



Original research article

# Vibrational resonance in groundwater-dependent plant ecosystems

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## ABSTRACT

We report the phenomenon of vibrational resonance in a single species and a two species models of groundwater-dependent plant ecosystems with a biharmonic oscillation (with two widely different frequencies  $\omega$  and  $\Omega$ ,  $\Omega \gg \omega$ ) of the water table depth. In these two systems, the response amplitude of the species biomass shows multiple resonances with different mechanisms. The resonance occurs at both low- and high-frequencies of the biharmonic force. In the single species bistable system, the resonance occurs at discrete values of the amplitude  $g$  of the high-frequency component of the water table. Furthermore, the best synchronization of biomass and its carrying capacity with the biharmonic force occurs at the resonance. In the two species excitable and time-delay model, the response amplitude ( $Q$ ) profile shows several plateau regions of resonance, where the period of evolution of the species biomass remains the same and the value of  $Q$  is inversely proportional to it. The response amplitude is highly sensitive to the time-delay parameter  $\tau$  and shows two distinct sequences of resonance intervals with a decreasing amplitude with  $\tau$ .

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## 1. Introduction

The study of the response of a system to a small variation of environmental changes is important since environmental drivers often fluctuate. The fluctuation can be periodic or nonperiodic (noise). In certain ecosystems, a small change in one or more environmental parameters leads to considerable changes on their structure and function. It has been noted that many systems have relatively high levels of diversity for an intermediate level of a disturbance (Roxburgh et al., 2004). The impact of the environmental variations/fluctuations has been analysed on food web stability (Vasseur and Fox, 2007), species coexistence in Holt–McPeck systems (Lai and Liu, 2005) and the stability of recovery (Steneck et al., 2002). Without invoking interaction between environmental noise and competition, it has been shown that environmental fluctuations enhance coexistence of species which either prefer or tolerate different environmental conditions (D'Odorico et al., 2008).

In the present work, we consider groundwater-dependent plant ecosystems. It is important to analyse the influence of the variation of various environmental factors, particularly, the changes in the water table depth, in order to get a deep understanding of the

response of various ecosystems. We point out that vegetation–water table interactions is very common in many ecosystems like wetlands, salt marshes and riparian forests. As a matter of fact, it is considered as one of the key mechanisms influencing the dynamics of vegetation (Naumburg et al., 2005; Elmore et al., 2006; Munoz-Reinoso and de Castro, 2005). Appropriate theoretical models are of great use for exploring various possible dynamics that can emerge from vegetation–water table interactions. In this connection, Ridolfi et al. (2006, 2007) have proposed two vegetation–water table models based on realistic ecological assumptions. The first model describes the vegetation biomass dynamics of only one species (dominant species). In this model the rate of change of the species biomass depends on the existing biomass and the carrying capacity of the system. The resultant model is a first-order nonlinear ordinary differential equation with a periodic driver. It accounts for multistable states in the dynamics of wetland forests and riparian ecosystems (Scheffer et al., 2001). The second model describes the two phreatophyte species interacting with a water table. In these two models, one of the factors that can change the carrying capacity of biomass is the depth of the water table. Change in the water depth due to seasonal rainfall oscillations and other sources is represented by a periodic function of time. It is also found to display coexistence of two species and chaotic dynamics (Ridolfi et al., 2007).

The influence of the environmental variability, treated as a disturbance or a kind of noise, in the above two models has been analysed recently by Borgogno et al. (2012). Specifically, they have shown the occurrence of stochastic and coherence resonances.

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When a bistable or an excitable system driven by a weak periodic force is subjected to an additive noise, it can exhibit an enhanced response at an optimal noise intensity. This phenomenon is termed as stochastic resonance (Gammaitoni et al., 1998; McDonnell et al., 2008). Very recently, noise-induced spatio-temporal patterns in wetland vegetation dynamics have been reported (Scarsoglio et al., 2012). In a subthreshold excitable system, a noise-induced resonance can be realized in the absence of external periodic driving and is known as coherence resonance (Pikovsky and Kurths, 1997). Interestingly, it has been shown that deterministic resonances can be observed even in monostable nonlinear systems driven by a biharmonic force in the absence of external noise and is called vibrational resonance (Landa and McClintock, 2000). The analysis of vibrational resonance has received a great deal of attention in recent years. Particularly, its occurrence has been investigated in a spatially extended system in the presence of noise (Zaikin et al., 2002), Duffing oscillator (Blekhman and Landa, 2004), two-coupled overdamped anharmonic oscillators (Gandhimathi et al., 2006) and monostable systems (Jeyakumari et al., 2009). Experimental evidence of vibrational resonance was demonstrated in analogue simulations of the overdamped Duffing oscillator (Baltanas et al., 2003), a bistable optical cavity laser (Chizhevsky and Giacomelli, 2006) and an excitable electronic circuit with Chua's diode (Ullner et al., 2003). The influence of time-delayed feedback on vibrational resonance was studied numerically (Yang and Liu, 2010) and theoretically (Jeevarathinam et al., 2011). Further, biharmonic force induced enhanced signal propagation was found to occur in one-way coupled systems (Yao and Zhan, 2010) and in a coupled network of excitable neuronal systems (Yu et al., 2011).

In the present work, we consider the two groundwater-dependent plant ecosystem models of Ridolfi et al. (2006, 2007) and investigate the emergence of vibrational resonance. It has been pointed out that the dynamics of vegetation have a time scale greater than one season and much greater than man-induced periodic disturbances (Ridolfi et al., 2007). We wish to mention that high-frequency oscillation of beach water table due to wave runoff and rundown has been observed and analysed (Waddell, 1976; Li et al., 1997). Interestingly, similar high-frequency oscillation of underground water table (in addition to the low-frequency periodic oscillation of water table due to seasonal variation) can occur due to evaporation, inflow and outflow of water and temperature fluctuation. It can also be artificially realized through irrigation or pumping from the aquifer. Furthermore, a water table rise and drop can be induced by vegetation removal and planting, respectively. Thus, planting additionally short-lived species interacting weakly with species *A* can also lead to a high-frequency variation of the water depth. Therefore, it is realistic to include a biharmonic force in the water table with two well-separated frequencies. The first model describing the dynamics of the biomass *V* of a single species has bistable states. When the biharmonic force is included in the water depth the system shows an oscillatory variation of *V*. As the amplitude of the high-frequency force is varied, the system exhibits multiple vibrational resonance with a decreasing response amplitude at successive resonances for certain range of fixed values of amplitude of low-frequency force. The second model describes the dynamics of two species, say *A* and *B*, interacting with the water table, and where the evolution of *B* depends on  $A(t - \tau)$  and  $\tau$  is the time-delay parameter. Unlike the single species model, the two species model is an excitable system (such a system have only one stable equilibrium state, but external perturbations above a certain threshold can induce large excursions in phase space, which takes the form of spikes or pulses). For a fixed time-delay, both *A* and *B* display a certain number of resonances when the amplitude of the high-frequency force is varied. The resonance

profiles of *A* and *B* are similar except that at resonance the amplitude of *A* is always much higher than that of *B*. Here the resonance intervals are not sharp but wide. The response amplitude is inversely proportional to the period of the variation of *A* and *B*. The delay parameter  $\tau$  has a strong influence on the response amplitude. The response amplitude at successive alternative resonances decreases when the value of the delay parameter increases.

## 2. Vibrational resonance in a single species model

To start with, first we briefly introduce the model (Ridolfi et al., 2006, 2007) in order to prepare the readers for the study of vibrational resonance.

### 2.1. Description of the model

The dynamics of phreatophyte biomass *V* of a single species (or total plant biomass neglecting interspecies interactions) is expressed as (Ridolfi et al., 2006, 2007)

$$\frac{dV}{dt} = V(V_{cc} - V), \quad (1)$$

where the growth rate of *V* is assumed to be proportional to the existing biomass and the available resources  $V_{cc} - V$  with  $V_{cc}$  being the carrying capacity of the ecosystem, that is, the maximum amount of vegetation sustainable with the available resources. Based on experimental evidences, an appropriate form of  $V_{cc}$  shows a quadratic dependence on the water table depth *d*. Taking into the effect of periodic oscillations in the rainfall regions leading to periodic variations of water table depth, Borgogno et al. (2012) considered the form of  $V_{cc}$  as

$$V_{cc} = \begin{cases} a[d(t) - d_{inf}][d_{sup} - d(t)], & \text{if } d_{inf} < d < d_{sup} \\ 0, & \text{otherwise.} \end{cases} \quad (2)$$

The form of  $V_{cc}$  given by Eq. (2) corresponds to the case of phreatophyte vegetation that depends on water uptake from the groundwater. In Eq. (2)  $d(t)$  is the water table depth, *a* is the sensitivity of carrying capacity to changes in the water table depth,  $d_{inf}$  is the threshold of vegetation tolerance to shallow water tables and insufficient aeration of the root zone and  $d_{sup}$  is the threshold of water depth below which tap-roots cannot extract water. The water table depth is given by

$$d(t) = d_0 + \beta V + F(t), \quad (3)$$

where  $d_0$  is the water depth in the absence of vegetation,  $\beta$  is the sensitivity of the water table to the presence of vegetation and  $F(t)$  describes the oscillatory variation of the water table. The choice  $F(t) = f \cos \omega t$  is considered in Borgogno et al. (2012). In the present work we choose  $F(t)$  as a biharmonic force with two widely differing frequencies:

$$F(t) = f \cos \omega t + g \cos \Omega t, \quad \Omega \gg \omega. \quad (4)$$

The explicit time-dependent variation of the water depth can be natural due to seasonal rainfall oscillations or man-induced perturbations (pumping from an aquifer).

The potential  $U(V)$  defined through  $dV/dt = -dU/dV$  in the absence of  $F(t)$  is depicted in Fig. 1a where  $d_0 = 0.5$  m,  $\beta = 0.5$  m,  $a = 26$  m<sup>-1</sup>,  $d_{inf} = 0.6$  m and  $d_{sup} = 0.9$  m the values of the parameters used in Borgogno et al. (2012).  $U(V)$  is of a double-well form. The equilibrium states can be obtained by setting  $dV/dt = 0$ .  $V_0^* = 0$ , representing the unvegetated state, is an equilibrium point. The other equilibrium states correspond to  $V_{cc} = V$ . In the plot between  $V_{cc}$  versus *V* the intersection points of the line  $V_{cc} = V$  with the curve of  $V_{cc}$  are the equilibrium states. Fig. 1b shows  $V_{cc}$  versus *V*. The equilibrium states are  $V_0^* = 0$ ,  $V_u^* = 0.28526$  and

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