Nonlinear Dynamics in the Trapping Movement of the Venus Flytrap

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Abstract— **Venus flytrap has long been regarded as one of the few plants capable of rapid movements for small animal trapping. It has three unique features. First, it has one of the fastest movements in the plant kingdom. Second, it exhibits a "decision-making intelligence" to determine, from a semi-closed state, whether to proceed to be completely closed or fully open. Finally, the Venus flytrap has a "memory" of touch that two mechanical stimuli within about 30 seconds are usually necessary to trigger the trap closing. The movement has significant advantages over motions generated by complex nervous interactions, as it does not involve sophisticated sensor or processor. Rather it relies on simple biochemical reactions that could be relatively easily engineered. This movement involves nonlinear dynamics that has not been well understood. A mathematical model describing the movement of the Venus flytrap was first proposed by the authors in [21]. This paper provides an in-depth nonlinear analysis of the dynamic process for better understanding of not only the fascinating plant trapping movements, but also the potentially bio-inspired control mechanism for industrial applications.**

I. INTRODUCTION

Venus flytrap is one of moving plants that can capture and digest insect prey. Each of its leaves consists of two lobes hinged at the midrib. Each lobe has few prey-sensitive trigger hairs on its inner surface and some finger-like cilia along its edge. When two lobes shut, the cilia interlock to prevent prey from escaping. By capturing and digesting insect prey, the Venus flytrap has more nutrition resource than non-carnivorous plants. Charles Darwin referred it as "*one of the most wonderful plants in the world*" [1]' because of its fascinating motion of opening and closing. Since then, researchers have studied both chemical signaling and its trap closing mechanics.

The Venus flytrap's motion consists in three distinct states [2], [3], [4], (1) fully open state before stimuli apply, (2) semi-closed state after stimuli apply and cilia interlock to restrain the prey and (3) fully closed state only if further stimuli follows to seal the restrained prey. The state transition in the Venus flytrap's motion involves complex dynamics. Especially at the semi-closed state, it exhibits "decision-making" intelligence and allows the flytrap either proceeding to the fully closed state or reverting back to the open state. The dynamical transition from the open to semi-closed states has been studied, but the transitions from semi-closed state to other states have been largely overlooked [5], [6]. At the semi-closed state, if the prey escapes, the flytrap will

return to the fully open state; while if the prey struggles to produce more stimulus, it will proceed to the fully closed state. Usually it takes 5-7 days to complete the digestion process and the flytrap reopens thereafter.

The mechanism of the Venus flytrap's opening and closing processes has drawn great attention of plant biologists for long time. It is known that through mechanical stimulus, the trigger hairs on the inner surface can generate receptor potentials (RP) followed by action potentials (AP) to initiate trap closure [7], [8]. In fact, these APs are similar to those found in mammalian muscle contraction and nerve impulse, and do not vary in the different types of cells within the trap [9]. Moreover, experiments show that besides APs, trap closure can be also initiated by constant injections of electrical charges with accumulated charge $14\mu C$ [10], which requires two mechanical stimuli within $\sim 30s$ at temperature $15 - 25°C$ [11], [12]. The charge accumulation involves interesting nonlinear dynamical effects which, unfortunately, has not been studied yet.

Each lobe contains two layers, inner layer and outer layer. Experimental study demonstrated that the trap closure is actively initiated by hydrodynamic flow between two layers. When the accumulated electrical charge reaches the threshold, it will trigger the ATP hydrolysis [13] and fast proton transport [4], [14] to generate a gradient to open the water channels. It is suggested [15] that the surface curvature of lobes and the water transport between two layers lead to the trap closure. But the feature of rapid closing motion is not captured.

Some models have been proposed to study the trap closure. Forterre *et al.* suggested that the trap closure require force generated by the bucking instability due to the leaf geometry [16]. Bobji modeled the Venus flytrap as a bistable vibrator with in both open and closed states stable [17]. Volkov *et al.* proposed a hydroelastic curvature model in which the lobes have curvature elasticity and different hydraulic pressures in two layers [18]. The model partially describes the closure process (from open to semi-closed states) after stimulation, but not the reopening and sealing processes (from semi-closed to other states). In [5], Markin *et al.* introduced a model with an intermediate state at which the mean curvature is zero. This additional state is not a semi-closed state, but a state between the open and semi-closed states.

Experiments show that the trap can snap to the semi-closed state in $0.1 - 0.3$s under sufficient stimuli. At this state, the cilia interlock with a visible gap between two lobes, which restrain big prey, but allow small prey to escape. Without further stimulus if the prey escapes, the trap will open within 1-2 days. With constant stimulation, however,

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the trap will close tightly to a sealed state that remains for 5-7 days. Due to this intermediate state [19], [20], the trap is capable of "making a decision" to reopen or seal. Studies on flytraps fed with ants have concluded that constant mechanical stimulation of the trigger hair causes fully trap closure, leading to secretion of digestive enzymes [3]. It is energetically costly for the plant to secrete digestive enzymes into an empty trap. Thus the decision-making capability is adaptively advantageous.

In [21], Yang, *et al.* proposed the first complete mathematical model to describe the closing and opening mechanisms of the Venus flytrap. However, as a paper with audience mainly for plant biologists, it has not taken full advantages of advanced nonlinear analysis to understand the biological process. This paper aims to pursue an in-depth study of the movement and to potentially inspire applications in control.

II. MODELING THE MOVEMENT OF THE VENUS FLYTRAP

It is believed [6], [10], [18], [22] that the dynamical transitions among the open, semi-closed and closed states is caused the water transportation between the outer and inner layers of the flytrap. Thus the water kinetics is crucial for modeling the flytrap movement. Denote by X_o and X_I the amount of water stored in the outer and the inner layers, respectively. Then the water dynamics in both layers is determined by

$$\begin{cases} \dot{X}_o = \frac{\alpha X_o^p}{X_o^p + X_I^p} + u_h + u_a - u_c - \mu X_o \\ \dot{X}_I = \frac{\alpha X_I^p}{X_o^p + X_I^p} - u_h - u_a + u_c - \mu X_I \end{cases} \quad (1)$$

where α is the supply rate from roots and μ the consumption rate through evaporation. The distributed water supply rates, $s_o = \frac{\alpha X_o^p}{X_o^p + X_I^p}$ and $1s_I = \frac{\alpha X_I^p}{X_o^p + X_I^p}$ with $p > 1$, to two layers reflect the fact that water supply favors the layer with more water. In addition, the water supply rates are also affected by hydraulic gradient u_h, osmotic gradient u_a and chemical signal u_c. These three effects usually take place in the different processes of flytrap movements and may depend on the stimulus strength. See [21] for more details.

Furthermore, once stimulated, the trigger hairs will generate receptor potential followed by action potential u_t. Let k_c and k_a be the dissipation rate and accumulation rate of the charge. Then the resulting charge accumulation can be written as

$$\dot{C} = -k_c C + k_a u_t \quad (2)$$

Given an accumulation threshold C_T, as the charge reaches the threshold ($C > C_T$), the voltage-gated channels connecting two layers will open. The hydraulic gradient u_h emerges and causes the water transport from the inner layer into the outer one until the channels are closed at time T_0 or hydraulic pressure becomes zero or negative. Because the aquaporin channel allows only one-direction water flow from inner to outer layers, the water transport rate due to the hydraulic gradient is given by

$$u_h = \begin{cases} k_t \max\{X_I(t) - X_o(t), 0\} \delta_t(t), & C \geq C_T, \\ 0, & C < C_T; \end{cases}$$

where the voltage opening is assumed to be an impulse

$$\delta_t(t) = \begin{cases} 1, & 0 \leq t \leq T_0, \\ 0, & t > T_0. \end{cases}$$

On the other hand, we assume (a) that transport rate u_a driven by the osmotic gradient depends only on the water volume X_I in the inner layer and is given by

$$u_a = \begin{cases} k_f X_I(t) \delta_t(t), & C \geq C_T, \\ 0, & C < C_T; \end{cases}$$

and (b) that the chemical signal starts at T_{start} and lasts within the time period T_D and the associated transport rate is given by $u_c(t) = k_d \delta_c(t)$, where k_d is the water flow coefficient by chemical energy and

$$\delta_c(t) = \begin{cases} 1, & T_{\text{start}} \leq t \leq T_{\text{start}} + T_D, \\ 0, & \text{Otherwise.} \end{cases}$$

Recall the water supply rates $s_o = \frac{\alpha x^p}{1 + x^p}$ and $s_I = \frac{\alpha}{1 + x^p}$, where $x = \frac{X_o}{X_I}$. As $x > 1$ but close to 1 and $p \gg 1$, then $s_o \sim 0$ and $s_I \sim \alpha$ and vice versa. While if p is close to 1, then s_o and s_I are significantly different only if x is very small. In other words, even if one layer contains slightly less water than the other one, their supply rates can be very different when p large. Therefore $p > 1$ is an important parameter for the water supply rates and determines the favorability of the water supply to the layer with more water. Indeed, if the stimulus is absent, any value of $p > 1$ yields essentially the same dynamics; otherwise, different values of p may lead to distinct dynamics. As discussed above, $p \gg 1$ and $X_I > X_o$ imply that the supply rate s_o to the outer layer will be very small compared to s_I. Thus most water supply goes quickly to the inner layer, which may inhibit the transition of flytrap from the open state to the semi-closed state.

III. ANALYZING THE NONLINEAR TRAPPING DYNAMICS

The nonlinear dynamic behavior of the Venus flytrap is described by model (1). And by definition of $\delta_t(t)$ and $\delta_c(t)$, one has

$$\lim_{t \to \infty} u_h(t) = \lim_{t \to \infty} u_a(t) = \lim_{t \to \infty} u_c(t) = 0$$

uniformly in $X = (X_o, X_I)$. Thus system (1) is asymptotically autonomous and its limiting system is given by

$$\dot{X}_o = \frac{\alpha X_o^p}{X_o^p + X_I^p} - \mu X_o, \quad \dot{X}_I = \frac{\alpha X_I^p}{X_o^p + X_I^p} - \mu X_I. \quad (3)$$

By [23], the long term behavior of the flytrap determined by (1) can be characterized by its limiting system (3), which also describes the water dynamics without stimuli. This also makes sense biologically. In reality, stimulus can exist only in the finite time, when the prey is trapped and struggling. After the prey is digested, no further stimulus is available before any new prey is trapped. Hence after stimulus is triggered by the trapped prey, the long time behavior of the flytrap can be characterized by the case that no prey is trapped.

It can be shown that system (3) has three steady states: open state $S_1^0 = (0, c)$, closed state $S_3^0 = (c, 0)$ and semi-closed state $S_2^0 = (\frac{c}{2}, \frac{c}{2})$. The stimulus-induced supply rate $u = (u_h, u_a, u_c)$ drives the flytrap to transit between any two states. Principles of the state transitions will be illustrated to connect the plant's biological functions.

A. Conservation of Water

It can be imagined biologically that the amount of water in each layer is largely determined by the water transport between two layers, but the total amount of water $Y = X_o + X_I$ is not. This is because water transport takes place only within and between the two layers but it will not produce or consume any water in the layers. Indeed the total amount Y depends only on the water supply and consumption. It is mathematically determined by $\dot{Y} = \alpha - \mu Y$ and hence $Y = c = \frac{\alpha}{\mu}$ is stable. In other words, the total amount of water is conserved when the water supply is balanced by the consumption, and the steady state $Y = c$ is stable in the sense that such a balancing can be soon recovered after certain variation in the amount of water stored in the layers. Therefore, without loss of generality, we assume that the total water in the two layers is conserved.

B. Bistability without External Stimulus

Experimental studies have confirmed that the Venus flytrap stays open when no stimulus is present. It is reasonable to consider the open state as a stable state. Due to the conservation of water, system (3) can be reduced to

$$\dot{X}_I = f_0(X_I) = \frac{\alpha X_I^p}{(c - X_I)^p + X_I^p} - \mu X_I. \qquad (4)$$

For $p > 1$, all the steady states are isolated. Both closed state S_3^0 and open state S_1^0 are stable and semi-closed state S_2^0 is unstable.

Apparently the semi-closed state separates the stability regions of two stable states of system (4). The initial state will determine which stable state the system will approach eventually, as shown in Figure 1. The feature of bistability accounts for the biological fact that water supply favors the layer with more water. If the inner (outer) layer contains more water than the outer (inner) layer, more water will flow into inner (outer) layer and fill it up so that the flytrap opens (closes).
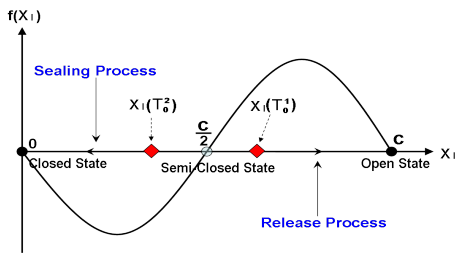

Fig. 1. Phase diagram of system (4) showing bistability. Red diamond $X_I(T_0^2)$ ($X_I(T_0^1)$) is in the stability region of closed (open) state and the flytrap will approach closed (open) state.

C. Dynamic State Transition

1) Capture process (from open to semi-closed states): Suppose that open state is the initial state, $X(0) = S_1^0$. By charge accumulation, a stimulus $C > C_T$ is applied to the flytrap and triggers the water channel opening so that water is transported under the hydraulic pressure u_h to close the trap for capture, until the channel closes at time $T_0 = T_0^1$.

Without other stimulus, the trap movement with hydraulic effect is described by

$$\dot{X}_I = f_1(X_I) = f_0(X_I) - k_t(2X_I - c)H(2X_I - c) \qquad (5)$$

where $H(x)$ is Heaviside function. Because open state S_1^0 is not a steady state of system (5) but semi-closed state S_2^0 may or may not be, the flytrap moves from open state toward semi-closed state for capture, as seen in Figure 2. Precisely it can be proved that if $p > 1$ is not very large, then X_I approaches S_2^0 if system (5) starts with open state, that is, $X_I(0) = c$. The data used in [21] are in such case.
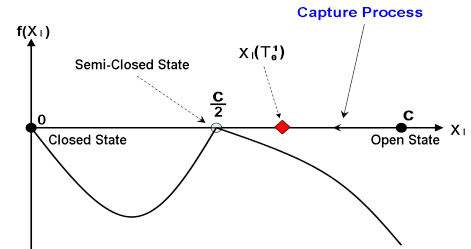

Fig. 2. Phase diagram of system (5) when hydraulic gradient takes into effect, which changes the phase diagram so that open state is not a steady state. The flytrap moves toward the semi-closed state for capture.

By comparison, if $p > 1$ is sufficiently large, then an additional steady state emerges and blocks the transition to the semi-closed state. This is because large p yields large water supply rate s_I into the inner layer, which can compete with hydraulic effect and interfere with the state transition.

2) Release process (from semi-closed to open states): The release process is also governed by system (4) because no further stimulus is applied. Note that the initial state in the release process is exactly the ending state $X(T_0^1)$ in the capture process. Because the flytrap does not cross the semi-closed state and still remains in the stability region of the open state, it will move back to the open state when no further stimulus is available. This process shows the transition of flytrap from semi-closed state to the open state, see $X_I(T_0^1)$ in Figure 1.

3) Sealing process (from semi-closed to fully closed states): If the trapped prey continuously struggles, more stimuli will evoke to reopen the voltage-gated channels. This extends the opening period T_0 of water channel from T_0^1 to $T_0^2 > T_0^1$ to push the lobes crossing the semi-closed state by transporting more water to the outer layers. Meanwhile, as the pressure between the inner and outer layers is negative, the resulting osmotic pressure prevents the backward water transportation [21]. Thus, in the sealing process, the osmotic

pressure plays a key role and the model is

$$\dot{X}_I = f_2(X_I) = f_1(X_I) - k_f X_I. \tag{6}$$

Dynamically, osmotic effect u_a changes the phase diagram further (Figure 3) so that semi-closed state is not s steady state and consequently the system can go across it and reach $X_I(T_0^2)$, which is in the stability region of closed state.
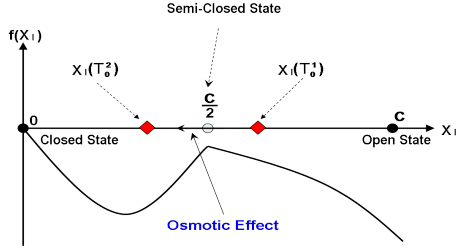

Fig. 3. Phase diagram of system (6) as osmotic gradient takes place and transition across the semi-closed state follows.

After the flytrap enters the stability region of closed state, it continues the transition to the fully closed state even though the stimuli vanish, as indicated by $X_I(T_0^2)$ in Figure 1.

4) Reopening process (from fully-closed to open states): After the prey is digested in the fully closed traps, the lobes start reopening and recover the open state for new trapping event. Assume that the reopening process is initiated by chemical signal $u_c(t)$, which yields a modified system

$$\dot{X}_I = f_3(X_I) = f_0(X_I) + k_d \delta_c(t). \tag{7}$$

Figure 4 shows that the chemical signal modifies the phase diagram so that no steady state exist. Consequently system (7) becomes monotone so that the transition to the open state is straightforward.
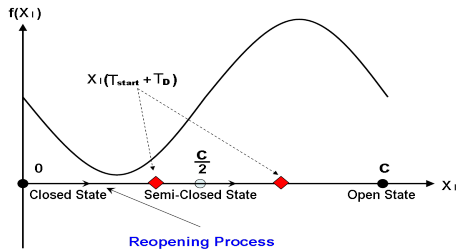

Fig. 4. Phase diagram of system (7) with chemical signal, which changes the phase diagram such that no steady state exists to block the transition to the open state.

It is readily to see that the chemical signal strength k_d and duration T_D are very important for the flytrap reopening. As k_d is small, the weak signal may be overcome by the water supply to outer layer and interfere with water transport to the inner layer. Suppose that the chemical signal starts at T_{start}, then the flytrap will move to $X_I(T_{\text{start}} + T_D)$ when it vanishes. If T_D is long enough, $X_I(T_{\text{start}} + T_D)$ can reach the stability region of the open state; otherwise, it remains in the stability region of the closed state, as shown in Figure 4. After chemical signal vanishes, certainly the former case

will lead to the flytrap reopening just as the release process illustrated in Figure 1.

D. Three Typical Features of the Venus Flytrap

In this section, we consider the three important features of the Venus flytrap's motion: (1) "memory" of touch, (2) fast closing movement and (3) "decision-making intelligence".

1) Memory of Touch: The Venus flytrap can detect a prey by the hair triggering mechanism. One hair touch by the prey generates a RP followed by an AP $u_t = Ae^{-Bt}$ Vols with $A = 0.15$ and $B = 2000$ as measured at $15 - 25°C$. The AP leads to charge accumulation, so that if the total charge is above threshold $14\mu C$, then the flytrap closure is initiated.

Denote by $\bar{C}_m$ the maximum of total charge accumulation C_m with $m + 1$ hair(s) triggered. Using the data provided in [21] and $k_c = 0.05$ and $k_a = 0.15$, one has

$$\bar{C}_0 = C_0(t_0) \approx 11.25\mu C < C_T = 14\mu C,$$

which implies that one trigger is not enough to initiate the flytrap closure and the second triggering is needed. A delay threshold $\bar{\tau}$ is required such that the second trigger must occur within $\bar{\tau}$ to accumulate sufficient charges and initiate the closure. By the same data set, $\bar{\tau} \approx 28.15$, which is consistent with the experimental observation.

Biologically, the Venus flytrap puts a "memory" every time when the prey touches a hair. The memory fades in time. The shorter the delay τ is, the stronger the combined effect of the memories is. On the other hand, more triggers produce higher maximum of charge accumulation. Thus, the trigger time delay and the number of triggers are two important factors for charge accumulation. The former is related to the memory of the flytrap, and the latter is related to the activities of the prey. The flytrap records the prey's activities and calculates the overall trigger effect for a decision-making whether or not the closure is initiated.

2) Fast Closing: In the capture process with the osmotic effect taken into account, i.e., $\dot{X}_I = f_2(X_I)$, let τ_t be the transition time from open state $X_I = c$ to semi-closed state $X_I = \frac{c}{2}$. With the data provided in [21], it can be estimated that $\tau_t = 0.203$ second, which indicates that the transition from open state to semi-closed state is rapid. Therefore the flytrap can trap the prey rapidly by fast closing the lobes.

In fact, this transition time τ_t depends decreasingly on both hydraulic and osmotic effect, but increasingly on the water consumption μ. Interestingly, however, τ_t is independent of the water supply rate α. Biologically, this may be due to the weak root system of the Venus flytrap. One of the common features of carnivorous plants is weak root system [24]. The carnivorous plant need catch and digest prey animal for more nutrient. But meanwhile, weak root system results in slow water supply. Therefore during the fast closing motion, slow water supply has no significant impact on the closing time.

3) Decision-Making: The decision-making intelligence benefits from bistability or the biological fact that water supply favors the layer with more water. By discussion in the previous sections, it is easy to see that there exists a time threshold $\bar{T}$. When the water channel is open in time $T_0 = \bar{T}$,

the flytrap moves exactly to the semi-closed state. Therefore the water channel opening time will lead to the decision-making. After the capture process, the flytrap will be either fully closed if $T_0 > \bar{T}$ or completely open if $T_0 < \bar{T}$.

When the hair is triggered by the prey to generate APs that cause the water channel opening and water transport from the inner into the outer layer, the Venus flytrap will start closing until the water channel is shut down at time T_0. On one hand, if the prey escapes, then no sufficient stimulus is generated to keep the water channel open in sufficiently long time, i.e., $T_0 < \bar{T}$. Thus the flytrap cannot close effectively to cross the semi-closed state and eventually moves back to the closed state. This is the release process as discussed in III-C.2. On the other hand, however, if the trapped prey keeps struggling, it will cause more stimuli and keep the water channel open in a longer time, i.e., $T_0 > \bar{T}$. Then the flytrap can close sufficiently by crossing the semi-closed state. In contrast, now the outer layer contains more water than the inner layer and hence the flytrap will continue to move to the closed state after stimulus vanishes. This is the sealing process discussed in III-C.3. Overall, the decision can be made either directly through the water channel opening time, or indirectly by the trapped prey's action, escape or struggling.

IV. CONCLUSION

It is revealed by nonlinear analysis of the Venus flytrap that the stimuli due to different effects, as the controls applied to the flytrap, can change the phase diagram in different stages of motion to achieve the state transition. Biologically, mechanical stimulus caused by the trapped prey can lead to the stimulus strength accumulation, so that the water channel is open when it exceeds the threshold. In this case, hydraulic gradient induces rapid water transport from the inner layer into the outer layer, and osmotic pressure further pushes more water into the outer layer, which makes flytrap lobes fully closed by keeping favored water supply into the larger layer. After the prey is digested, a chemical signal induces the water channel open and allows water transport from the outer back to the inner layers. Eventually the Venus flytrap transits back to the open state.

It is concluded from this study that the unique naturally occurring biological movement exhibits interesting nonlinear dynamical properties. The fascinating Venus flytrap movement does not involve any sophisticated sensors or processors, rather simple biochemical reactions that can always be easily engineered. This has significant advantage over actions caused by complex nervous interactions. As an alternative for sophisticated grabbing or trapping, this simple plant movement may offer new insights for bio-inspired solutions for control, including capture of moving objects and as a biological trapper for environmental toxicity monitoring. A motor-driven Venus flytrap trapper has been proposed and implemented. The movie of the trapper movement is available at http://web.utk.edu/~mjzhang/Projects.html. The trapper mimics the control mechanism of the Venus flytrap in nature. Further inspiration based on the simple plant movement and decision-making principles would be an interesting topic for researchers in dynamics and control.

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