Towards a framework for collective behavior in growth-driven systems, based on plant-inspired allotropic pairwise interactions

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Abstract
A variety of biological systems are not motile, but sessile in nature, relying on growth as the main driver of their movement. Groups of such growing organisms can form complex structures, such as the functional architecture of growing axons, or the adaptive structure of plant root systems. These processes are not yet understood, however the decentralized growth dynamics bear similarities to the collective behavior observed in groups of motile organisms, such as flocks of birds or schools of fish. Equivalent growth mechanisms make these systems amenable to a theoretical framework inspired by tropic responses of plants, where growth is considered implicitly as the driver of the observed bending towards a stimulus. We introduce two new concepts related to plant tropisms: point tropism, the response of a plant to a nearby point signal source, and allotropism, the growth-driven response of plant organs to neighboring plants. We first analytically and numerically investigate the 2D dynamics of single organs responding to point signals fixed in space. Building on this we study pairs of organs interacting via allotropism, i.e. each organ senses signals emitted at the tip of their neighbor and responds accordingly. In the case of local sensing we find a rich state-space. We describe the different states, as well as the sharp transitions between them. We also find that the form of the state-space depends on initial conditions. This work sets the stage towards a theoretical framework for the investigation and understanding of systems of interacting growth-driven individuals.

1. Introduction
In the past couple of decades, there has been an increasing interest in the investigation of collective behavior in systems composed of motile self-propelled entities. Examples of collective behavior are widespread in biological systems, including colonies of bacteria [1, 2], motile cells [3, 4], swarms of insects [5, 6], schools of fish [7, 8], or flocks of birds [9, 10], as well as physical systems including nematic fluids [11, 12], shaken metallic rods [13–16], and nano-swimmers [17]. Despite the diversity of these systems, generalized minimal models have shown that collective behavior may emerge as a results of local interactions between individuals [7, 18–27]. Indeed these models are able to reproduce complex behavior using similar minimal rules. For example in the archetypal Vicsek model [28] a particle assumes the average direction of the particles in its close neighborhood, while in the Couzin model [24] an individual is attracted to neighboring individuals and aligns to them. These simple systems all exhibit complex collective behavior, as well as transitions between disorganized and organized states. The sensory processes involved in biological systems are taken into account by introducing specific attraction, repulsion and alignment interactions [18, 21, 24]. Furthermore this understanding is at the basis of the field of swarm robotics [29].

However a variety of biological systems are not motile, but sessile in nature, relying on movement resulting from continuous growth in the direction of environmental stimuli. For example, in their search for nutrients, plant roots and fungal hyphae change their morphology by growing differentially, and neuronal
axons grow towards a chemical signal. Examples also include artificial systems such as recently developed self-growing robots based on additive manufacturing technology [30]. In many cases, groups of such growing organisms form striking structures that provide a biological function or are beneficial for the survival of the group, as in the case of plant root systems that adapt their structure according to water content [31, 32]. Another remarkable example is the development of the functional architecture of the nervous system, where axons grow, in a coordinated fashion, into networks that span large distances. The manner in which these complex structures form is not yet understood, however it has been suggested that both neuronal and plant systems may exhibit collective behavior [33–37], in line with evidence for interactions between growing organs mediated by complex signaling [36–40].

The few currently-available models of interacting growth-driven systems [33, 41–44] consider the dynamics of the tip alone, disregarding the fundamental implications of growth, namely the accumulation of past trajectories of individuals, which couples space and time, and constrains possible future trajectories. Indeed in elongating organs changes of curvature at the base have a long-range effect on the position and orientation of the apical tip [45].

The goal of this work is to provide a general framework for the study of collective dynamics in interacting systems where movement is due to growth. We will build on the established mathematical description [46, 47] of the kinematics of the growth-driven response of plants towards distant external stimuli, called tropisms. This minimal model does not rely on biological details, and therefore may apply to any rod-shaped system which senses signals and responds by growing in the direction, e.g. plant organs, neurons, fungi and self-growing robots. We will generalize this model to the case of a response to a stimulus emanating from a neighboring organ. We will investigate the dynamics of a single organ in response to a static point stimulus, where perception is either local or at the tip alone. Finally, we will consider pairwise interactions, where two organs sense each other and respond accordingly, yielding a complex state-space. Though we refer to plants throughout the paper, the results are general and can be applied to any similar growth-driven system, such as neurons, fungi, self-growing robots etc.

2. A minimal model for allotropism: the growth-driven reorientation of plants in response to signals emitted by neighboring plants

Tropisms are the response of plant organs to a distant directional stimulus, e.g. shoots grow towards a source of light (positive phototropism), and grow away from the direction of gravity (negative gravitropism) [48]. As mentioned in the Introduction, collective dynamics of plant organs are expected to emerge as a result of local plant-plant dynamical interactions, where for example one plant root senses a signal emanating from a neighboring root and, similarly to common tropic responses, reorients its growth according to the direction of the stimulus. Indeed plants are able to sense diverse signals emitted by neighboring plants, transmitted either above or below ground [49–51]. These signals can be classified as: (i) indirect signals, corresponding to environmental factors modified by the presence of neighbors, such as light and uptake of nutrients; and (ii) direct signals, corresponding to molecules directly produced by neighboring plants, such as aerial volatile organic compounds (VOCs), soluble root exudates, or microbiome and other intermediates. Furthermore, there are observations of self-recognition in plants [52], as well as recognition of kin [53–55]. Depending on the type of interaction, it is not always clear where the sensing occurs, or where the signal is emitted. Similarly to tropic responses, plant organs are assumed to grow to or away from such signals emanating from neighboring organs. However, the kinematics of these responses are expected to be different: the source of such a stimulus is in proximity of the organ, meaning that it will reach different points along the organ at different relative angles (illustrated in figure 1(a)), as opposed to a tropic response where the stimulus is infinitely distant, yielding a parallel vector field which therefore approaches any point on the organ from the same angle and intensity. We name this response allotropism, from the greek word ἀλλός (állos) for other or another.

As discussed in the Introduction, here we adopt a geometrical framework we recently developed for the study of plant tropisms [46, 47], the gravipropriocceptive model, or ‘AC’ model, and its variations. Though this model is general, making minimal assumptions about the building blocks of the system, it successfully accounts for the experimentally observed gravitropic kinematics of different organs from 11 angiosperms [46]. It also accounts for phototropic responses, as well as the equilibrium observed between phototropism and gravitropism in avena coleoptiles [47]. The model can be extended to take an explicit account of the effects of growth [56], as well as kinematics in 3D [57], and has also been generalized to take into account time varying stimuli [58]. Given the geometrical definitions illustrated in figure 1(a), the AC model relates perception and movement in tropisms, e.g. gravitropism or phototropism, with the following equation:

$$\frac{\partial \kappa(s, t)}{\partial t} = -\beta \sin(\theta(s, t) - \theta_p) - \gamma \kappa(s, t),$$  \hspace{1cm} (1)

where $0 \leq s \leq L$ is the curvilinear abscissa along the organ of size $L$, and $\theta(s, t)$ is the local angle that the organ forms with the vertical at point $s$ and time $t$. The curvature $\kappa(s, t)$ is the spatial rate of change of $\theta(s, t)$ along $s$, and is defined as $\kappa(s, t) = \frac{d\theta(s, t)}{ds}$. $\theta_p$ is the direction of an infinitely distant stimulus, such as light or gravity. The left-hand-side corresponds to the tropic
response, as expressed by the change of curvature in time. The right-hand-side corresponds to external and internal signals governing this response.

The term $\beta \sin(\theta(s, t) - \theta_p)$ accounts for the perception of an infinitely distant external stimulus such as gravity or light; the organ senses the stimulus locally along the organ, and tries to curve to align in the direction of the stimulus with a sensitivity $\beta$. The sign of $\beta$ also indicates whether the tropism is positive or negative (e.g. plant roots and shoots exhibit positive and negative gravitropism, respectively, where the former grow towards the gravitational signal, and the latter grow in the opposite direction). The perception of stimuli in plant organs generally occurs either locally, or at the tip alone (apical sensing), in which case we replace the sensing term with $\beta \sin(\theta(L, t) - \theta_p)$. For example in the case of phototropism, photoreceptors are either distributed at the tip alone, or along the whole growth zone as in the case of Arabidopsis [59–64]. The perception of gravity, on the other hand, is related to the presence of statoliths within specialized cells called statocytes; these are generally found throughout the growth zone for aerial organs, and restricted to the tip for roots [65, 66].

The second term $\gamma \kappa(s, t)$, is the proprioceptive term, and can be viewed as an internal restoring force expressing the plant’s resistance to being bent. $\gamma$ represents the proprioceptive sensitivity, associated with the ability of plants to perceive their own curvature and to respond accordingly to remain straight. Intuitively, a higher $\gamma$ represents stronger postural control, where the organ resists bending much in response to a stimulus. This proprioceptive term is central for the regulation of posture in plants and is a critical part of the tropic movement [46, 57, 67].

We note that equation (1) holds within a zone of length $L_{gz}$ from the tip, i.e. $0 \leq s \leq L - L_{gz}$, where growth occurs. Outside of the growth zone no response is possible, and equation (1) is reduced to $\frac{\partial}{\partial t} \kappa(s, t) = 0$. In this model growth is considered inherently as the driver of the tropic movement, focusing on the limit where elongation is negligible compared to the timescale of the tropic response (non-elongating organs). It was shown experimentally that this approximation is sufficient to describe gravitropism, and the effects of growth can be neglected [56]. For the sake of simplicity we adopt this limit here, which will provide an intuitive understanding of the system, and can be easily transferred in future to elongating organs as shown in [56].

The AC model for tropisms is limited to the case of distant stimuli yielding a parallel vector field, such as gravity or sunlight, which approach any point along a plant from the same angle, and at the same intensity. In other words the affecting stimulus is invariant per translation and rotation in the plane perpendicular to the direction of the stimulus. However, as mentioned earlier, when considering interacting neighboring plant organs, such as one root sensing the exudates secreted from a neighboring root [68], the signal emanates from a nearby source on the neighboring root tip, and approaches different points along the root from a different angle and intensity, as illustrated in figure 1(a). Moreover, the signal perceived by an organ is going to change dynamically as the organs move in space. Hence the translational and rotational invariances are no longer always valid throughout the dynamics.

Different types of signals, such as those discussed in the Introduction, may generally be classified as

Figure 1. Geometrical definitions. (a) Geometry of point tropism. The median line of an organ is in a plane defined by the coordinates $(x, y)$, and described by the parameter $s$ which runs along the organ taking the value $s = 0$ at the base, and $s = L$ at the apical tip, equal to the total length. At each point $s$ an angle $\theta(s, t)$ is defined with reference to the direction $y$. The base of the organ is clamped at $(x(s = 0, t), y(s = 0, t)) = (x_0, y_0)$, at an angle $\theta(s = 0, t) = \theta_0$. The position of the point signal is marked $(x_p, y_p)$. At each point $s$ of the organ, the distance to the point signal is $r(s, t)$ while the orientation of this element with respect to the point signal is $\theta(s, t)$. (b) Geometry of two interacting organs based on allotropism, the growth-driven response of a plant organ to another. The bases of the left and right organs are clamped at $(x_1(0), y_1(0)) = (-\Delta x/2, 0)$ and $(x_2(0), y_2(0)) = (\Delta x/2, \Delta y)$, respectively. The positions of the signaling apical tips are then $(x_1(L), y_1(L))$ and $(x_2(L), y_2(L))$. Each organ senses the signaling tip of the neighboring organ.
those emanating from extended areas of the organ (e.g. microbiome), or from the tip (e.g. root exudates). For the sake of simplicity we will focus here on the case of a signal emanating from a point placed at the tip of a neighboring organ, which will allow to get a an intuitive picture of the ensuing interaction and dynamics. Mathematically, this can easily be generalized to an extended zone by considering it as just the integration of many consecutive points along the line. We now generalize the previously described model so as to capture the tropic response to a stimulus emanating from a single point, which we will term point tropism.

Using the geometrical definitions illustrated in figure 1(a), and assuming the signal point is fixed in space at $\mathbf{x}_0 = (x_0, y_0)$, point tropism can be described by the following equation:

$$\frac{\partial \kappa}{\partial t} = -\lambda \left( r_0 \right) \sin \theta_p(s, t) - \gamma \kappa(s, t), \tag{2}$$

where all variables are identical to equation (1), apart from the signal perception term $\lambda \left( r_0 \right) \sin \theta_p(s, t)$. $\theta_p(s, t)$ is the angle at which the stimulus reaches an element of the organ at point $s$ at time $t$, defined as the difference between the angle of the organ and that of the signal point, as illustrated in figure 1(a):

$$\theta_p(s, t) = \theta(s, t) - \arctan \left( \frac{x(t) - x(s, t)}{y(t) - y(s, t)} \right). \tag{3}$$

Here $(x(t), y(t))$ is the position of the point signal and $(x(s, t), y(s, t))$ is the spatial position of an element of the organ at point $s$. In contrast to the AC model for regular tropisms such as gravitropism, the perceived angle is not constant along the organ even when the organ is straight, as illustrated in figure 1(a), and the closer the point stimulus is, the greater the variance along the organ.

$\lambda \left( r_0 \right)$ represents the sensitivity of the plant organ to the signal, and may depend on the distance between the sensing organ element and the signal point

$$r_0(s, t) = \sqrt{\left( x(t) - x(s, t) \right)^2 + \left( y(t) - y(s, t) \right)^2}. \tag{4}$$

Attractive responses, where the organ bends towards the stimulus, are described by $\lambda > 0$, and repulsion with $\lambda < 0$. $\lambda$ can also depend on time $\lambda(r, t)$, e.g. in the case of a diffusive signal which changes over time and space. Here we will consider a value constant in both space and time, focusing on attractive responses, since repulsive responses are more trivial, as we will discuss later. In line with biological observations [69] the signal is weighed by a sine function and cannot be linearized as has been done previously for the tropic case [46, 47] since angles cannot be assumed to be small. Equation (2) assumes local sensing, however for the apical case the sensing term is replaced with $-\lambda \sin(\theta_p(L, t))$. As with equation (1), the intuition behind equation (2) lies in recognizing that the right-hand-side expresses sensing of external signals, represented by the term $\lambda \sin(\theta_p(s, t))$, and internal signals associated with proprioception, $\gamma \kappa(s, t)$. On the other hand the left-hand-side represents the growth-driven response represented by the change in curvature $\frac{\partial \kappa(s, t)}{\partial t}$. We note that for distant stimuli this model coincides with that for regular tropisms. Initial conditions assume that at time $t = 0$ the organ is straight, $\kappa(s, t = 0) = 0$, placed at some angle $\theta_0$ from the vertical $\theta(s, t = 0) = \theta_0$, and clamped at the base, i.e. $\theta(s = 0, t) = \theta_0$.

Following dimensional analysis carried out in the AC model [46], we derive characteristic length and time scales. The length scale is identified by considering the steady state, and substituting $\frac{\partial \kappa(s, t)}{\partial t} = 0$ in equation (2). This allows to express $\kappa(s, t)$ as a function of the other terms, and taking $\sin \theta_0 = 1$ yields the maximal curvature value. Its inverse corresponds to the radius of curvature, a characteristic length scale termed the convergence length $L_\kappa = 1/\kappa_{\text{max}} = \gamma/\lambda$. There are two time scales: one is associated with the time it takes for the organ to reach its steady state, termed the convergence time and defined as $T_c = 1/\gamma$. The other is associated with the time it takes the organ to align in the direction of the stimulus for the first time, termed the arrival time, as is defined as $T_v = 1/\lambda L_{\gamma}$. The ratio between the convergence length and the length of the growth zone, as well as the ratio between the convergence time and arrival time, introduces a dimensionless number $Z$ [67], which describes the balance between the sensitivity to external stimuli and proprioception, and is linearly related to the maximal curvature:

$$Z \equiv \frac{L_\gamma}{L_c} = \frac{T_c}{T_v} = \frac{\lambda L_{\gamma}}{\gamma} = \kappa_{\text{max}} L_{\gamma}. \tag{5}$$

Now that the mathematical model is in place, we will proceed to describe the dynamics of a single organ as a response to a point signal fixed in space, both for apical and local perception.

3. Single organ dynamics with fixed point stimulus

We now consider the response of a single organ to a point stimulus fixed in space, focusing on the case of a constant attractive interaction $\lambda > 0$. In what follows we perform out analysis with values of $Z$ in the biologically relevant range $1 \leq Z \leq 10$ [46], where the limits $Z = 1$ and $Z = 10$ represent the extreme cases of strong and weak postural control. Numerical simulations are based on a simple forward integration Verlet algorithm, identical to what was used in previous work [46, 47]. A steady state is defined as the configuration at which $\frac{\partial \kappa}{\partial t} = 0$ and the organ stops moving.
We first focus on the case of apical sensing, where only the apical tip can perceive the direction of the signal, substituting $\theta_0(L, t)$ in equation (2). This means that the whole organ responds to the same signal, and thus the dynamics are expected to converge smoothly to the steady state, and the curvature is constant along the organ [47]. Given an initially straight and vertical organ, with $\kappa(s, 0) = 0$ and $\theta(s, 0) = 0$, the position of the apex is then limited to a set of possible positions, and is calculated analytically in the supplementary material (SM) (stacks.iop.org/BB/14/055004/mmedia). Figure 2(a) shows the steady state configurations of organs with different values of $Z$, with point stimuli placed at different positions (represented by a red dot). The configurations are overlaid on the said trajectory of all possible apex positions, plotted in solid black.

When a signal is placed outside of the trajectory of possible apex positions (top figure in figure 2(a) with $x_p = L$ and $y_p = 0$), we note that in the absence of postural control (proprioception), $\gamma = 0$ and $Z = \infty$, the organ curves and stops when the apical tip of the organ is aligned with the direction of the point signal. As $Z$ decreases (proprioception increases), the organ is not able to completely align its tip with the stimulus directions, and stops before that. If the point signal intersects the line of possible apex positions (middle figure in figure 2(a) with $x_p = 2L/\pi$ and $y_p = 0$), then in the absence of proprioception the apical tip will reach the position which by definition means the tip is aligned with the direction of the signal. As before, higher proprioceptive sensitivity does not allow organs to reach the stimulus. Finally, when the point is within the trajectory of possible apex positions (bottom figure in figure 2(a) with $x_p = L/4$ and $y_p = 0$), the organ may loop in order to align with the point stimulus.

We now continue to the more complex case of local sensing, where sensing is no longer limited to the apex, but rather occurs locally along the organ as described in equation (2). Similarly to the apical case, we start by analyzing the steady state with signal points placed at different positions, as shown in figure 2(b). Each row corresponds to different values of $Z$, and each column corresponds to a signal placed vertically from an organ’s base at distances $y_p = 0.1L, 0.5L, L, 2L$ and $y_p = \infty$ corresponding to normal tropism. Each shown configuration represents the steady state for an initially straight organs $\kappa(s, t = 0) = 0$ placed at different base angles: $\theta_0 = k \pi/6$ for $k = 1, 2, 3, 4, 5$, and the color code represents the value of local curvature along the organ normalized by the maximal curvature $\kappa(s)/\kappa_{\text{max}}$, exhibiting large variations. This demonstrates that in the case of local sensing the proximity of

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**Figure 2.** Steady state analysis of point tropism. (a) Apical sensing: steady states of dynamics of initially straight and vertical organs, $\theta_0 = 0$, in response to a point signal (red dot) placed at different positions ($y_p = 0$ and $x_p = L, 2L/\pi, L/4$ from top to bottom). Colors reflect different values of $Z$. The black curves represent the possible apex positions of steady states compatible with the initial conditions, as described in the text and calculated in the SM. (b) Local sensing: steady states for an initially straight organ clamped at different angles at the base $\theta_0 = k \pi/6$ with $k = 1, 2, 3, 4, 5$, for $Z = 1, 3$ and 10 (from top to bottom), as a response to point signals placed at different distances from the base marked by a red dot ($x_p = 0$ and $y_p = \infty, 2L, L, L/2, L/10$ from left to right). The colors denote the local curvature normalized by the maximal possible curvature $\kappa(s)/\kappa_{\text{max}}$. (c) Local sensing: normalized curvature map $\kappa/\kappa_{\text{max}}$ of the steady states for an organ clamped at the base with $\theta_0 = \pi/6$, as a function of the position along the organ $s$ and the position of the point tropism ($x_p = 0$ and $0 < y_p < 2L$).
the point signal introduces local perturbations in the curvature along the organ, associated with the variations in the perceived stimulus angle. When the point signal is infinitely distant \( y_T = \infty \), the steady state configuration corresponds to the AC model \([46]\). The organ curves to reach the vertical and higher values of \( Z \) yield a shorter convergence length \( L_c \). However contrary to the AC model the length of the curved zone is not constant for a given \( Z \), increasing for large base angles \( \theta_0 \) due to the sine function.

The local effects on curvature are represented in detail in figure 2(c), where the normalized curvature \( \kappa(s)/\kappa_{\text{max}} \) of the steady state configuration of an organ, initially clamped at an angle \( \theta_0 = \pi/6 \), is plotted as a function of position along the organ \((0 \leq s \leq L)\), and position of the point signal with \( x_P = 0 \) and \( 0 \leq y_P \leq 2L \) (again for \( Z = 1, 3, 10 \)). For large values of \( y_P \) the curvature is concentrated near the base and decreases exponentially towards the tip. As the point signal comes closer, with \( y_P < L \), a peak in curvature is observed in the region closest to the signal point, in line with the observation that close to the signal point the perceived angle of the signal varies greatly (illustrated in figure 1).

The diverse configurations resulting from local curvature perturbations mean that an analytical map of possible positions of the apical tip, as we found in the apical case, is harder to establish, and we will resort to a numerical analysis of the space of possible steady state positions of the apex for initially vertical and straight organs. We expect this to depend on both \( Z \) and the distance to the point signal. Let us first consider the case of an infinitely distant signal. Figure 3(a) shows different trajectories of all possible apex positions for different values of \( Z \), where the base of the organ is placed at the origin \((0, 0)\). The color scheme represents the angle of the point stimulus relative to the origin \( \theta_{op} \). When \( Z = \infty \) the solution is a circle of radius \( L \), starting straight ahead for a signal placed in direction \( \theta_{op} = 0 \) (dark blue) and ending in the opposite direction for \( \theta_{op} = \pi \) (yellow). This is the case since with no prior-ception the curvature can be infinitely concentrated near the base, and the organ aligns perfectly with any stimulus direction. As the proprioceptive sensitivity increases, and \( Z \) decreases, the range of possible positions is reduced, forming a closed curve. This reflects the point, that with proprioception, when a signal is placed almost directly behind the organ (high values of \( \theta_{op} \) marked in yellow), the organ is not able to bend enough and a different configuration is preferable. We note that the outer trajectory is common to all values of \( Z \).

In order to study effects of the distance of the stim-ulus to the organ, in figure 3(b) we plot possible steady state apex positions placed at a given distance \( r_P(L) \) from the stimulus, as defined in equation (4). Trajecto ries are plotted for distances \( r_P(L)/L = 0.01, 0.1, 1, \infty \). For \( Z = 3 \) the range of possible solutions does not vary significantly, while for \( Z = 10 \) the inner curve is affected (associated with larger angles), while only small variations are observed on the outer part, (associated with smaller angles). From these analyses we deduce that the outer curve for a large value of \( Z \) is a good approximation for the possible steady state apex positions, apart from cases of stimuli placed behind the organ at large angles relative to the organ base. This will be instrumental in understanding the steady state configurations in the case of two interacting organs, as detailed in the next section.

4. Allotropic interaction between two organs

Building on our understanding of the dynamics and steady states of organs in response to a point stimulus fixed in space, we now proceed to the case of pairs of
interacting organs. Continuing with the argument laid for point tropism, for the sake of simplicity we assume that the signal for allotropism is emitted at the apex, which can be generalized to extended regions on the organ. Each organ then perceives the neighbor’s signal either apically or locally. The position of the point signal is then no longer fixed in space, but rather moves with the organ’s apex. We consider two organs vertically aligned \( \theta_1(s, 0) = 0 \), separated by a distance \( \Delta x \) and \( \Delta y \), as illustrated in figure 1(b), so that they are symmetrically positioned around the origin, i.e. the left organ is placed at \( x_1(s = 0) = -\Delta x/2 \) and \( y_1(s = 0) = 0 \), while the right organ is placed at \( x_2(s = 0) = \Delta x/2 \) and is placed at some position in the \( y \) direction at \( y_2(s = 0) = \Delta y \).

Following equation (2) we now have two equations of motion, one for each organ, coupled through the perceived angle of the stimulus emitted by each other’s tip:

\[
\begin{align*}
\frac{\partial \theta_1(s, t)}{\partial t} &= -\lambda \sin \theta_{12P}(s, t) - \gamma \kappa_1(s, t), \\
\frac{\partial \theta_2(s, t)}{\partial t} &= -\lambda \sin \theta_{21P}(s, t) - \gamma \kappa_2(s, t).
\end{align*}
\]

Here \( \theta_1(s, t) \) and \( \theta_2(s, t) \) are the local angles of the left and right organ, respectively, and \( \kappa_1(s, t) \) and \( \kappa_2(s, t) \) are the respective local curvatures. We assume here that both organs have the same dynamical value \( Z \) (as well as \( \gamma \) and \( \lambda \)). The angle of the stimulus emitted by the tip of the right organ as perceived by the left organ is \( \theta_{12P}(s, t) \), while \( \theta_{21P}(s, t) \) is the opposite. Following equation (3) they are therefore defined as

\[
\begin{align*}
\theta_{12P}(s, t) &= \theta_1(s, t) - \arctan \left( \frac{x_2(L, t) - x_1(s, t)}{y_2(L, t) - y_1(s, t)} \right), \\
\theta_{21P}(s, t) &= \theta_2(s, t) - \arctan \left( \frac{x_1(L, t) - x_2(s, t)}{y_1(L, t) - y_2(s, t)} \right).
\end{align*}
\]

As in the previous section, we first consider apical perception, replacing the perception angles in equation (7) with \( \theta_{12P}(L, t) \) and \( \theta_{21P}(L, t) \). We simulated pairs of organs placed at different relative positions, \( 0 \leq \Delta x \leq 2.3L \) and \( -2.3L \leq \Delta y \leq 2.3L \), where negative values of \( \Delta x \) just yield mirror configurations.

For each simulation we take note of the apex position of the left organ in its steady state configuration, \( x_1(s = L) \) and \( y_1(s = L) \), and figure 4(a) plots these values for \( Z = \infty \), as a function of relative organ position \( \Delta x \) and \( \Delta y \). The values of the right organ \( x_2(L) \) and \( y_2(L) \) for a given value of \( \Delta y \) are equivalent to the values of \( x_1(L) \) and \( y_1(L) \) for \( -\Delta y \), since these are identical flipped configurations. These maps can be considered as the state-space of the steady state shapes of two interacting organs as described by the position of their tips, for different initial pairwise configurations, and will be useful in our understanding, particularly in the more complex case of local sensing.

In order to understand the state-space in figures 4(a) and (b) displays four examples of steady state shapes of simulated pairs of interacting organs from different points in the state-space in figure 4(a), namely \( \Delta x = 0.2L, 1.4L, 2L \), with \( \Delta y = 0 \) for all (i.e parallel organs). The different colors correspond to different values of \( Z \). Following figure 2(a) the organs are overlaid on the trajectory of possible apex positions in steady state. When the organs are far away (\( \Delta x = 2L \)), and in the absence of proprioception \( Z = \infty \), the curvature of both organs is such that their apices are aligned to each other, i.e. \( \theta_{12P} = \theta_{21P} = 0 \), the perceived stimulus is zero, and the organs stop moving. Similarly to figure 2(a), organs with proprioception stop to curve before their apiacal part are aligned. This is reflected in the associated point in state-space, with \( x_1(L) < 0 \) (the apex of the left organ does not pass the center line between the organs), while \( y_1(L) > 0 \) (the apex is in the upper quadrant). Since the organs are placed in parallel, they are the mirror image of each other, and therefore \( \kappa_1(L) > 0 \) and \( \kappa_2(L) > 0 \).

From figure 4(b) we see that at some relative distance \( \Delta x \) the curves of possible apex positions will intersect. We can calculate this distance by considering that the first point of contact will be at the outermost point along the curve, which is reached by an apex in the case that the two apices are aligned with each other, with \( Z = \infty \). In this case the apices are horizontal, and therefore the organs cover a quarter of a circle. In this case the distance along the x-axis from the organ base to the apex position \( x_1(L) - x_1(0) \) is just the radius of curvature of the organ, given by \( \rho = 2L/\pi \). Hence when organs are placed at smaller distances, the trajectories of their possible steady state apical positions intersect. For \( \Delta x > 4L/\pi \) they align towards each other before reaching the intersection point, and stop there (as shown for \( \Delta x = 1.4L \)). For \( \Delta x < 4L/\pi \) they reach this intersection point before they are able to align, where they touch. If a point signal is placed at the apex, then by definition the apex is aligned towards it, and again the perceived signal is zero. Hence the organs will stop at the intersection point, as shown for \( \Delta x = L \) and \( \Delta x = 0.2L \). Organs with apical sensing do not overshoot the desired solution in the direction of the stimulus [47], and it is therefore expected that the organs will indeed stop at the first point where the signal is minimized.

The case of local perception provides a more complex picture due to the local curvature perturbations discussed earlier for single organs in proximity of a point stimulus. Following the analysis for apical sensing, we plot in figure 5 the state-space represented by \( x_1(L) \) and \( y_1(L) \) of steady state shapes of interacting organs, for both \( Z = 3 \) and \( Z = 10 \). For \( Z = 3 \) the state-space is smooth, and solutions are continuous. Comparing the state-space with that for apical sensing, we note that the picture is qualitatively similar, producing very similar dynamics. For \( Z = 10 \) the picture is dramatically different. First, we observe that at certain relative positions no convergence is observed, represented in black. In these cases both organs oscillate periodically without reaching a steady state, which will be discussed later. Furthermore, the state-space is
no longer continuous, exhibiting discontinuous jumps between types of steady state forms, as exemplified in specific examples shown in figure 6. These discontinuities are distributed with a roughly circular geometry.

Following the analysis for apical sensing, we plot the said examples of steady state forms of interacting organs in figure 6, overlaid on the numerical approximation of the outer trajectory of possible steady state positions of apices, as discussed in figure 3. We recall that this is a good approximation as long as signals are not placed behind the organ base, and while this approximate trajectory does not represent the full picture, it does provide some intuition when discussing the different classes of steady states.

Going back to the state-space in figure 5, the outermost area, defined for organs whose bases are placed at a distance roughly larger than $\Delta r = \sqrt{\Delta x^2 + \Delta y^2} > 1.9$, represents the simplest case of organs placed at large distances. The organs are too far away to intersect or align, and this is equivalent to the pattern observed when $Z = 3$. An example of a relevant steady state configuration is shown in plot (9) of figure 6.

Next we consider the steady state shapes defined for organs placed at distances roughly within $0.6L < \Delta r < 1.2L$. At these distances the apex trajectories intersect, as can be seen in examples (2) and (5) in figure 6, and the apices touch at the first intersection point. Let us consider the symmetric cases where $\Delta y = 0$ (e.g. configuration (2)). We see in the state-space that $x_1(L) = x_2(L) = 0$, i.e. the tips touch at the center-line, while $y_1(L) > 0$ and $y_2(L) > 0$. Since the values of $x_1(L)$ and $y_1(L)$ change in a continuous manner, we can assume that in all configurations within this range the organ tips converge at the first intersection point.

We now proceed to consider the steady state forms for organs placed at distances approximately within $1.2L < \Delta r < 1.7L$. Also within this range the...
apex trajectories intersect, as can be seen in examples (3) and (6) in figure 6. We note that for examples (7) and (8), which belong to this state, the curves are no longer a good approximation due to the large angles, and a more detailed approximation is required. Looking at the state-space we see that for values of about $|\Delta y| < 0.5$, we have $y_1(L) < 0$ and $y_2(L) < 0$, i.e. both tips point down, clearly shown in examples (3) and (6). We note that the apices touch at the bottom intersection point—a class of steady state forms which was not observed in previous cases. This means that during their dynamics the organs did not stop at the first intersection point they encountered, but continued to the next. This is also true for the other examples in this class of steady state forms, (7) and (8). As argued before, since the values of $x_1(L)$ and $y_1(L)$ change in a smooth manner within this range, we can assume that in all configurations within this range the organ tips converge at the second intersection point.

Finally for very short distances, roughly $\Delta r < 0.5L$ we see a more complex behavior. For symmetric cases the tips touch at the first intersection point as in example (1). Upon breaking the symmetry they no longer stop at the first intersection point, and continue to the second, as shown in example (4).

In order to understand why in certain configurations organs do not stop at the first intersection point, but rather continue to the second, we need to discuss the dynamics of the organs. The fact that discontinuities are observed at roughly fixed distances, suggests that the base-to-base distance is a dominant factor. Figure 7(a) shows snapshots of the dynamics of four symmetric configurations from different points in state-space, where the evolution of time is represented by color code. Figure 7(b) shows the locally perceived angle along the organs, and figure 7(c) shows the local change in curvature. Let us consider the first example of two organs placed at $\Delta x = 1.2L$ apart. We observe
that after leaving their initially straight conformation the organs cross each other, and exhibit damped oscillations as they converge to the final steady state configuration. This is related to the overshooting behavior found to be characteristic of local sensing organs with low proprioception (high values of $Z$) in regular tropic models [46]. Indeed with no proprioception ($Z = \infty$), it was shown that when a stimulus is placed in a perpendicular direction from the organ, as the organ approaches the direction of the stimulus the basal part continues to curve. The organ overshoots the stimulus direction, then crosses back, overshooting it in the opposite direction etc, yielding oscillations which go on indefinitely, while their amplitude decreases with time. Considering the dynamics of the organs placed at $\Delta x = 1.2L$, we observe that when the organs overshoot they cross each other upwards, so that the apices are above the rest of the organs. The apices therefore pull the organs back up towards the first intersection point. However for larger distances, such as $\Delta x = 1.3L$, by the time they cross each other, which is after the first intersection point, they have already curved enough so that they cross each other downwards, with the apices below most of the organ, thus pulling the organs towards the next intersection point. This is illustrated in figures 7(b) and (c), where for $\Delta x = 1.2L$ the perceived angle goes from negative to positive values after a single time step, translated to changes in the direction of curvature propagating from the tip. For $\Delta x = 1.3L$ the change in perceived angle occurs much later. We note that this argument suggests that the form of the state-space also depends on initial conditions, or the history of the system dynamics. In the SM we show an example of organs placed at $\Delta x = 1.68L$, but with an initial configuration placed at the first intersection point. Instead of continuing to the next intersection point as expected from the state-space, they remain stable at the first intersection, since the organs did not cross each other downwards.

Lastly figure 7 also shows an example of the non-converging oscillating dynamics, associated with the black colored outer ring in figure 5, defined roughly for $1.7L < \Delta r < 1.9L$. Within this range the apices are extremely close to each other, but can barely touch. Figures 7(b) and (c) illustrates that in this particular configuration, as opposed to the stable dynamics, the value of the perceived angle propagates from the apex all the way to the base. Namely, at every point in time the perceived angle at the base and at the tip are in opposite directions, directly translated to curvature changes in opposite directions (this can be seen by drawing a straight line at any time in the respective $\theta_P(s, t)$ and $\frac{\partial \kappa(s)}{\partial t}$ map). We note that this is a result of the proximity of the signal point to the organ, which leads to large variations in the locally perceived angle.

Figure 6. Examples of steady state configurations of pairs of interacting organs with local perception. Organs are placed at different base-to-base distances sampling the state-space in figure 5. Simulations were run with $Z = 10$, with $\Delta x = 0.3L$, $L$, $1.6L$ from left to right, and $\Delta y = 0, 0.3L, 1.2L$ from bottom to top. The organs are overlaid on the approximated curve of possible steady state apex positions (which is common to all distances, as shown in figure 3(b)). Each configuration is numbered and marked on the respective position in the state-space in figure 5.
and local curvature. This is further exemplified in the SM where we show how oscillations can be initiated as a result of this geometrical argument.

5. Discussion and conclusion

In this paper we addressed the concept of collective or swarming dynamics in systems where movement is not due to self-propulsion, but rather due to growth. The goal of the paper is to develop a mathematical framework which will allow to rigorously investigate this phenomenon in future. Here we take inspiration from plant tropisms - the growth-driven response of plants to external stimuli such as light and gravity, where a robust mathematical model has recently been developed. However the resulting framework is applicable to other systems which move by growing, including biological systems such as neurons and fungi, and robotic systems [30, 70, 71].

Within this work we have introduced two new concepts related to plant tropisms: point tropism and allotropism. Point tropism refers to a nearby signal source whose signal propagates radially and therefore affects different point on an object from different angles. This is in contrast to regular tropism, where the signal source is generally assumed to be far away (gravity, the sun), yielding a parallel signal field which affects objects from the same angle. This scenario is relevant for tropisms towards localized sources, for example plant roots searching for water or nutrients. We analyzed the dynamics of a single organ responding to a fixed point both for the case of apical sensing and local sensing. We were able to analytically characterize the possible configurations in the simpler case of apical sensing. However we found that in the case of local sensing, where sensing occurs along the whole organ, the proximity of the signal leads to local perturbations in the curvature of the organ, yielding complex dynamics and configurations. We made a numerical analysis which allowed to make an approximation of possible shapes of steady state organs.

We termed allotropism the observed growth-driven responses of plant organs in the direction of their neighbors, for example a root growing towards or away from a neighboring root. Here we assume that a pair of organs can sense a signal emitted from a point fixed at their neighboring organ’s tip, thus coupling the point tropism dynamics of both organs. We discussed the applicability of such an assumption in the Introduction. We ran simulations for pairs of organs placed at various relative positions in space, both in the case of apical and local sensing, and considered the state-space as represented by the position of the apices in the steady state shape. We found that in the case of apical sensing the state-space is continuous, and the different types of configurations can be easily understood from the point-tropism analysis for single organs. However for local sensing we found that proprioception, the resistance of the organ to bending, has a significant effect. For high proprioceptive values the state-space is qualitatively very similar to that of the apical sensing. However for low proprioceptive values organs overshoot the direction of the stimulus, and this yields new classes of steady state forms which were not pos-
sible otherwise, including non converging dynamics. Indeed the state-space now exhibits discontinuities between classes of steady states roughly correlated to the base-to-base distance between the organs.

We found that the possible steady state positions are determined by the intersection points of the approximated curves of possible steady state apex positions of each organ (a property of the single organ). We suggest that the discontinuities between these classes of steady states are due to the tendency of organs to overshoot their stimulus at high values of $Z$, which causes them cross each other, effectively pulling each other towards one of a few possible steady state positions. This argument also suggests that the form of the state-space should depend on the initial conditions, which we verified in the SM. Lastly we also observed non converging dynamics associated with self-sustained oscillations of the organs. These oscillations seem to occur when the organs are placed at a distance such that the value of the perceived angle propagates from the apex all the way to the base, and the perceived angle at the base and at the tip are in opposite directions. This is a result of the proximity of the signal point to the organ.

We can interpret these results in terms of bifurcation theory. Effectively, the possible steady state forms or stable solutions, associated with different intersection points of the tip position trajectories, correspond to different attractors. Different initial conditions belong to different attractor basins. A bifurcation occurs when a change in the relative distance between organs causes the stability of an equilibrium solution to change, i.e. along the discontinuities. The oscillatory states may be interpreted as Hopf bifurcations [72]. A formal analysis can be performed by studying the eigenvalues of the dynamical system. However since these equations are PDEs, with derivatives both in time and space, this analysis is non-trivial and therefore beyond the scope of this paper.

The analysis brought here focused on the case of constant attractive interactions, however the interactions can easily be replaced with a repulsive interaction, or a more complex distance-dependent interaction, such as those generally used in common models for collective behavior [18, 24, 73]. The case of constant repulsion is trivial since organs will belong to different attractor basins. A bifurcation occurs when a change in the relative distance between organs causes the stability of an equilibrium solution to change, i.e. along the discontinuities. The oscillatory states may be interpreted as Hopf bifurcations [72]. A formal analysis can be performed by studying the eigenvalues of the dynamical system. However since these equations are PDEs, with derivatives both in time and space, this analysis is non-trivial and therefore beyond the scope of this paper.

The analysis brought here focused on the case of constant attractive interactions, however the interactions can easily be replaced with a repulsive interaction, or a more complex distance-dependent interaction, such as those generally used in common models for collective behavior [18, 24, 73]. The case of constant repulsion is trivial since organs will always align in opposite directions, and the signal will never be close enough to cause local curvature perturbations.

Future work may include many possible generalizations. Here we focused on the limiting case where the elongation rate of the organ is negligible compared to the bending dynamics. However this can be generalized to explicitly account for growth following previous work [56]. In addition, elasticity [74] and more complex integration of stimuli [58] can be integrated, as well as a generalization to 3D [57]. Moreover, this model assumes the signal is emitted from a point at the tip, however it is possible to consider the signals emitted from a more extended part of the organ $s_1 < s < s_2$, by assuming the signal is additive. In this case the signal angle $\theta_p(s, t)$ is rewritten:

$$\theta_p(s, t) = \theta(s, t) - \int_{s_1}^{s_2} \arctan \left( \frac{x'(s') - x(s)}{y'(s') - y(s)} \right) ds'$$

i.e. effectively a point stimulus taken as an average over the extended signal, and the dynamics are governed by the same equations as before. In other words, considering a signal which emanates from an extended zone is not expected to dramatically change the results we have obtained for a single point signal.

Lastly, this work brought an analysis of the dynamics and state-space of steady states of pairs of interacting organs. The mathematical framework presented here allows to take the next step and investigate collective behavior or swarming of multiple organs, by simply generalizing equation (6) to $N$ interacting organs, each of which follows the following ODE:

$$\frac{d\theta_i(s, t)}{dt} = -\lambda_{rps} \sum_{j \neq i} \sin \theta_{ij} - \gamma \kappa_i(s, t)$$

where $\lambda_{rps}$, expressing the interaction between individuals, can depend on space and time following common models for collective behavior. The ideas presented here will hopefully spark interest in the concept of collective behavior in a class of systems with inherently different dynamics, and are relevant both for researchers working on biological systems where movement is due to growth, as well as for the growing community of plant-inspired robotics.

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