for the transect A-B under low fire conditions (black line), and the transect in the absence of fire (grey line). Panels (c) and (d) give *T* and *G*, respectively, for the transect C-D, under high fire condition.

AF_DMC_VR_DD_SRJ_Figure_4a.eps
(a)

AF_DMC_VR_DD_SRJ_Figure_4b.eps
(b)

Figure 4 Stability map in the parameters space rainfall-fire for two values of the tree fire sensitivity parameter δ_F: 0.05 in panel (a), and 0.35 in panel (b). Panels show the transect P-Q for $0.2 \leq f \leq 1$ y^{-1} and $p = 650$ mm y^{-1}.

Figure 1



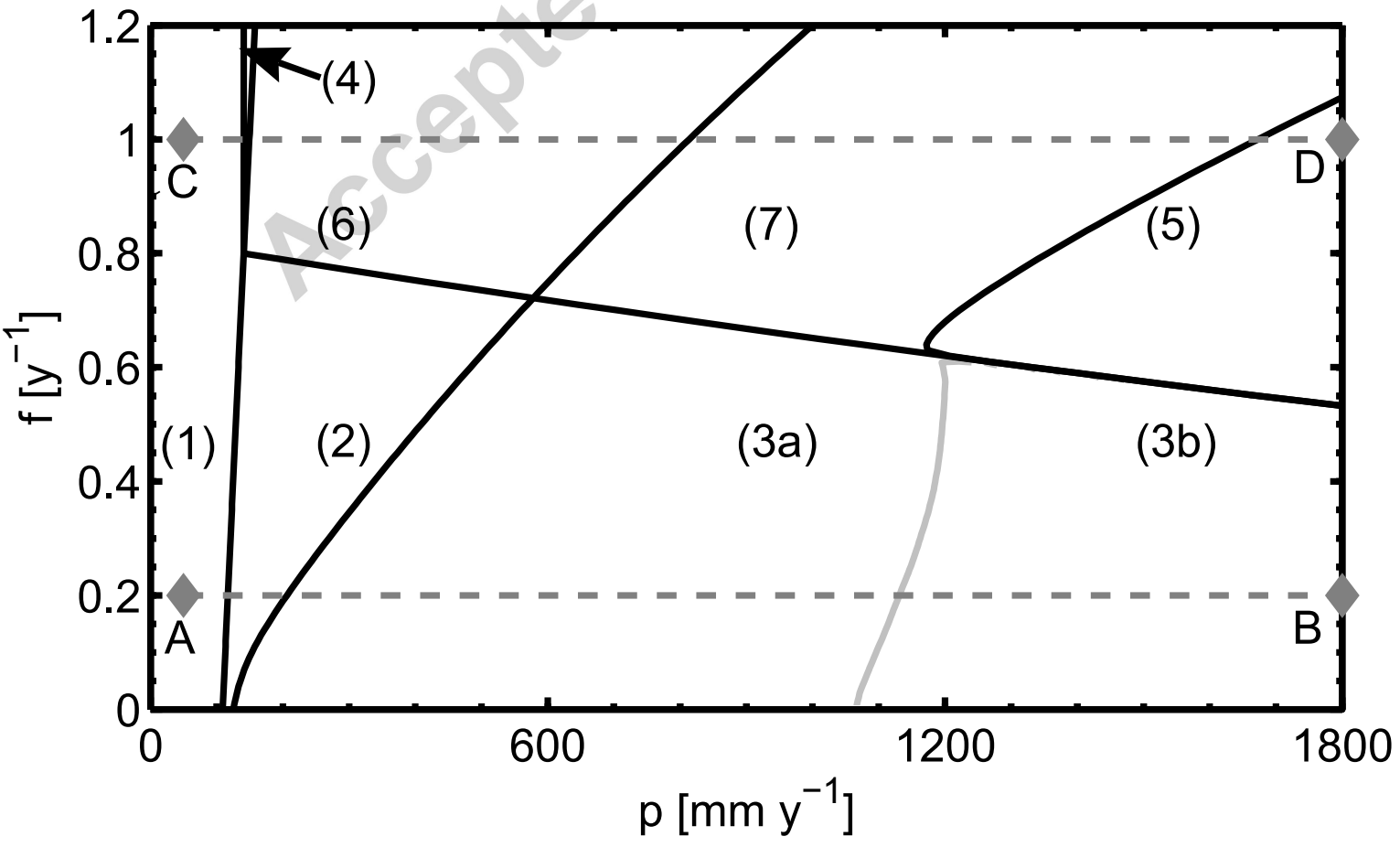


Figure 3a

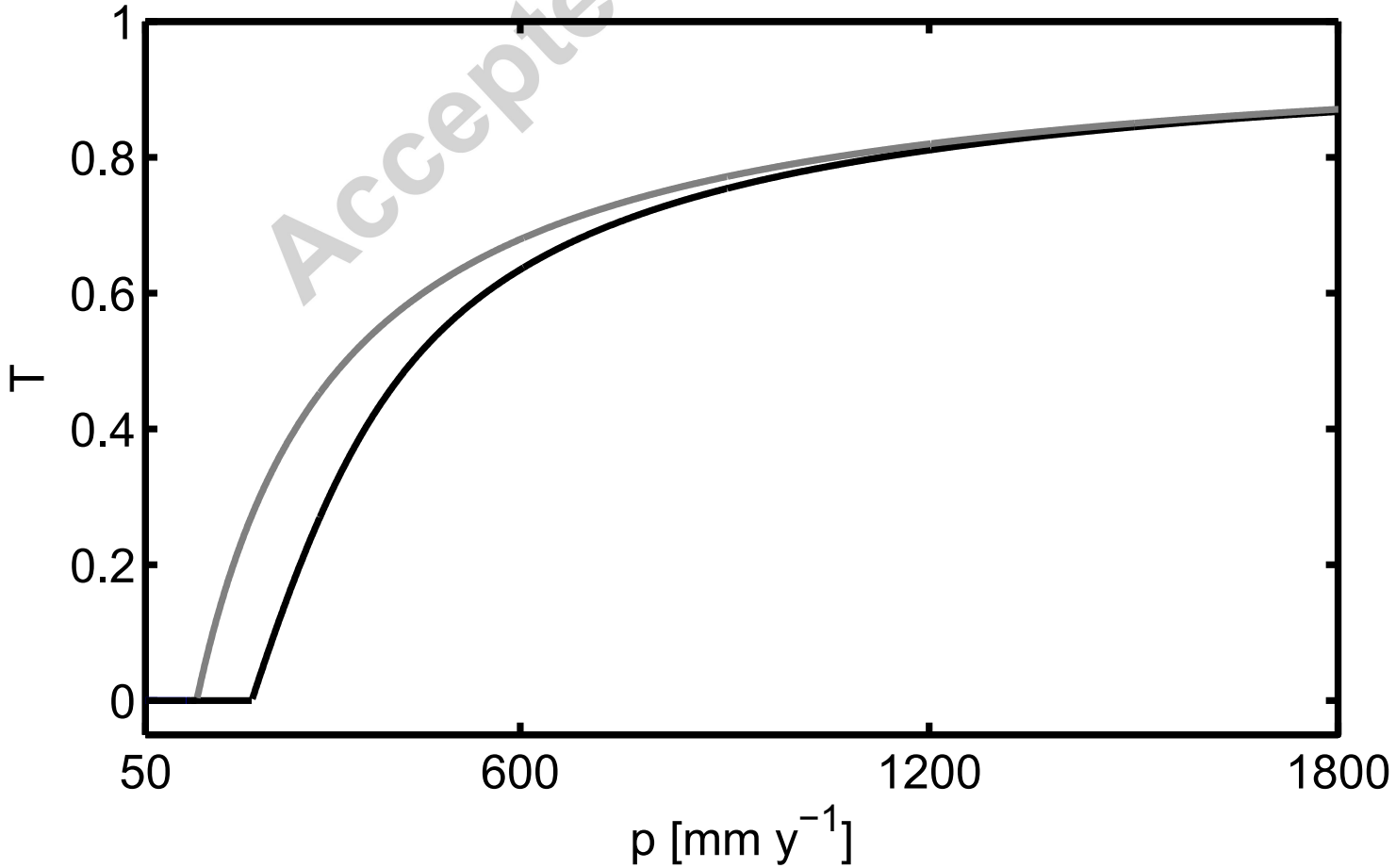
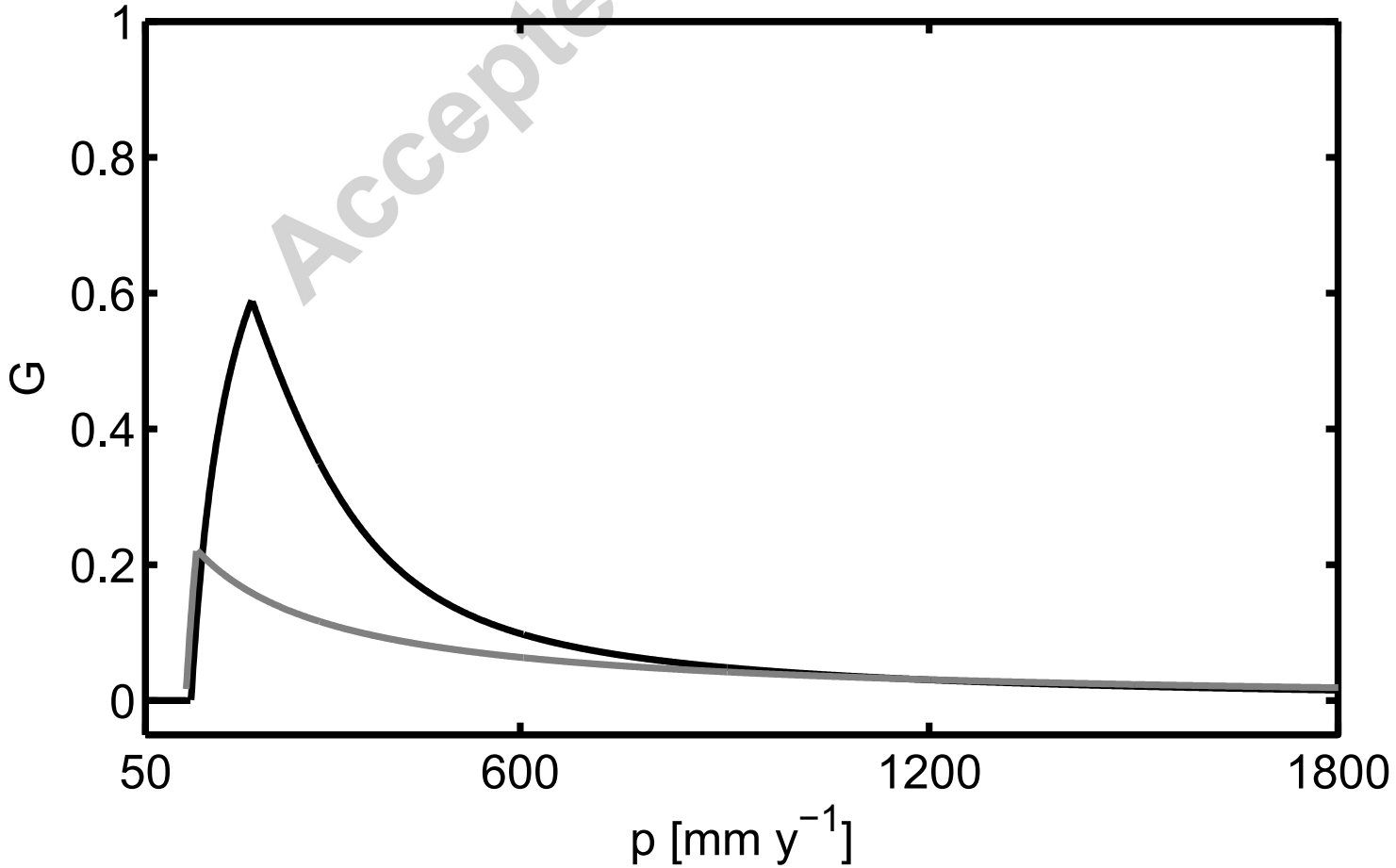


Figure 3b



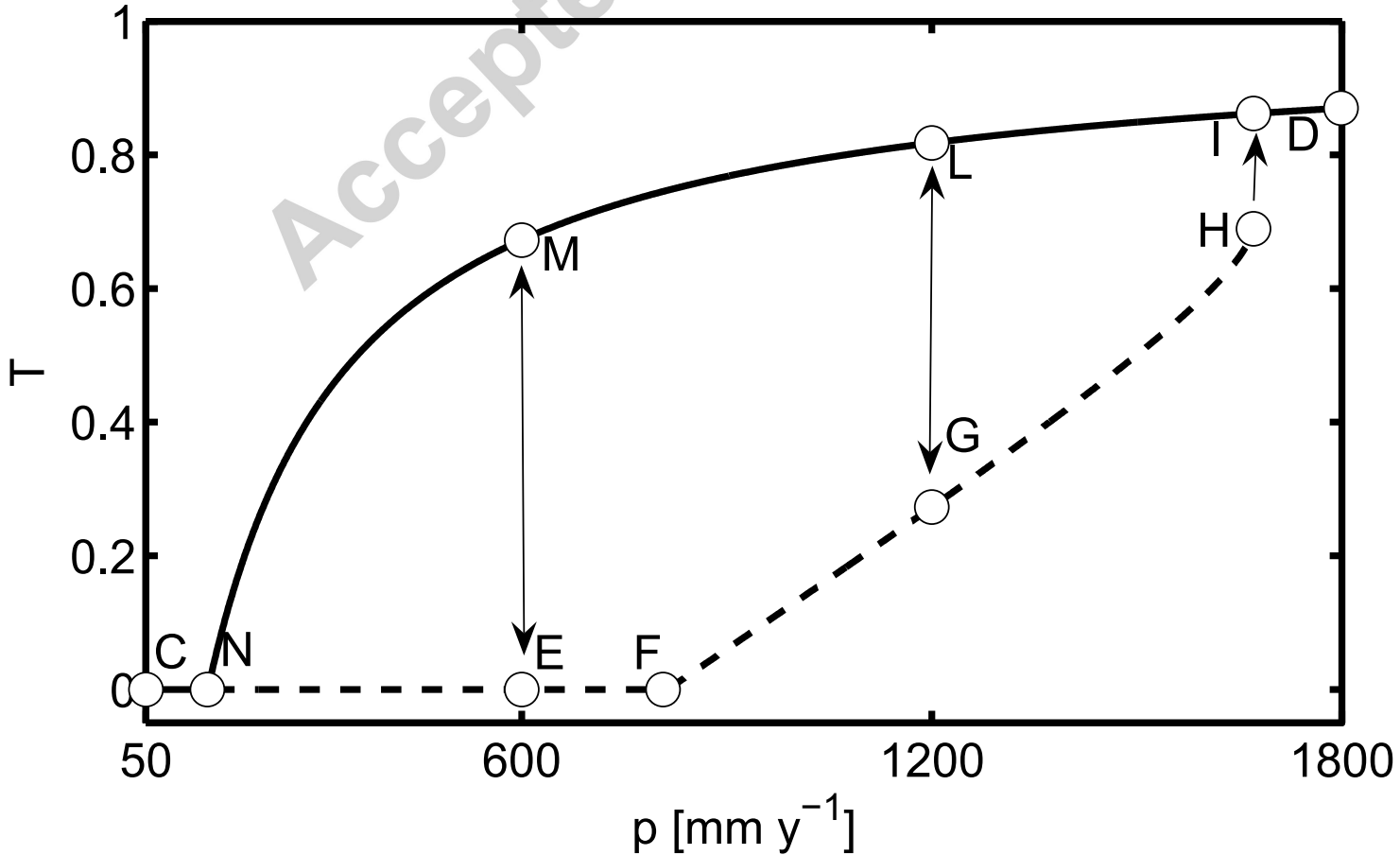


Figure 3d

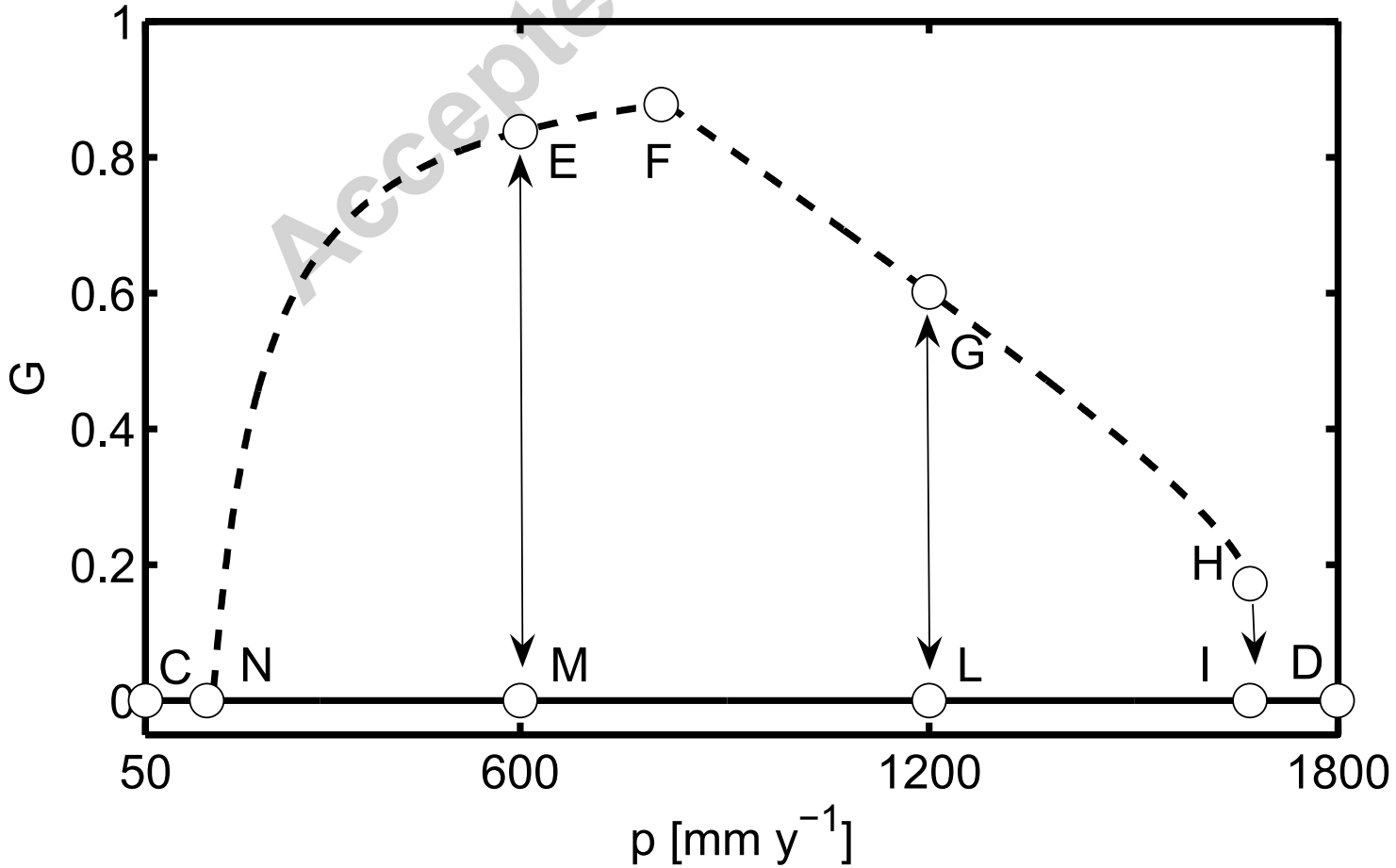


Figure 4a

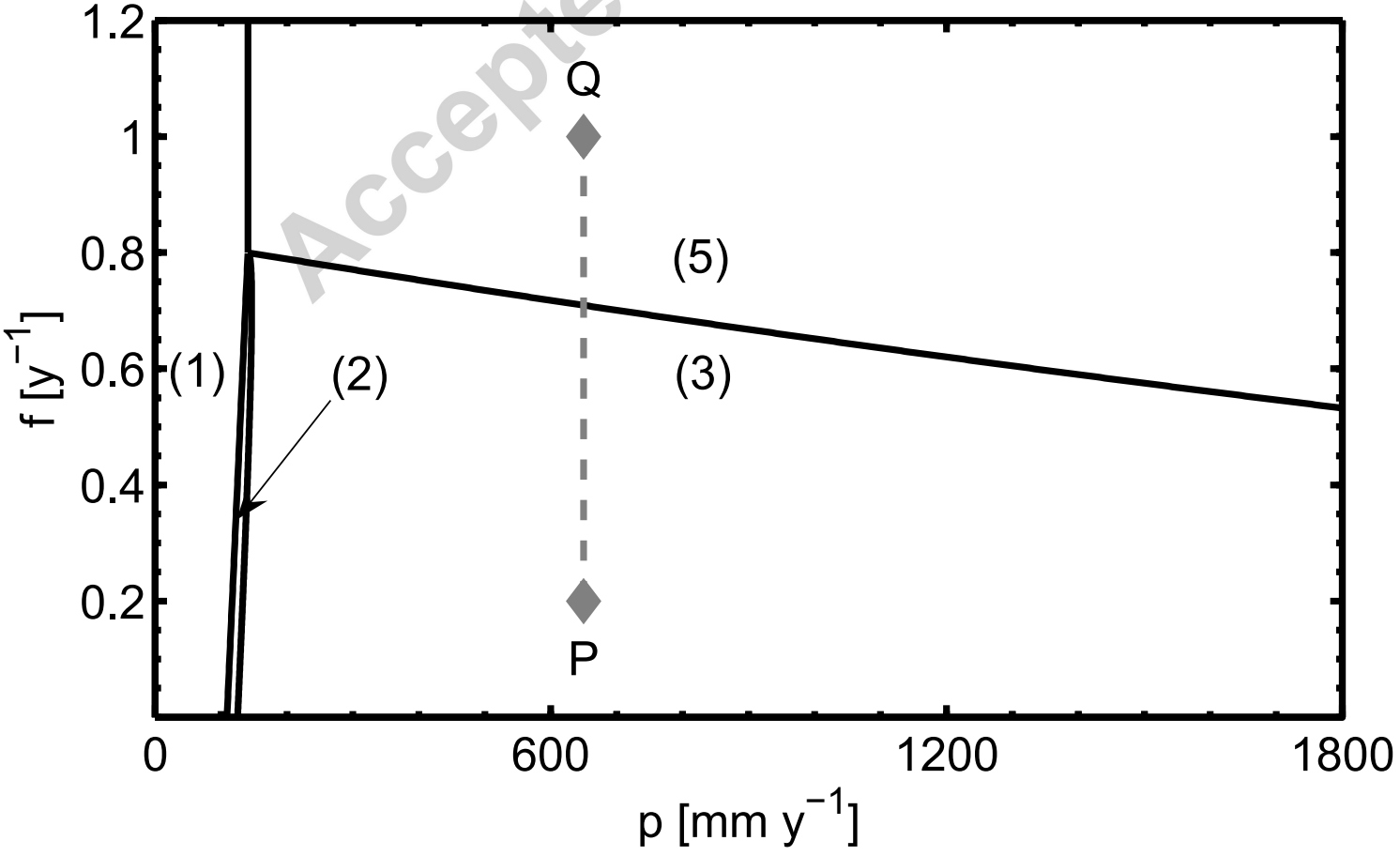


Figure 4b