

Modeling biomass competition and invasion in a schematic wetland

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[1] Plants growing along hydrologic gradients adjust their biomass allocation and distribution in response to interspecific competition. Furthermore, susceptibility of a community to invasion is to some extent mediated by differences in growth habit, including root architecture and canopy height. With reference to the study of a schematic wetland, the aim of this paper is (1) to test, via numerical modeling, the capacity of native plants to counteract an alien dominant species and cause eco-hydrological shifts of the ecosystem by changing their growth habit (e.g. allocating biomass below ground and by so doing changing the evapotranspiration locally) and (2) to test the impact on biodiversity of management practices that alter nutrient supply. The results demonstrated that unique combinations of vegetation types characterized by different growth habits may lead to different vegetation patterns under the same hydrologic forcing, and additionally, the vegetation patterns may change in response to major hydrological shifts, which could be related to diverse wetland management and restoration practices.

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1. Introduction

[2] One of the greatest threats to habitat loss in wetland communities is the spread of invasive plants [Zedler and Kercher, 2005; Lacoul and Freedman, 2006] which tends to reduce native plant diversity. Nevertheless, “novel ecosystems” could also be valued on the basis of their being better or worse than what existed before, and even an invasive species could be allowed to thrive in wetlands because it provides a great habitat for birds [Marris, 2009]. Exotic plant invasions locally reduce native plant diversity. However, contrary to what diversity-productivity experiments would predict, net primary productivity may increase with exotic invasions [Rout and Callaway, 2009]. Since eliminating competition has a high management cost, and often physical and chemical requirements of even a few plants are imprecise, the wetland designer should not attempt to maintain a system with few known plants [Kadlec and Wallace, 2009]. Although, there is increasing concern about the problem of preserving wetland biodiversity, and wetland restoration often aims at creating well functioning plant communities far from a monoculture of invasive species. Creating conditions favorable to the maintenance of biodiversity may assist in enhancing resilience of native wetland communities to biological invasions. Furthermore, ecohydrological interactions associated with periodic flooding or water table draw down can change biotic interactions in wetland communities and favor biodiversity [Bornette and Puijalon, 2009]. Biodiversity in wetlands is often structured around a community zonation associated with variable surface and soil saturation at different elevations [Zedler and Kercher, 2004; Zedler,

2000]. This zonation can be reinforced (or eroded) by spatially variable nutrient supply. In managed or constructed wetlands, water depth, flow rate and nutrient supply may be amenable to some degree of human control [Persson and Wittgren, 2003]. This paper seeks to identify whether variation in these parameters alters ecosystem resilience to invasion by altering the spatial structure of water table depth and species distribution in a wetland. Specifically the paper will address the development of a new ecohydrological model which simulates competitive interactions between two vegetation types in association with the interaction between plant water uptake and the depth of the water table. This new model extends previous studies by addressing these questions in a spatially explicit manner, allowing the dynamics of zonation to be explored for the first time.

[3] Investigating the processes, feedback mechanisms and relevant interrelations between hydrology and ecology has inspired many theoretical studies based on mathematical biology and hydrology, and led to effective eco-hydrological models of diverse environments [Borgogno *et al.*, 2009; Peterson *et al.*, 2009; Murray *et al.*, 2008; Rietkerk *et al.*, 2004]. The goal of eco-hydrological modeling of the wetland systems is to provide support for restoration and management practice, or timely forecasting of fateful ecosystem changes. Among others, more specifically, Vervoort and van der Zee [2009], Muneeppeerakul *et al.* [2008], and Ridolfi *et al.* [2006] have analyzed the coupled water table and vegetation dynamics, in order to capture the essential features of the ecosystem and reproduce time series of vegetation density, soil moisture and other relevant variables. Among the appealing topics that are crucial for the maintenance of wetlands there are: the spontaneous development of heterogeneous biomass patterns, the steady, oscillatory or chaotic behavior of the relevant state variables, the maintenance of bio-diversity and the dominance of one species over the others. These topics may be easily studied by simple models

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that capture the essential interdependencies among biotic and hydraulic state variables. Trying to control the invasion of exotic plants by managing water level and nutrient supply is certainly an appealing link between restoration ecology and hydrology. The possibility of forecasting, by numerical modeling, the characteristic features of those plants that could counteract dominant invasive species under controlled hydrologic regimes is definitely attractive. Even though more information about eco-physiological properties is needed in order to draw a general conclusion on the effects of plant invasion on an ecosystem [Laio *et al.*, 2007], simple bucket models [Krasnostein and Oldham, 2004; Brotsma and Bierkens, 2007; Muneeppeerakul *et al.*, 2008; Vervoort and van der Zee, 2009] may be valuable instrument to investigate the interplay of hydrological forcing and biological reaction under controlled wetland operation conditions.

[4] Several experimental and theoretical studies have investigated the interrelation between nutrient concentration, hydroperiod and plant competition (see, e.g., Zedler and Kercher [2005] for a review). Phreatophytic vegetation adjusts its root growth to the level of the water table and changes in groundwater depth will cause root growth redistribution to maintain water uptake in unsaturated zones above the water table [see Naumburg *et al.*, 2005, and references therein]. Wetzel and van der Valk [1998] demonstrated the importance of canopy architecture for biomass allocation. Plants growing along hydrologic gradients adjust their biomass allocation and distribution in response to interspecific competition [Carter and Grace, 1990; Grace and Wetzel, 1982]. Recently, the experiment conducted by Touchette and Romanello [2009] confirmed the importance of morphological and physiological plasticity in plant invasions [Schweitzer and Larson, 1999; Richards *et al.*, 2006]. DeMeester [2009] investigated whether higher nitrogen availability promotes invasive species dominance by a greenhouse competition experiment and showed that there are unique competition effects in aboveground biomass and in below-ground dynamics for every invasive-native species combination.

[5] The water table dynamics can have adverse impacts on plants in two ways: periods of prolonged saturation and periods of prolonged drought cause physiological stress. There is an optimal soil moisture regime for any given plant species. A key factor behind zonation is the tolerance for different mean soil moisture contents. The interplay between this genetically determined optimal soil moisture, the dynamics of plant soil moisture utilization and the resupply of soil moisture by rainfall and streamflow forms the nexus of this modeling effort. Indeed, since the water table depth may be influenced by plant transpiration, some wetland plants may contribute creating and maintaining environmental niches for themselves or other competing plants [see Ridolfi *et al.*, 2007, and references therein]. The model has been applied to an ecosystem where there is a native vegetation type and a second dominant species. The two plants may act as ecosystem engineers since they affect the water table depth by evapotranspiration. Little is known about phreatophytic reaction to invasion. Different vegetation types seem to react differently to invasion. A feedback likely exists between strategic biomass allocation and eco-hydrological shifts of the ecosystem. Based on the experimental results summarized in the previous paragraph, it has been postulated that the relation between biomass growth and stress, as well as

the one between root growth and stress may be positive or negative depending on the combination of competing plants that share the same resources.

[6] The new model presented here is built upon the hypothesis that one species, that is expected to be the invasive species, has broader tolerance limits with respect to soil saturation, and submersion. The common feature of the surface water depth gradient (instead of the soil saturation gradient) leading to zonation, competition and segregation of wetland plants could have been considered by easily modifying the model function that characterizes the biomass carrying capacity (not shown here). To constrain the problem it is assumed that invasive species may out-compete the native one by inducing stress for light or water. Several hypotheses on the competing species survival strategies have been tested. 1. What is the effect of a preferential allocation of biomass below ground of the native and invasive species? 2. What is the effect of an invasive species resulting in an increase in mean evapotranspiration? 3. What is the effect of the other species transpiring more? 4. What is the effect of increased nutrient availability on the organization of the two vegetation types, if only one vegetation type may profit of this opportunity? The answer to these questions has been evaluated based on the analysis of the different vegetation patterns predicted by numerical simulation at the end of one growing season. At that time, the biomass distribution reaches a steady state in many cases, despite the hydrological forcing varies in time. In a few cases the biomass density of the two vegetation types oscillates with the same frequency of the hydrologic forcing, but different initial conditions and intensity and frequency of rainfall may reverse this model outcome. Provided that the initial condition and the hydrologic forcing are the same, the simulated vegetation patterns, depend on the unique competition outcome of each species' diverse combination, such that the loss of the native species results in major shifts of the ecosystem in terms of vegetation and soil moisture patterns. The model presented here allows just a discussion of the relative fixed physiological characteristics on invasion and must be considered as a starting point for a more realistic description of the dynamics of plant response to water and nutrient availability.

2. Methods

[7] The spatially extended model described here results from the combination of two hydrological mass balance equations for soil moisture and groundwater depth [see, e.g., Brotsma and Bierkens, 2007] and two biomass balance equations, mimicking the growth and the competition between two different vegetation types, [see, e.g., Ridolfi *et al.*, 2007], as well as biomass spreading.

[8] The model is used here to investigate the task of controlling invasive plant spreading by regulating nutrient supply and by realizing ad hoc combinations of invasive and native species. Only one growing season is considered.

2.1. Water Table Dynamics

[9] Groundwater flow is modeled with the partial differential equation

$$W_s \frac{\partial H}{\partial T} = K_s \frac{\partial}{\partial X} \left[H \frac{\partial H}{\partial X} \right] + Q_v \quad (1)$$

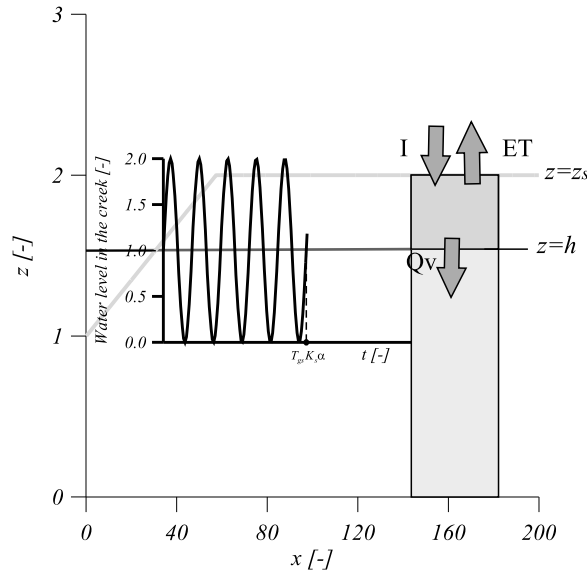


Figure 1. Schematic representation of the cross section of the wetland (gray line). (left) The fluctuations of the water level in the creek are represented as a function of time. (right) Relevant hydrological fluxes across the soil surface (ET and I) and across the water table (Q_v) are represented.

where H is the elevation of the water table over a horizontal bedrock, K_s is the saturated hydraulic conductivity of the soil, W_s is the saturated soil moisture content that is assumed to coincide with the drainable porosity of the soil and Q_v is the vertical exchange flux with the above unsaturated zone and is modeled by applying Darcy law. Space and time are indexed by X and T respectively.

$$Q_v = -K(W) \cdot \frac{Z_s + \Psi(W) - H}{Z_s - H} \quad (2)$$

where $K(W) = K_s \exp[\alpha \Psi(W)]$ is the unsaturated soil conductivity, α is the inverse of the mean capillary rise that depends on the soil capillary force, $\Psi = \alpha^{-1} \ln(W/W_s)$ is the negative pressure head in the unsaturated zone, as a function of soil moisture W , according to *Gardner* [1958]; Z_s is the surface elevation. In $X = 0$ and where $Z_s \leq H_c$ the water table H coincides with a creek water level H_c that rises after every rainfall event as a result of the drainage of storm water from an upstream catchment (Figure 1). On the opposite boundary a no-flow boundary condition has been imposed.

2.2. Soil Moisture Balance

[10] The water balance within the unsaturated zone is given by

$$\frac{\partial}{\partial T} [(Z_s - H) \cdot W] = [I - ET - Q_v] + (Z_s - H) \left[V_w \frac{\partial W}{\partial X} + D_w \frac{\partial^2 W}{\partial X^2} \right] \quad (3)$$

where Z_s is the soil elevation, W is the soil moisture content, I is the net infiltration, ET the evapotranspiration

and Q_v is given by equation (2). By expanding the left hand side term by the chain rule, the soil moisture balance equation may be easily derived:

$$(Z_s - H) \frac{\partial W}{\partial T} = W \cdot \frac{\partial H}{\partial T} + [I - ET - Q_v] + (Z_s - H) \cdot \left[V_w \frac{\partial W}{\partial X} + D_w \frac{\partial^2 W}{\partial X^2} \right] \quad (4)$$

[11] The net infiltration I equals the difference between the rainfall and runoff productions. It is evaluated by applying Darcy's law to the unsaturated zone with unit gradient (negligible standing water depth during infiltration) when the water table is below the soil surface ($H < Z_s$) and thus, it was estimated as

$$I = \min[K(W), \text{Precipitation}] \quad (5)$$

whereas $I = 0$ if the water table reaches the soil surface or it is submerged ($H \geq Z_s$).

[12] The evapotranspiration ET is evaluated as the sum of the evaporation E and root water uptake $E_i(W_{ri}) \cdot N_i$ realized by two plants whose density is N_i with $i = 1, 2$:

$$ET = E + E_1(W_{r1}) \cdot N_1 + E_2(W_{r2}) \cdot N_2 \quad (6)$$

The terms $E_1(W_{r1}) \cdot N_1$ and $E_2(W_{r2}) \cdot N_2$ represent the evapotranspiration losses due to root uptake over depth r_1 and r_2 respectively. Depending on soil saturation, they may be less or equal than the potential evapotranspiration values $E_i(\max)$, according to *Feddes et al.* [1978] root water uptake reduction function (see Figure 2):

$$E_i = E_i(\max) \cdot f_i$$

$f_i = 0$	if $W_{ri} \leq W_{ai}$
$f_i = \frac{W_{ri} - W_{ai}}{W_{bi} - W_{ai}}$	if $W_{ai} < W_{ri} \leq W_{bi}$
$f_i = 1$	if $W_{bi} < W_{ri} \leq W_{ci}$
$f_i = \frac{W_{di} - W_{ri}}{W_{di} - W_{ci}}$	if $W_{ci} < W_{ri} \leq W_{di}$
$f_i = 0$	if $W_{ri} \geq W_{di}$

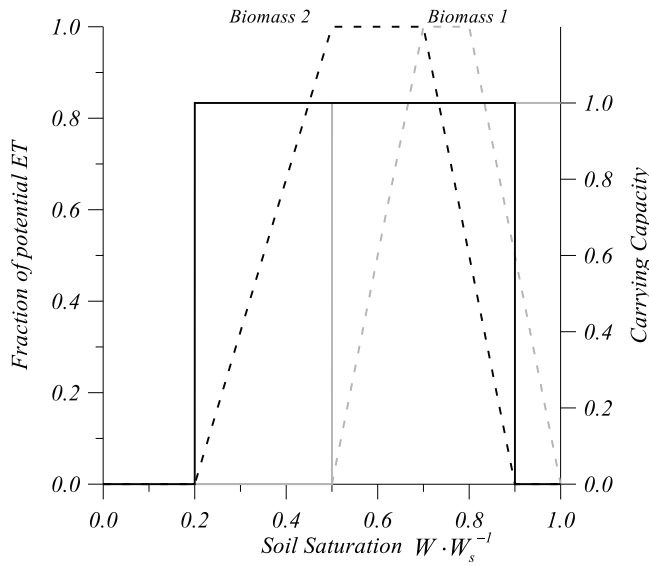
(7)

with $i = 1, 2$. The parameters W_{ai} and W_{di} represent respectively the species specific wilting point and anaerobiosis point respectively. Biomass 1 is adapted to higher soil saturation and thus its mean root length is $r_1 = 0.5$ m, whereas $r_2 = 0.2$ m [see *Muneepeerakul et al.*, 2008, and references therein]. W_{r1} and W_{r2} are the average soil moisture evaluated over the mean root depth of the two plants (respectively r_1 for the first and r_2 for the second type of vegetation), according to the following expressions:

$$W_{ri} = r_i^{-1} \cdot \int_0^{r_i} W(Z) \cdot dZ$$

$$= W \quad \text{if } r_i \leq Z_s - H$$

$$= r_i^{-1} [W \cdot (Z_s - H) + W_s \cdot (r_i - Z_s + H)] \quad \text{if } r_i > Z_s - H \quad (8)$$



Biomass 1 Biomass 2

$W_a \cdot W_s^{-1}$	0.5	0.2
$W_b \cdot W_s^{-1}$	0.7	0.5
$W_c \cdot W_s^{-1}$	0.8	0.7
$W_d \cdot W_s^{-1}$	1.0	0.9

Figure 2. Carrying capacity (continuous line) and evapotranspiration function of biomass 1 and 2 (dashed gray and black lines, respectively).

with $i = 1, 2$. The terms $V_w \frac{\partial W}{\partial X}$ and $D_w \frac{\partial^2 W}{\partial X^2}$ are respectively soil moisture advective and diffusive fluxes, where V_w and D_w might be expressed as functions of the saturated conductivity K_s and the inverse of the capillary rise α^{-1} by combining Richards equation [Richards, 1931] and Gardner's exponential relations for K_s and W_s as a function of Ψ [Gardner, 1958] according to Ursino [2005]. Here average values over depth ($Z_s - H$) are considered: $D_w = K_s(W_s \alpha)^{-1}$ and $V_w = -\frac{dZ}{dX} K_s(W_s)^{-1}$.

2.3. Biomass Dynamics

[13] The biomass growth of two vegetation types (with densities N_1 and N_2) is described by the simple Lotka-Volterra competition model [Lotka, 1925; Volterra, 1926], with saturation dependent carrying capacity. The classic Lotka-Volterra set of equations incorporates both inter- and intraspecific growth limitation:

$$\begin{aligned} \frac{\partial N_1}{\partial T} &= G_1 \cdot N_1 \cdot \frac{[L_1(W_{r1}) - N_1]}{C_1} - M_1 \cdot N_1 \\ \frac{\partial N_2}{\partial T} &= G_2 \cdot N_2 \cdot \frac{[L_2(W_{r2}) - (\beta N_1 + N_2)]}{C_2} - M_2 \cdot N_2 \end{aligned} \quad (9)$$

where G_1 and G_2 are the growth rates and L_1 and L_2 are the saturation dependent carrying capacities of the two plants. In the first of (9) the species growth is inhibited by intraspecific competition while in the second the growth is inhibited by

intraspecific competition and a degree of interspecific competition whose magnitude depends on β .

[14] The coexistence of the two vegetation types, in this case may be demonstrated to be possible and stable just for $L_2 > L_1$ [see, e.g., Gillet, 2008]. Otherwise, just the dominant species survives in the absence of water stress. The water table depth may be influenced by plant transpiration and soil saturation may affect the carrying capacity of the two competing plants. This means that one of the two vegetation types may contribute to creating and maintaining environmental niches for itself or other competing species by root up-taking according to Ridolfi et al. [2007]. The feedback between biomass growth and soil moisture content is accounted for by L_1 and L_2 that depend on the average soil saturation in the root zone (W_{r_i} in equation (8)), and account for the loss of the carrying capacities when the soil moisture is below the wilting point W_{a_i} or above the anaerobiosis point W_{d_i} , according to the following expression:

$$L_i = H(W_{r_i} - W_{a_i}) \cdot H(W_{d_i} - W_{r_i}) \cdot C_i = \ell_i \cdot C_i \quad (10)$$

where $i = 1, 2$, and $H(\cdot)$ is the Heaviside's step function (see Figure 2).

[15] DeMeester [2009] observed that wetland restoration activities are increasing available nitrogen, and favoring invasive species which in turn detracts from the restoration success. Variations of β with the nutrient concentration have not been considered here, although they may also occur. The Lotka-Volterra model does not explicitly consider changes in resources utilized by the competitors (typically nutrients in the case here). The fact that anthropogenic sources are altering resources availability e.g. nutrients (indexed by S) into wetlands, may be accounted for by assuming either that the carrying capacity may change with the nutrient concentration $C_i = C_i(S)$ or that the growth rate increases in a Monod fashion with nutrient level, in analogy with other competition scenarios [see, e.g., Scheffer et al., 1993]:

$$G_i C_i^{-1} = G_i^0 \frac{S}{S + k_s} \cdot C_i^{-1} \quad (11)$$

where G_i^0 is a reference growth rate, S is the concentration of any relevant nutrient component, k_s the half-saturation constant. In the case study discussed in this paper, even significant variations of $G_{1,2}$ (up to one order of magnitude), evaluated according to equation (11), had a negligible impact on the results (not shown here), since the model is evaluated at a state (in many cases steady) that is determined by the carrying capacity. Conversely, the model predicted major changes in vegetation patterns by assuming that a hydrological shift of the water quality could increase the carrying capacity of the species whose capacity of adaptation to the changed environment improves its ecological performance. Given the complexity of vegetation dynamics in wetlands, ascribing nutrient and water related changes only to the carrying capacity is just a mathematical convenience but, it makes possible to explore canonical features of the dynamics in schematic, hypothetical cases.

[16] Macrophytes rely partly on water drift for seed dispersal and on the ability of plants to break themselves up and regrow from broken dispersed fragments, and partly on endozoochory by animals. Here dispersion is simplistically modeled by the diffusive term $D_i \frac{\partial^2 N_i}{\partial X^2}$, with $i = 1, 2$. Modeling the non isotropic reproductive behavior of each species [Thompson *et al.*, 2008] could have had an impact on zonation, although, for the sake of simplicity, this has been neglected here. In order to account for biomass dispersion, the classical model (9) has been modified as follows:

$$\begin{aligned} \frac{\partial N_1}{\partial T} &= G_1 \cdot N_1 \cdot \frac{[L_1(W_{r1}) - N_1]}{C_1} - M_1 \cdot N_1 + D_1 \frac{\partial^2 N_1}{\partial X^2} \\ \frac{\partial N_2}{\partial T} &= G_2 \cdot N_2 \cdot \frac{[L_2(W_{r2}) - (\beta N_1 + N_2)]}{C_2} - M_2 \cdot N_2 + D_2 \frac{\partial^2 N_2}{\partial X^2} \end{aligned} \quad (12)$$

2.4. Model Parametrization

[17] Soil parameter values are $W_s = 0.4$, $K_s = 2 \cdot 10^{-6} \text{ m s}^{-1}$ and $\alpha = 1 \text{ m}^{-1}$. Net inflow (effective rainfall minus evaporation: $I - E$) during the growing season is 50 mm (it is modeled as a sinusoidal function) and it is characterized by average frequency of 1 month^{-1} over the 5 months of the growing season (T_{gs}). Cumulative evapotranspiration of the wetland competing plants at carrying capacity ($E_{1,2} C_{1,2} T_{gs}$) was set either at 50 or 500 mm, with $T_{gs} = 5$ months. The water level in the creek varies with the same frequency of the rainfall events rising up to the maximum soil elevation and lowering to the minimum level ($1 \leq H_c \leq 2 \text{ m}$, see Figure 1).

[18] In the particular case here, the growth rate of species 2 may be limited by the presence of species 1 (if $\beta = 1$, otherwise $\beta = 0$), but the opposite never happens, mimicking the fact that the invasive species may be taller and thus, a superior competitor for light, and does not suffer for the proximity of the native species that tend to be rather displaced.

[19] The growth rate was set at: $G_{1,2} = 2 \cdot 10^{-8} \text{ s}^{-1}$, and the mortality due to senescence was neglected since the simulation time is only one growing season, thus $M_1 = M_2 = 0 \text{ s}^{-1}$. The absolute value of the carrying capacity $C_{1,2}$ does not have an impact on the results, once the maximum evapotranspiration at carrying capacity ($E_{1,2} C_{1,2}$) is fixed. The coefficients of diffusion are $D_1 = D_2 = 2 \cdot 10^{-9} \text{ m}^2 \text{ s}^{-1}$.

[20] Several simulations have been done to address the research questions on vegetation patterning (see Section 1). The following mechanisms of interaction between vegetation types have been considered: 1) the density of the subdominant species (species 2) may be reduced by the presence of the dominant species (species 1); 2) one of the two vegetation types may create opportunities by lowering the water table (by evapotranspiration); 3) a shift of nutrient concentration may increase the carrying capacity of one species.

2.5. Dimensionless Model Balance Equations

[21] Assuming that the characteristic water budget parameters $(K_s \alpha)^{-1}$ and α^{-1} are respectively the time and the length scale and the carrying capacity C_i of each species scales the related biomass density N_i , the dimensionless form of the proposed eco-hydrological model consists of the following set of balance equations for groundwater depth (h), soil moisture (w), the first (and eventually dominant) plant biomass density (n_1), and the second plant biomass

density (n_2). The spatially explicit model is defined in 1D as a function of space x and time t :

$$\begin{aligned} \frac{\partial h}{\partial t} &= \frac{\partial}{\partial x} \left[h \frac{\partial h}{\partial x} \right] + q_v \\ \frac{\partial w}{\partial t} &= \frac{w}{(z_s - h)} \frac{\partial h}{\partial t} + \frac{1}{(z_s - h)} \cdot [i - e - \gamma e_1(w_{r1}) \cdot n_1 \\ &\quad + e_2(w_{r2}) \cdot n_2 - q_w] + v_w \frac{\partial w}{\partial x} + d_w \frac{\partial^2 w}{\partial x^2} \\ \frac{\partial n_1}{\partial t} &= g_1 \cdot n_1 \cdot [\ell_1(w_{r1}) - n_1] + d_1 \frac{\partial^2 n_1}{\partial x^2} \\ \frac{\partial n_2}{\partial t} &= g_2 \cdot n_2 \cdot [\ell_2(w_{r2}) - n_2 - \beta \gamma n_1] + d_2 \frac{\partial^2 n_2}{\partial x^2} \end{aligned} \quad (13)$$

The dimensionless groups in model (13) are: $i = \frac{IW_s}{K_s}$, $q_v = \frac{Q_v W_s}{K_s}$, $e = \frac{EW_s}{K_s}$, $e_{1,2} = \frac{E_{1,2} C_{1,2} W_s}{K_s} f_{1,2}$, $\gamma = \frac{C_1}{C_2}$, $v_w = -\frac{dz}{dx}$, $d_w = 1$, $g_{1,2} = \frac{G_{1,2}}{\alpha \cdot K_s}$, $m_{1,2} = \frac{M_{1,2}}{\alpha \cdot K_s}$, $d_{1,2} = \frac{D_{1,2} \alpha}{K_s}$.

[22] Parameters q_v , e , v_w , and d_w characterize the hydrological functioning of the ecosystem. The two dimensionless functions e_1 and e_2 link the biological growth to the hydrologic regime, whereas g_1 and g_2 represent the ratios between the characteristic timescale of soil moisture dynamics and the timescales of the two biomass dynamics. Finally γ , the ratio between the maximum carrying capacities of the two competing vegetation types accounts for the fact that one of the two may be an opportunistic plant that takes particular advantage from the environmental standing conditions when nutrient supply is increased. Although dimensional parameters are chosen on the base of literature values, no specific site is taken here as a reference scenario, and mainly relevant processes and strategies are discussed. Thus, the analysis was conducted in dimensionless form to focus on the relative impact of different model functions and parameters and major variations of parameters have been analyzed to demonstrate the possible related shift of the ecosystem. More specifically, model (13) has been integrated to evaluate the impact of significantly different $e_{1,2}$ and γ on forecasted vegetation patterns at the end of one growing season. Dimensionless parameter values are listed in Table 1. An Euler explicit method with discrete time step $\Delta t = 5 \cdot 10^{-4}$ and space step $\Delta x = 0.1$ was adopted.

3. Results

[23] Model (13) may be used to investigate the task of controlling invasive plant spreading by regulating water table depth, time of submersion, and nutrient supply and by realizing ad hoc combinations of invasive and native species based on their capability of affecting the ecosystem water budget.

[24] Here, the focus is on the combination of plants and on nutrient availability. Only one growing season is considered, during which a minimum amount of precipitation occurs. After rainfall the water level in the creek rises up to the upper soil level, and then lowers again, to mimic the inflow from a drainage catchment, affecting the water table elevation just close to the creek, since, due to the relatively low K_s , the upslope part of the transect remains hydraulically disconnected from the lower one that is periodically submerged (Figure 1).

Table 1. Dimensionless Parameters

Parameter	Value	Notes
γ	1	Figures 3 and 4
β	1	Figures 3b, 3d, 3f, 4b, 4d, and 4f
γ	10	Figure 5
γ	0.1	Figure 6
$i-e$	8×10^{-4}	Average value
Species 1		
g_1	10^{-2}	
d_1	10^{-3}	
e_1	$8 \times 10^{-4} \times f_1$	
e_1	$8 \times 10^{-3} \times f_1$	Figures 3c, 3d, 4c, 4d, and 5
Species 2		
g_2	10^{-2}	
d_2	10^{-3}	
e_2	$8 \times 10^{-4} \times f_2$	
e_2	$8 \times 10^{-3} \times f_2$	Figures 3e, 3f, 4e, 4f, and 6

[25] The simulation results demonstrated that the unique combination of competing plants, with their physiological characteristics, and the existing environmental conditions determine the vegetation patterns at the end of the growing season, despite the fact that the hydrologic forcing is always the same. Figure (3) shows the different vegetation patterns at the end of the simulation time, starting at the beginning of the growing season with the same homogeneous distribution: $n_1 = n_2 = 0.5$. Close to the creek and far from the creek vegetation types that are adapted to different saturation ranges find their favorable environment according to the subsurface soil moisture patterns and to their competitiveness, but the capability of one species to affect the water table depth may change completely the vegetation patterns.

[26] Although the transect is never completely submerged, it is all saturated in the base case study (Figures 3a and 3b), and species 1 which has broader tolerance limits with respect to soil saturation, invades the entire transect (Figures 3a and 3b), resulting in a monoculture if dominant ($\beta = 1$, Figure 3b). The model outcome changes completely if evapotranspiration of one species is different from the other or one carrying capacity is increased to mimic different survival strategies in changing environments.

3.1. Enhanced Potential Evapotranspiration of One Species

[27] An interesting case study is the one in which the dominant species (species 1 when $\beta = 1$) is adapted to a higher saturation degree and possesses traits that attain higher potential evapo-transpiration values. As its biomass increases to the detriment of the other species, the soil moisture at its standing place diminishes due to the high evapotranspiration, and consequently, the environmental conditions start to become more favorable to the previously displaced plant. Thus, while the dominant vegetation type tends to colonize neighboring zones it creates soil moisture conditions that are more favorable to the re-establishment of the competing plants [Ridolfi *et al.*, 2007].

[28] If species 1 succeeds in enhancing evapotranspiration, by so doing it creates an opportunity for species 2 to establish in the upper and dryer part of the transect (Figures 3c and 3d). Even if species 1 limits the growth of species 2 ($\beta = 1$, Figure 3d), the latter cannot be displaced in the upper part of

the transect. A completely different scenario results if species 2 manages to enhance evapotranspiration to survive and thus attempts to create itself more favorable environmental conditions (Figures 3e and 3f). Species 2 from its upper zone natural location lowers the water table much more than the dominant species, ultimately acting to its own detriment and finds a niche close to the creek in the higher zone adjacent to biomass 1 (Figure 3e). When biomass 1 dominates ($\beta = 1$), the native species is displaced from its niche, the dominant species invades the whole transect and the water table rises up to the soil surface (Figure 3f) as in the base case (Figure 3b). Increasing evapotranspiration does not help biomass 2 in this case.

[29] Figure 4 shows the phase plane corresponding to the Figure 3 scenarios: the biomass density of species 1 has been plotted versus the biomass density of species 2, at different distances from the creek (namely: $x = 20, 40, 60, 80$). Figure 4 shows how, when species 1 does not invade the upper part of the transect (Figures 4c–4e), the biomass density of one or both plants oscillates in response to the oscillating environmental forcing ($i - e$). The environment is extremely sensitive to even small hydrological shifts.

3.2. Increased Carrying Capacity of One Species

[30] Increasing nutrient supply may create an opportunity for the species that would more efficiently allocate these resources in the standing environment. In order to simulate major ecosystem changes deriving by possible water quality shifts, the carrying capacity of one plant at a time (the opportunist) is increased by a factor 10.

[31] Opposite to the case study of Figures 3a and 3b, the model outcome is the clear zonation of the two vegetation types (Figures 5 and 6), indeed the water table is considerably lower, due to the enhanced carrying capacity of the dominant species, leading to higher evapotranspiration. When $\beta = 0$, biomass 1 creates an opportunity for biomass 2, but if the two compete e.g. for light, and biomass 1 is a superior competitor ($\beta = 1$, Figure 5, right), biomass 2 is completely displaced, despite the favorable soil saturation.

[32] When biomass 2 is the one that profits from the water quality shift and increases its carrying capacity (Figure 6), it cannot create an opportunity for itself. In this case the upper part of the transect hosts a minimum amount of vegetation and both vegetation types find their niche close to the creek, since biomass 2 that is naturally located in the drier zone, is too effective in lowering the water table, and by so doing it creates unfavorable conditions for both vegetation types.

[33] In this case study, the higher biomass density achieved by the opportunist species results in a disadvantage for both vegetation types (Figures 5 and 6). Indeed, increased biomass density leads to increased dimensionless evapotranspiration and thus pushes the environment toward a drier scenario. Even though other resources may be abundant, water turns out to be the main growth limiting resource.

3.3. Hydrologic Forcing and Initial Condition

[34] The impact of the intensity and frequency of rainfall and the initial condition (Figures 4d and 4e) is briefly discussed in this Section. In Figures 4d and 4e the system is particularly sensitive to the hydrological forcing and does not reach a steady state unless the frequency and intensity of rainfall are set at different values (Figures 7 and 8). Although,

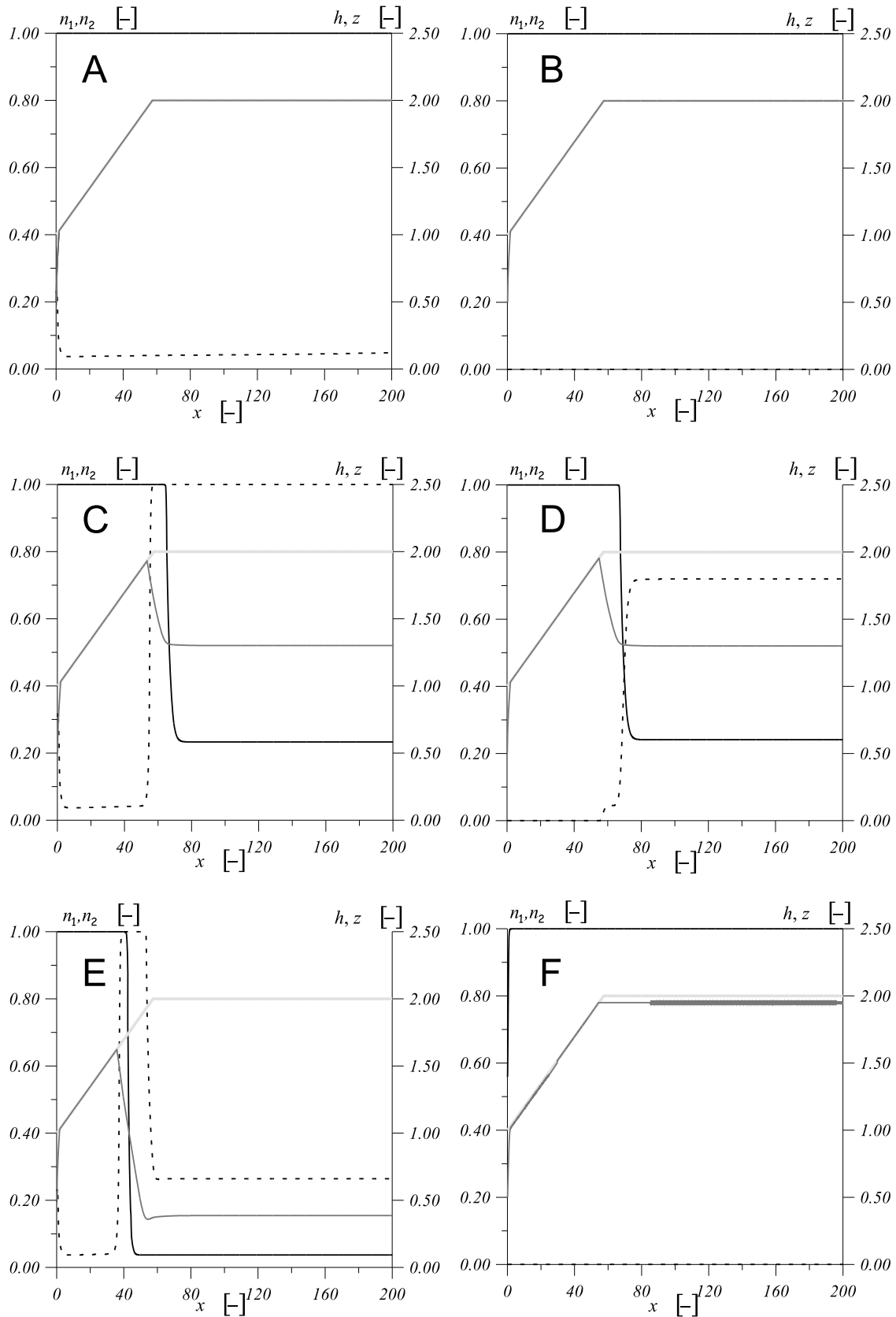


Figure 3. Biomass patterns: biomass density of species 1 (black solid line) and biomass density of species 2 (black dashed line). Gray lines are water table depth (dark gray) and soil elevation (light gray). (a, c, and e) Parameter $\beta = 0$. (b, d, and f) Parameter $\beta = 1$, species 1 dominates species 2. Figures 3c and 3d show potential evapotranspiration of biomass 1 is increased by a factor 10. Figures 3e and 3f show potential evapotranspiration of biomass 2 is increased by a factor 10.

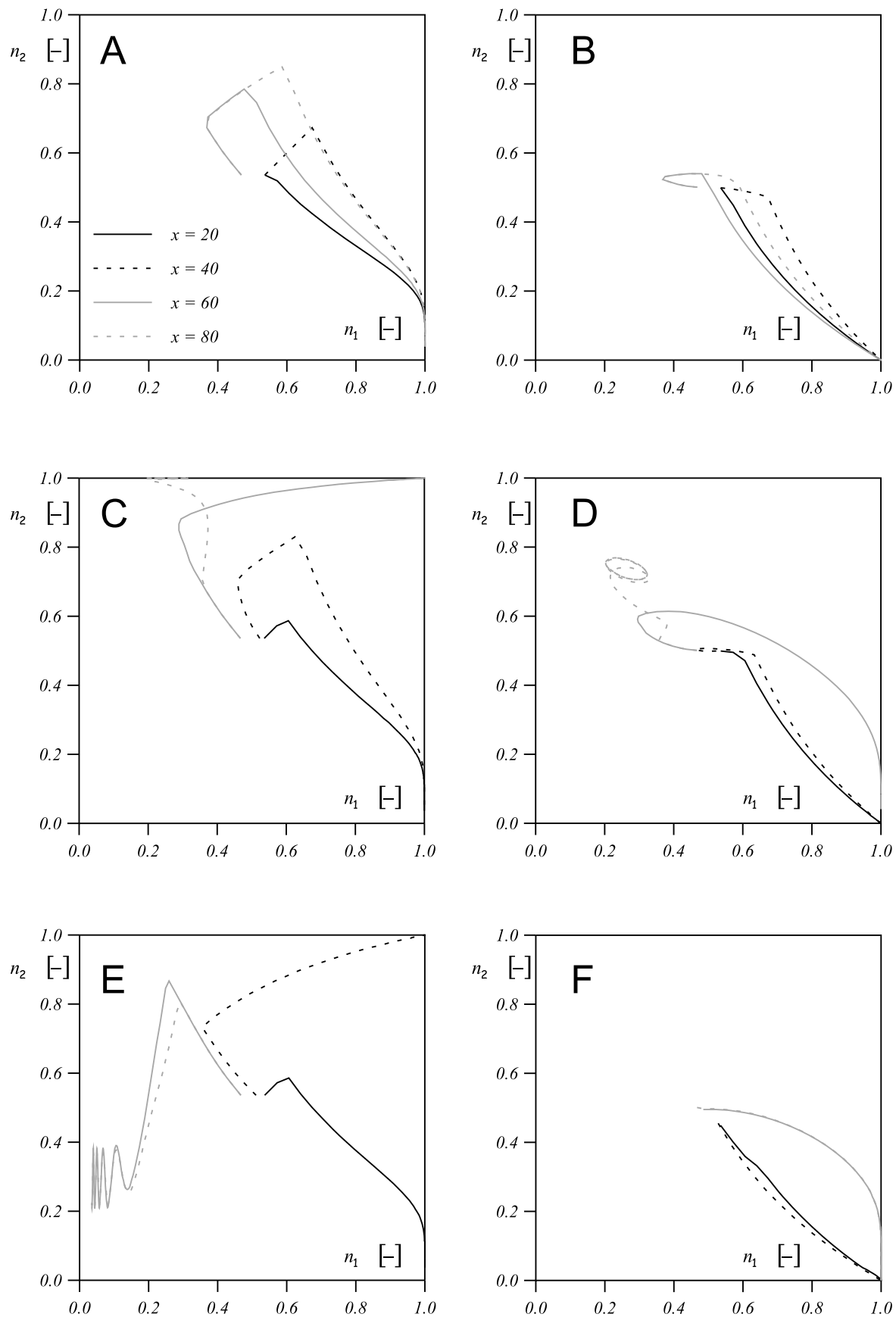


Figure 4. Phase plane corresponding to Figure 3 scenarios. Biomass density of species 1 versus biomass density of species 2, at different distances from the creek ($x = 20, 40, 60, 80$) during one growth season, starting at equal biomass density $n_1 = n_2 = 0.5$ at $t = 0$.

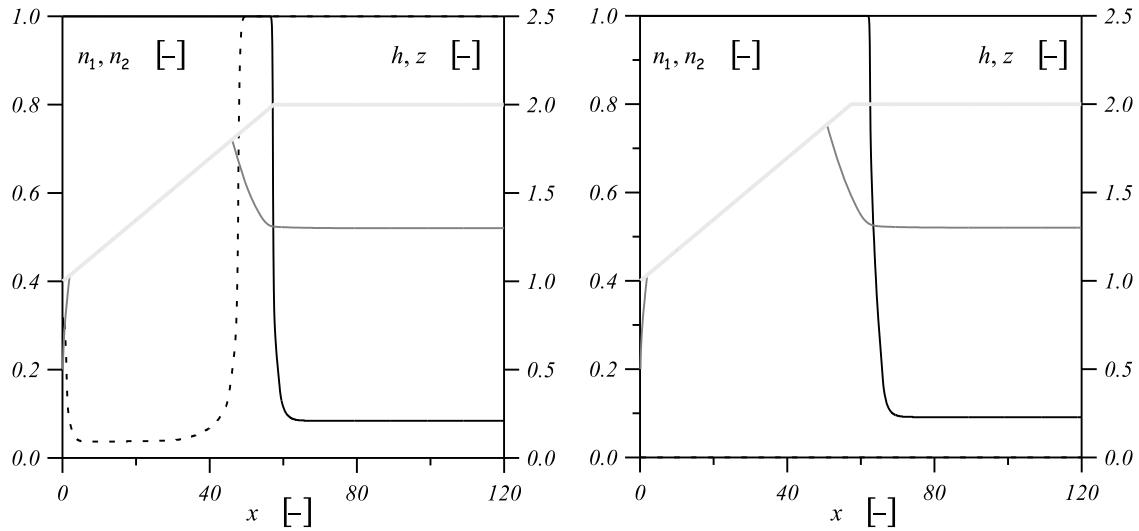


Figure 5. Biomass density of species 1 (black solid line) and species 2 (black dashed dashed). Gray lines are water table depth (dark gray) and soil elevation (light gray). (right): Species 1 dominates species 2. (left): Opportunist species 1 benefits from an hydrologic shift (increased carrying capacity of species 1).

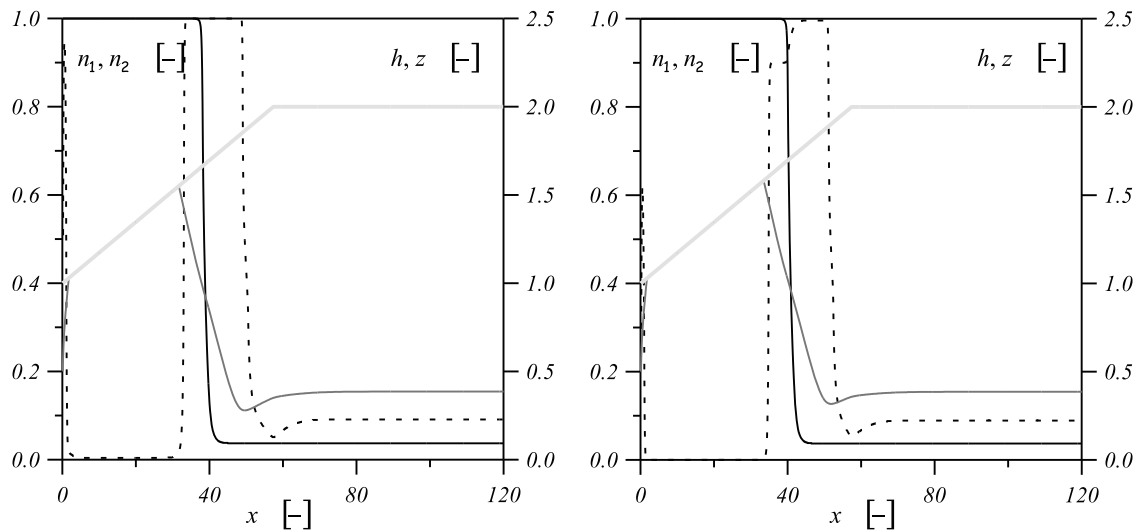


Figure 6. Biomass density of species 1 (black solid line) and species 2 (black dashed dashed). Gray lines are water table depth (dark gray) and soil elevation (light gray). (right): Species 1 dominates species 2. (left): Opportunist species 2 benefits from an hydrologic shift (increased carrying capacity of species 2).

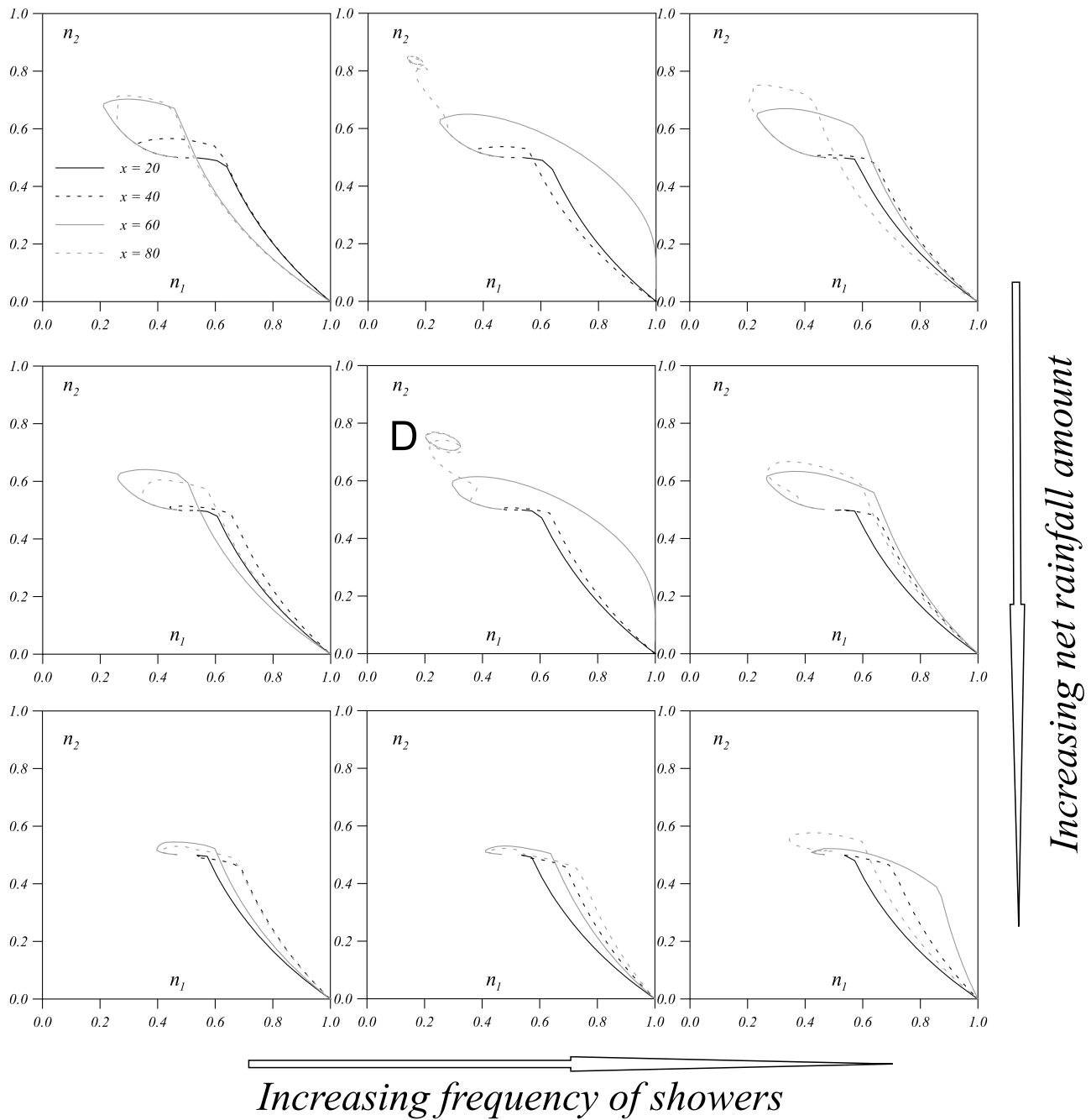


Figure 7. Phase plane corresponding to Figure 3d. Biomass density of species 1 versus biomass density of species 2, at different distances from the creek ($x = 20, 40, 60, 80$) during one growth season, starting at equal biomass density $n_1 = n_2 = 0.5$ at $t = 0$ for different hydrologic forcing. (left to right) Half frequency of showers, same frequency as in Figure 3d, double frequency. (top to bottom) Half intensity of rainfall, same intensity as in Figure 3d, double intensity.

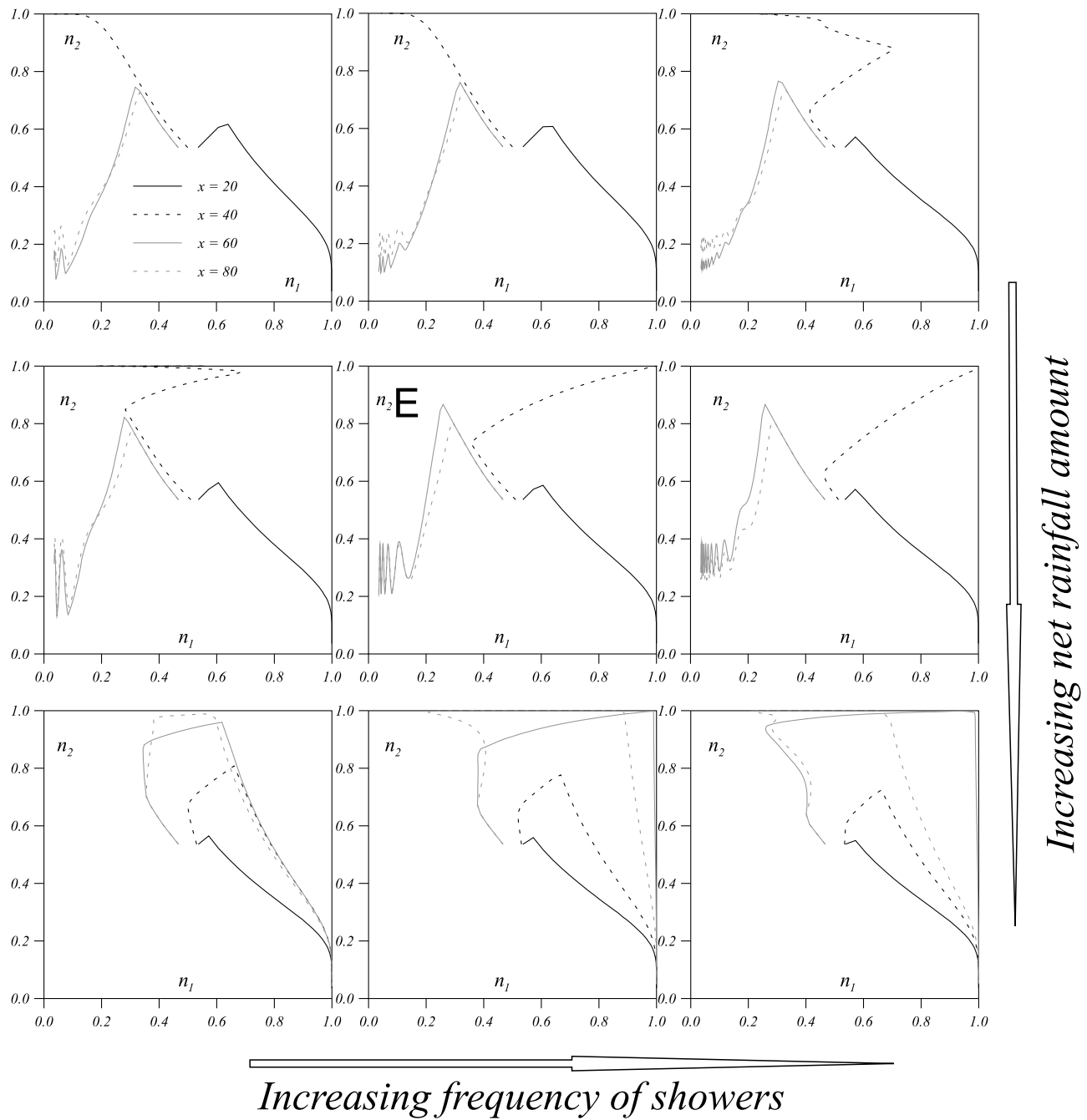


Figure 8. Phase plane corresponding to Figure 3e. Biomass density of species 1 versus biomass density of species 2, at different distances from the creek ($x = 20, 40, 60, 80$) during one growth season, starting at equal biomass density $n_1 = n_2 = 0.5$ at $t = 0$ for different hydrologic forcing. (left to right) Half frequency of showers, same frequency as in Figure 3e, double frequency. (top to bottom) Half intensity of rainfall, same intensity as in Figure 3e, double intensity.

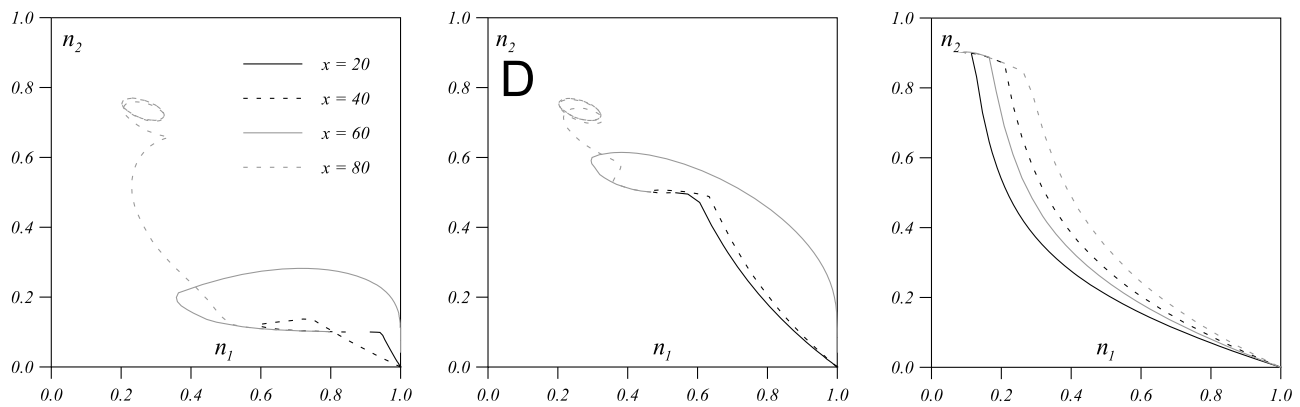


Figure 9. Phase plane corresponding to Figure 3d. Biomass density of species 1 versus biomass density of species 2, at different distances from the creek ($x = 20, 40, 60, 80$) during one growth season, starting at different biomass densities at $t = 0$. (left) Here $n_1 = 0.9, n_2 = 0.1$; (middle) $n_1 = n_2 = 0.5$ as in Figure 3d; (right) $n_1 = 0.1, n_2 = 0.9$.

there is not a unique threshold value of frequency and intensity of rainfall that makes the system insensitive to the fluctuations of the hydrological forcing, and allows it to reach the steady state at the end of the growing season. These threshold values, depend on the characterization of the biomass dynamics. In Figures 9 and 10 the model outcome, again referred to in Figures 4d and 4e, is shown for different initial conditions. Similarly, there is not a unique combination of initial biomass densities that determines whether the system reaches a steady or an oscillating state at the end of the simulation time.

4. Discussion and Conclusion

[35] A new spatially explicit model for the soil-water-vegetation interaction in a schematic wetland has been presented. A few examples have identified important interrelations between the hydrologic and biotic processes. The model outcome demonstrates that the zonation of two competing species strongly depends on their physiological characteristics, given the hydrologic forcing (previous studies focused mainly on the impact of different hydrologic regimes on vegetation patterns [see, e.g., Muneepeerakul *et al.*, 2008]).

This means that the susceptibility of a community to invasion is to some extent mediated by differences in growth habit, including root architecture and canopy height.

[36] Depending on the fixed evapotranspiration and carrying capacity of two competing vegetation types, the simple model introduced here forecasted the maintenance of biodiversity and zonation or the dangerous shift to a monoculture of the invasive species. In some cases the biomass distribution was particularly sensitive to the hydrologic forcing, and the system did not reach a steady state biomass distribution at the end of the simulation time. Frequency and intensity of rainfall showers as well as the initial biomass distribution could reverse the model outcome. Changes in evapotranspiration may be ascribed to preferential allocation of biomass below ground, a survival strategy that has been observed to be typical of some wetland species under stress [Naumburg *et al.*, 2005], or when coupled with certain invasive plants [DeMeester, 2009], and increasing carrying capacity may be attributed to opportunistic adaptation to changing environments.

[37] The results suggest that wetland managers may expect to affect vegetation patterns by regulating water and nutrient levels as well as creating a unique combination of different

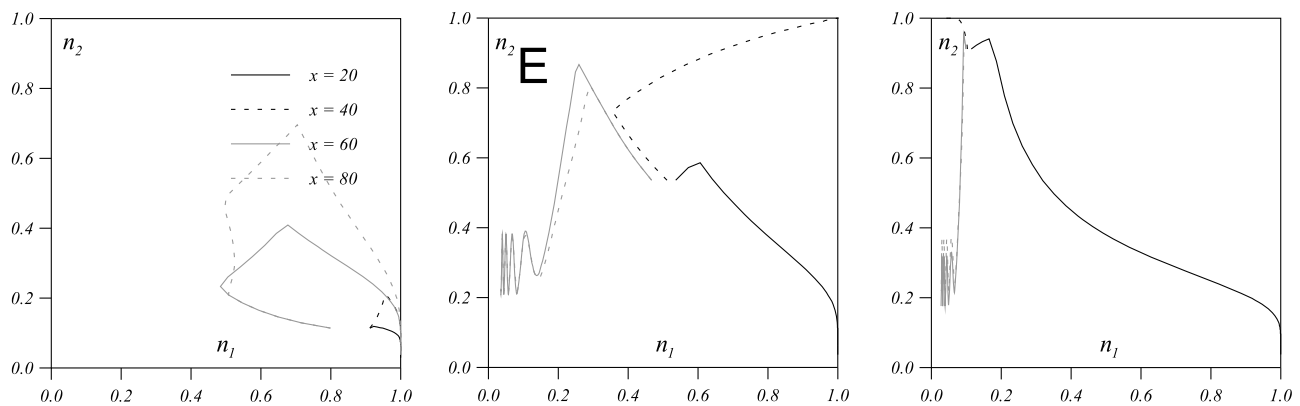


Figure 10. Phase plane corresponding to Figure 3e. Biomass density of species 1 versus biomass density of species 2, at different distances from the creek ($x = 20, 40, 60, 80$) during one growth season, starting at different biomass densities at $t = 0$. (left) Here $n_1 = 0.9, n_2 = 0.1$; (middle) $n_1 = n_2 = 0.5$ as in Figure 3e; (right) $n_1 = 0.1, n_2 = 0.9$.

vegetation types, provided that the plants with the required characteristics exist. Although the model, certainly needs to be greatly elaborated on to be of use as a predictive tool. The biology in the model needs to be explicitly linked to the forcing variables of interest and the dynamics of nutrients, the vegetation dispersal, and the stochastic nature of the hydro-logic forcing should be accounted for.

[38] The validation of these conclusions by rigorous field and laboratory experiments focused on detecting changes of above and below ground biomass allocation in changing environments would confirm the possibility of employing simple spatially extended models as wetland management and restoration tools.

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