Biological efficiency in processing information in green plants

Dorje C. Brody¹ and Anthony J. Trewavas²

1School of Mathematics and Physics, University of Surrey, Guildford GU2 7XH, UK
2Institute of Molecular Plant Science, University of Edinburgh, Edinburgh, UK

The detection and processing of environmental information is a fundamental attribute of all living systems. This article approaches the question of how efficiently plants process that information, considering it likely that differential efficiency among different species may help explain differential survival. The primary routes of information transfer, that is, signal transduction, are relatively well understood. It is pointed out, based on current understanding, that erasure of such information may be of equal importance to its acquisition. This in turn could provide a simple means of quantifying the acquisition of information by a plant and the efficiency in doing so. However, wild plants live in an environment that is noisy. A useful analogy to deal with such situations can be found in quantum theory of open systems, wherein processes are both well-characterized and well understood, unlike those in plants. This paper develops this theme from quantum information processing and provides a mean of transferring such quantum characterization to biological dynamical situations. The article concludes with discussion on communication theory, indicating that there is a dearth of experimental results that can currently be used to investigate information processing but suggesting how progress can be made in this important programme.

© 2023 The Authors. Published by the Royal Society under the terms of the Creative Commons Attribution License http://creativecommons.org/licenses/by/4.0/, which permits unrestricted use, provided the original author and source are credited.
1. Introduction

Plants in wild circumstances commonly experience fluctuating environments that can threaten the survival of any individual and thus limit their capability to reproduce. Within reasonable environmental limits, plants react to such variations by changing their behaviour adaptively, improving their probability of survival [1]. They detect and transduce the information they receive from their environment and use that processed information to establish counter-reactions in behaviour to improve survival. Unlike animals that can move out of danger, plants in general cannot move away from extreme threats except via distribution of seed or pollen or the production of dormant underground organs such as tubers, fleshy roots and stolons that weather the hazard and produce new shoots when conditions change. When milder threats are experienced from numerous biological and abiological sources, developing plants counteract by changing development either by changing phenotype (phenotypic plasticity) or altering their molecular physiology to improve the probability of survival [2].

These considerations lead to the question of how efficiently plants manage to process information so as to enhance survival probability. In fact, the criterion of efficiency is not immediately apparent, when it concerns the processing of environmental cues by plants. The objective of this paper is to clarify the notion of efficiency, and the implications of being efficient, by developing a framework that allows us to model dynamical behaviours of plants as a result of processing information. We will find that such dynamical models have precise analogies in the modelling of open quantum systems, and that conversely, new physical intuitions can be gained about open quantum systems—such as the meaning of decoherence—by applying mathematical techniques of quantum theory in modelling the dynamics of biological systems.

2. Are responses by plants to changes in environmental information efficient or optimal?

In 1871, Charles Darwin [3] commented that ‘intelligence is based on how efficient a species become at doing the things they need to survive’, leading to the general recognition that ‘adaptive behaviour is the essence of (biological) intelligence’ [4–6]. Human intelligence, as commonly measured by intelligence quotient, assesses only scholastic ability [4]. Plants use the information that they receive from their noisy environment to construct adaptive responses. Those species that do so more efficiently may benefit in the struggle for existence. But in establishing the reality of Darwin’s view, there is a necessity to quantify the environmental information that any plant experiences and in turn be able to measure how efficiently it is processed. It is obvious that all plants experience information from their environment and that is commonly stated, but without attempts to quantify what is experienced, the term really has little scientific use. Many areas of plant science would benefit if quantifying the information content of signals could be achieved, as would understanding of biological intelligence.

Optimization criteria (least cost, maximal benefit) are often used as an indirect measure of fitness [7]. The marginal value theorem [8] has been used to indicate that some birds and mammals forage for food optimally; that is, least energy was used for maximal energy gain. Similar optimal behaviour in energy gain has been reported for the parasitic plant, Cuscuta, that chooses its prey and ensures maximal energy return [9]. Detection and exploitation of soil minerals by plant roots again fits the marginal value requirements indicating optimal mineral gain for minimal energy outlay [10]. In the latter case, this process might also be modelled effectively using predator-prey dynamics. Optimal sensing capability for both chemical and mechanical signals has been reported in some animal cells [11].

In wild circumstances, a degree of uncertainty will inevitably exist as regards perception of any signal. Environments can vary almost instantaneously but transiently, as with sun flecks, sudden gusts of wind or showers, or touched by a passing animal or trampled on, providing uncertainty in the detected information. Such uncertainties can be measured quantitatively in terms of the
Wiener–Shannon entropy [12]. Now in a generic more stable situation the detection of a signal, for instance, the orientation of the light source, can be obscured by noise, such as scattered photons, particularly in crowded plant circumstances. Upon processing of the environmental information this uncertainty should reduce, the distribution of the light source, for example, becoming sharper, so that the entropy decreases—or else adaptation is impossible.

We consider that regarding the information a plant holds on the condition of its environment, the detection and processing of noisy new information is efficient if on average the entropy decreases maximally, thus reducing the uncertainty most effectively. Such an efficient transformation will minimize a distance measure called the Kullback–Leibler divergence between the distribution before the signal detection (the initial perception about the environmental conditions) and the distribution afterwards. This efficiency condition is known in brain science as the ‘free energy principle’ [13]; whereas in quantum theory it can be shown to be equivalent to the ‘von Neumann–Lüders postulate’ [14]. The applicability of the free energy principle to model the behaviour of plants has indeed been suggested [15].

The important consequence of an efficient signal detection is that the state of a plant, as represented by the information it holds about the environmental conditions, will change minimally in such a way that it is consistent with the detection of new signals indicating a change in the environmental condition. In brain science this concept is sometimes heuristically characterized as minimizing surprises [13], but more importantly for all biological systems including green plants the efficiency condition implies that responses to changing environments are the most conservative ones that is nevertheless consistent with the arrival of new information. Because every response by a plant entails energy consumption, an efficient signal processing will result on average in the least energy consumption.

3. Signal transduction pathways in plant cells

Intensive research in the last 30 years has identified the central role of cytosolic calcium [Ca^{2+}]_i in transducing most environmental signals experienced by plants [2,16]. Signals are perceived by specific receptors often located in the plasma membrane. Occupied receptors, it is assumed, form membrane patches that initiate intracellular calcium transients, [Ca^{2+}]_i, within less than a second but lasting usually less than a minute. Inhibition of these transients prevents the subsequent physiological or phenotypic changes that normally occur hours, days or weeks later. These transients can oscillate if the environmental change is prolonged [2,16,17].

Cytoplasmic changes in [Ca^{2+}]_i are perceived by well over 100 proteins that bind Ca^{2+} directly. A variety of channels, pumps, exchangers and carriers are responsible for Ca^{2+} entry. These membrane-bound proteins help shape and change the internal spatial distribution generating a distinctive signature often characteristic of the specific signal. It is thought that different signals recruit different combinations of these Ca^{2+} binding proteins that continue information transfer into hundreds of protein kinases of differing kinds that manipulate further downstream change into altered ion fluxes, enzyme activities, cytoskeletal reconstructions and ultimately particular combinations of gene expression constructing traits.

4. The transient nature of the Ca^{2+} signal suggests that erasure of signal information may be as important as its acquisition

Whatever the mechanism by which information is detected, transmitted, processed, or stored, the amount of information processed could be estimated from dynamical behaviours resulting from the processing of information. The efficiency of biological computation could then be measured from the amount of energy consumed by the cells to process that information. These estimates could be made without necessarily any knowledge of detailed structures and mechanisms for achieving the detection of environmental conditions by plants [18].
The information-based approach to modelling biological dynamics, more specifically, provides a way to specify, as model inputs, the way in which noisy information about environmental conditions are conveyed to biological systems. Their dynamical behaviours are then deduced, using the efficiency criterion, as model outputs. The framework therefore permits a way of measuring information contents of environmental cues, or messages, that biological systems such as green plants experience.

When environmental conditions change, at least some or all of the processed information about previous conditions will presumably be erased, in the sense of reset of its state [19]. For instance, when a climbing plant detects an object that can support its growth, but then the object is removed to another position, it seems likely that this information is erased because the plant changes direction towards the new support position [20]. Otherwise, plant cells will require considerable memory capacity to store all the day-to-day processed information, which seems unlikely. Of course, if erasure of processed information results in energetic penalties, for instance, the leaf-folding behaviour of *Mimosa pudica* under false alarms, then there is an advantage in storing processed information, but even here the memory appears to be erased within 30 days [21]. However, if such processed information is regularly erased, then we can estimate the computational efficiencies of biological systems. This is because information erasure requires energy consumption indicated by additional heat production, and this can either be calculated or potentially measured, and compared with the total energy consumption and heat production of biological cells.

5. There are many parallels between quantum dynamics and information processing

Perhaps unexpectedly, the adaptive dynamics of biological systems have a deeper parallelism in quantum mechanics. Consider a quantum system, like a particle, in an external field, say, a photon field. For the state (wave function) of the system to evolve in time in accordance with the conditions of the external field, it is required to extract information about the condition of its environment. This information is typically noisy, but if we assume that nature is intrinsically efficient in the sense that dynamical evolution is dictated by the criterion of minimizing the degree of uncertainties about the condition of the environment, then the system must follow the dynamics that is consistent with optimal signal detection. Such a picture for the dynamics of a quantum system is not entirely dissimilar to, say, a plant cell extracting the information of the light source from the noisy interaction with a photon field for phototropic or heliotropic dynamics. Indeed, there is a great deal of parallelism between quantum and biological dynamics, and this can be exploited to pave the way towards a better understanding of information and signal transduction in biology, because the theory of quantum dynamics in noisy environments is well developed, while biological dynamics in equally noisy environments is not. Because discussion of quantum systems rarely enters consideration of systems behaviour in plant biology we have included figure 1 that indicates the potential relationships between the systems nature of plant individuals and the primary specific environmental locale for each member in the hierarchy.

One might ask how is such a characterization of quantum dynamics as extracting information from the environments compatible with the more traditional formulation of quantum systems by means of Schrödinger’s wave equation? And can we show that nature is indeed efficient in its ability to process information? If so, what are the implications in biology, if any, and what do we learn from these observations? Our aim here is to clarify some of these issues, with the view towards building a unified information-based approach to modelling both quantum and biological systems, and in particular, plant dynamics. We add parenthetically that when we speak about information processing at a quantum level, we are concerned with the processing of environmental information by the system, as opposed to the more familiar notion of quantum information theory [22], which deals with the processing of information by an external observer making use of quantum systems.
Figure 1. The relation of levels in plant biological system structures to the primary environment in which they are embedded. The left-hand side shows a typical hierarchical arrangement of some aspects of a simple system structure that underpin the organization of plant systems. The right-hand side shows the primary environment in which each individual system level is constrained in both behaviour and variation. Interactions between the constituents of any particular system level are usually considered to generate emergent properties that compose the level above. For example, the very complex interactions between thousands of cellular proteins are considered to construct the emergent property that is characterized as the cell.

6. Outline of our objectives

With these preliminaries, the main goals of the present paper, in more specific terms, can be summarized as follows.

1. We begin by explaining how the specification of the information flow can be used to model dynamic features of biological systems. In particular, focusing on the response of green plants to environmental cues, it is shown how the techniques of information and communication theory can be used to characterize their dynamics, even though in the context of signals from environments there are no agents purposely transmitting these signals. The sun does not emit photons with the purpose of letting green plants on Earth know of its whereabouts. Wind does not blow at high speeds for the purpose of stressing plant structures. The environments, in effect, carry the signals, but they are not purposefully built like a Shannon telephone line carrying signals. Nevertheless, the fact that information is transmitted and processed implies that techniques of communication theory remain applicable.

2. We then show that precisely the same mechanism of signal-detection-induced dynamics is already present at the quantum-mechanical level. This is done by examining a stochastic extension of the standard Schrödinger equation in which noise, as well as an underlying optimal signal detection, plays an important role. We will show, in particular, how signal detection by a quantum system leads to the so-called decoherence effects of quantum mechanics. We conjecture the converse, that any decoherence is accompanied by information acquisition by the system, is true and prove this in the case of two-level quantum systems.

3. We then discuss the advantages of applying models describing dynamics of quantum systems for the characterization of biological dynamics, especially when there is an
incompatibility between adaptation and the rate of change in the environment. This is a common situation arising in biology and ecology; and yet classical formulations are not well suited to model this. Such dynamical models not only allow for the prediction of future statistics but also enable the quantification of information contents that are otherwise difficult to estimate from experimental data.

4. We conclude with some discussion on open challenges in biology from an information-based perspective. Here we also discuss further on the issue of efficiency and its implications in biological systems, by highlighting the three key features of an efficient signal processing.

7. Processing of noisy information induces dynamics in biology

Information theory is traditionally concerned with the amount of information contained in a signal transmitted through a noisy channel, the informational capacity of the channel and corrections of errors [23,24]. These ideas refer to an established communication channel used by a sender and a receiver of the message, which, in biological contexts, might translate into signal transduction in molecular and cellular networks [25].

As well as internal communication channels, biological systems constantly extract information from their environments, in the absence of a transmitter of a message or a communication channel designed to deliver specific environmental cues [26]. Take, for instance, the case of green plants. Whether it is sunlight, scattered photons, volatiles, wind, water, soil nutrients or gravity, information about these environmental cues is processed effectively [27]. Even when there are well-defined communication channels, estimating the amount of information transmitted from data is not straightforward [28], so the problem becomes even less tangible when it comes to quantifying information processed by plants through what seems to be ambiguous communication channels. This is where a mathematical model can be exploited to better understand the link between information processing and resulting biological dynamics.

It is worth remarking here that while we frequently speak about a ‘biological system’ and its ‘environment’, the division of the two is entirely context dependent and there is no one definition of a biological system. For example, if the object of interest is the whole plant, then the associated environment consists of air and soil that carry chemical signals, electromagnetic and gravitational fields that carry signals required for phototropic or gravitropic motions, and any object that might influence the growth and survival of the plant. But if the system of interest concerns a single cell or a receptor inside of a cell, for instance, then their environments will inevitably contain other parts of the plant itself. When we consider plant efficiencies, typically we have in mind as the system the efficiency of an individual cell or a receptor, but in general the notion of a system will always depend on the context. In figure 1, we illustrate system-environment partitions across different scales. Part of our aim here is to promote an information-based modelling framework that is applicable universally across different scales.

Processing of information commonly leads to phenotypic changes and movements in plants. For instance, leaf blade reorientation towards the direction of the sun. Such a dynamical behaviour is induced by detection and processing of signals encoded in photons. Now in the conventional approach to mathematical modelling of biological dynamics, one typically attempts to model the resulting motion directly in the form of differential equations, which in some cases may be superimposed with additional noise terms. While such an approach of directly modelling observed dynamics has seen some successes in modelling certain specific systems, because models can always overfit to match simple dynamics, ultimately it appears futile to attempt to directly model dynamical behaviours of biological systems driven by processing of noisy information.

The reason is a simple one. What underlies biological dynamics is the noisy information about environmental conditions, which are processed to arrive at choices, and hence dynamics. The input, therefore, is the specification of noisy information, on which optimal signal detection can be applied to arrive at the output, and this leads to phenotypic change and/or movement.
This input–output transformation is typically highly nonlinear. Hence any attempt to model the output will fail to capture the input–output causal relation. In other words, direct modelling of the dynamics in most cases cannot replicate the underlying information-processing features.

The way forward, therefore, is to model the noisy flow of information, from which the implied dynamical behaviour of a given biological system can be deduced (rather than modelled) using the theory of optimal signal detection. In this way, the causal structure underlying the resulting biological dynamics becomes transparent.

8. Environment acting as a communication channel

Of course, in many cases there are no purposefully built communication channels when it comes to biological systems processing information about environmental cues, and this fact has perhaps prevented the application of communication theory to describe biological dynamics. To proceed, therefore, we must regard the environment as a whole, in effect, as playing the role of a communication channel. The idea is as follows. Take the case of a green plant. There is a range of quantities of interest that plants wish to identify, such as the location of the light source, the direction of the gravitational pull, the gradient of volatile concentration in the air or soil, the existence of plants or other objects in their vicinities, and so on [29]. We may refer to these quantities as ‘signals’ or ‘messages’, even though in none of these cases, an active agent is transmitting the signal. Yet, these signals do exist, not in abstraction but in reality, and they are carried by the environment (air molecules, photons, gravitons and so on) to reach, along with noise (e.g. scattered photons), the plant receptors.

From the viewpoint of communication theory, whether there are active transmitters of signals or purposefully built channels is immaterial, because information has been successfully transmitted, albeit superimposed with noise. It is the environment itself that generates what plants perceive as signals, and it is the environment itself that carries these signals along with noise.

9. Dynamics following from Bayesian updating

In many cases, the signal (i.e. the quantity of interest from the plant’s perspective) is given by a time series, and so is noise, but for an illustrative purpose take for simplicity the case in which they are fixed in time. In more specific terms, let $X$ be the random variable representing the signal, and suppose that it can take $N$ discrete values $\{x_i\}$ with the a priori probabilities $\{p_i\}$ (the continuous case can equally be treated). Similarly, let $\epsilon$ represent noise, with the density function $f(x)$. Information acquisition in signal detection is then modelled by learning the value $\xi = X + \epsilon$ of signal plus noise. The motion of plant (or any other biological system for that matter) resulting from information acquisition will then be consistent with the transformation from the a priori mean of $X$ to its a posteriori mean [12]:

\[
\sum_{i=1}^{N} x_i p_i \Rightarrow \sum_{i=1}^{N} x_i \left( \frac{p_i f(\xi - x_i)}{\sum_{j=1}^{N} p_j f(\xi - x_j)} \right).
\]

Here, the term given in the bracket on the right side is just the Bayes formula for the a posteriori probability of $X$, subject to the specification of partial information $\xi$ about $X$. The meaning of the Bayes formula is that among all probabilities that are consistent with the observed value of $\xi$, the a posteriori probability obtained by the Bayes formula is the closest to the a priori probability [14]. This ensures that the change from the a priori mean to the a posteriori mean, which in practical terms entails energetic costs because biological systems will transform their configurations accordingly, is minimized within the constraint of being consistent with the information acquired.

To gain a better intuitive understanding of the information-based formulation, consider the experiment on the parasitic plant Cuscuta pentagona (dodder) to demonstrate its ability to detect
the host location via inferring the gradient of volatile chemical concentration in the air [30]. The initial motion of the seedling as circumnutation is dictated by the genetic information already encoded in the plant (as opposed to processed information), and suggests that the \textit{a priori} distribution of the host location is uniformly distributed over a circle centred at the point of germination, on account of the symmetry of the configuration. But then the detection of volatiles in the course of nutation turns the \textit{a priori} distribution into the \textit{a posteriori} distribution, resulting in the observed directed growth orientation towards the host location [30]. The \textit{a posteriori} distribution can be estimated accurately by increasing the sample size considered in [30]. The amount of information processed can then be identified, in units of bits, by working out the relative entropy or entropy reduction associated with the \textit{a priori} and the \textit{a posteriori} distributions.

This example illustrates how a seemingly abstract mathematical idea of signal detection can be used to characterize the dynamical behaviours of biological systems. This quintessentially biological feature of ‘intelligently’ adapting to environmental conditions, in the sense of optimally processing noisy information so as to maximally reduce, on average, the degree of uncertainty as measured by entropy, however, can already be observed in more primitive systems of atoms and particles whose behaviours are described by quantum theory. That is to say, dynamical features of systems induced by signal transduction appears to be universal across all scales.

10. Role of environmental noise in quantum dynamics

In physical science, the dynamics of a system is determined by the specification of its energy. That is, once the system energy is specified, equations of motion for the state of the system unambiguously determine how the initial state evolves in time. From Hamiltonian mechanics to quantum theory, this approach has proven incredibly effective. Quantum theory, in particular, is one of the most stringently tested theories in science, enabling high-accuracy predictions for experimental data. Yet, there are reasons to doubt whether this energy-based description of physical systems, supplemented with an absolute determinism, in accordance with the Schrödinger equation, is complete in the quantum realm.

One of the central issues here is to explain the transition from quantum to classical, as exemplified by the so-called measurement problem of quantum theory [31]. While the dynamical evolution of a quantum system is deterministic, when an observable is measured by an experimentalist, the outcome of the measurement is random. Where, then, is this randomness come from? From the early days of quantum theory numerous attempts have been made to address this problem, accompanied by various interpretations of quantum theory [31]. One approach to overcome this issue is to take into account the impact of noise on the dynamics of the system [32].

Starting with the work of Ghirardi, Pearle, Diósi, Gisin and many others [33–39], this approach aims at bridging the gap between deterministic dynamics and random measurement outcomes by means of modifying the dynamical equation so that a stochastic term is included in the Schrödinger equation. Within such random dynamical models, there remain a wide range of choices, but what concerns us here is the so-called energy-based stochastic Schrödinger equation [40]. This family of models can essentially be derived by the requirement of energy and norm (total probability) conservation, but not requiring determinism (the inclusion of the latter will narrow the model further to the Schrödinger equation [41]). The energy-based models have the advantage that the Born probability rule of quantum mechanics—part of the postulates of quantum theory—can be derived dynamically [42].

Stochastic extensions of the Schrödinger equation can either be viewed as phenomenological models for describing measurements or models that represent the dynamics of open quantum systems interacting with noisy environment. In the case of energy-based models, which can be specified purely in terms of the Hamiltonian (energy) of the system, they can also be viewed as representing the dynamics of closed systems, regarding Schrödinger’s theory as an approximation to a more realistic description of the quantum world in which the role of noise is taken on board. This follows from the fact that energy expectation is conserved in such models.
Of course, any deviation from the noise-free deterministic ‘unitary’ dynamics (if the relative separation or difference of two wave functions remains constant in time, then the dynamics is called unitary) predicted by Schrödinger’s theory must be subject to scrutiny. This is because if the Schrödinger equation for the wave function of the system is replaced with a stochastic dynamical equation that reflects the impact of noise, then experimental predictions will in general deviate away. However, for a number of prototypical quantum systems for which ample experimental data exists, this deviation has been shown to fall within error bars, and hence not detectable, provided that the random dynamics of the wave function conserves energy expectation [43]. In other words, the energy-based models appear not to contradict the successful predictions arising from the traditional quantum theory, while incorporating the impact of noise.

This may seem surprising, but the intuitive reason is that the time scale for such a stochastic dynamics to deviate significantly away from unitarity is inversely proportional to the system’s energy variance [44]. Hence for a small quantum system, for which the energy variance is small, the stochastic evolution will maintain approximate quantum coherence for long times. On the other hand, if the system is coupled to a measurement apparatus, then the energy variance is amplified by the uncertainties of the macroscopic pointer state (the state of the pointer of the apparatus pointing in one direction or another will result in huge energy uncertainty), forcing the wave function to ‘collapse’ into one of the stable eigenstates instantly.

11. Characteristics of quantum dynamics induced by signal detection

What then is the main trait of such stochastic models? It can be shown that for the class of stochastic Schrödinger equations for which the energy expectation is conserved (the energy-based models), their solutions can be obtained by formulating underlying signal detection problems about the energy of the system [41,45]. Suppose that a quantum system (say, a particle) is immersed in an external field, and the interaction of the two is modelled by a Hamiltonian \( \hat{H} \), which characterizes the energy of the system. A simple example is an electron interacting with an external magnetic field. In this case, the internal state of the electron, known as the spin, will precess about the axis of the magnetic field at an angular frequency proportional to the strength of the field. The Hamiltonian \( \hat{H} \) of the system (i.e. the electron in this case) then takes the form \( \hat{H} = \mathbf{B} \cdot \hat{S} \), where \( \mathbf{B} \) denotes the external field vector, and \( \hat{S} \) denotes the vector-valued spin matrix. The idea of quantum mechanics is to regard the external field \( \mathbf{B} \) as being fixed (that is, the magnet that generates the field is assumed macroscopic and thus need not be subjected to a quantum-mechanical description), and treat the system as being ‘closed’ even though the energy of the system is determined by the interaction with the environment. Of course, for a composite system like two or more electrons there can be internal interactions that will contribute to the whole system energy, but it remains to be the case that for each subsystem it is the interaction between that subsystem and its environment that characterizes the subsystem energy.

More generally, we can think of the system energy \( \hat{H} \) as a matrix with eigenvalues \( \{E_i\} \), representing definite energy values. An energetically definite (certain) state of the system is represented by the eigenvector \( \{|E_i\} \) of \( \hat{H} \) corresponding to the eigenvalue \( E_i \). A generic state \( \{|\Psi\rangle \) of the system can be expanded in terms of the eigenvectors of the Hamiltonian:

\[
|\Psi\rangle = \sum_i \sqrt{p_i} |E_i\rangle.
\]

Here, we have ignored the phase factors that are quantum-mechanically important but not relevant to the ensuing discussion. The expansion coefficients \( \sqrt{p_i} \) are such that their squares add up to one. These are then interpreted as determining the probability of finding the system to be in the state with a definite energy. Such a generic state is therefore a state of indefinite energy. Our hypothesis then is that through interaction with the environment, the system acquires partial information about its own energy—partial because of the prevalence of noise.

Typically, the information acquisition occurs continuously in time, but for simplicity consider a ‘single-shot’ transfer of information. The (unknown) quantity of interest is the energy, which
we model by a random variable $H$ taking the value $E_i$ with the probability $p_i$. We let $\epsilon$ model the noise, which is assumed to be independent of the ‘signal’ $H$ and has the density $f(x)$. Then information transfer from the environment to the system can be modelled by the specification of the value $\xi = H + \epsilon$ of the sum of signal and noise. There are two unknowns, $H$ and $\epsilon$, and one known, $\xi$, so these data are insufficient to determine the value of $H$, but it can be used to reduce the uncertainty of $H$, just as in the biological case. Such a reduction results in updating the prior probabilities $\{p_i\}$ into posterior probabilities $\{\pi_i\}$. If this updating of information is efficient in that it maximally reduces the uncertainty, then $\pi_i$ must be the probability that $H = E_i$ conditional on the value of $\xi$, and this can be worked out by use of the above-mentioned Bayes formula. Hence the state of the system, after acquiring this information, and if nature is efficient, is given by

$$|\Psi'\rangle = \sum_i \sqrt{\pi_i} |E_i\rangle,$$

where the conditional probability $\pi_i = \pi_i(\xi)$ is a function of the information transmitted. The acquisition of information by the system, represented by the transformation $p_i \rightarrow \pi_i$, then results in the well-known decoherence effect of quantum theory, as described below.

### 12. Acquisition of noisy information leads to decoherence effects

From the perspective of an external observer (an experimentalist), it is useful to represent the state of the system in the form of a density matrix $\hat{\rho} = |\Psi\rangle \langle \Psi|$, where $|\Psi\rangle$ is the complex conjugate transposition of $|\Psi\rangle$. This is because the expectation of a physical observable, represented by a matrix $\hat{F}$, in the state $|\Psi\rangle$ is given by $\langle \Psi | \hat{F} | \Psi \rangle = \text{tr}(\hat{\rho} \hat{F})$, and this is the quantity that would be measured in laboratories. If the observer knows the state of the system, then writing the expectation in terms of a pure state $|\Psi\rangle$ or in terms of a density matrix $\hat{\rho} = |\Psi\rangle \langle \Psi|$ makes no difference. However, if the observer is uncertain about the state of the system, and the uncertainty being represented by a distribution over pure states, then we need to average not the wave function $|\Psi\rangle$ but the matrix $|\Psi\rangle \langle \Psi|$ using this distribution, and the resulting averaged matrix is what defines the density matrix. This follows on account of the fact that observable quantities are not linear but quadratic in the wave function, and the square of the mean is not the same as the mean of the square.

In the energy basis, the initial state $\hat{\rho}$ thus has the matrix elements $\sqrt{p_i}f_j$, which transform into $\sqrt{\pi_i(\xi)}\pi_j(\xi)$ after information acquisition. The external observer, however, has no information about the value of $\xi$, so at best they may consider the average $\mathbb{E}[\sqrt{\pi_i(\xi)}\pi_j(\xi)]$ over all values $\xi$ can take, and this gives the matrix elements of the state $\hat{\rho}' = \mathbb{E}[|\Psi\rangle \langle \Psi|]$ as represented by the observer after the information acquisition by the system. Here, $\mathbb{E}[-]$ denotes expectation over the random variable $\xi$, which in the present example has the density $p(\xi) = \sum_i p_i f(\xi - x_i)$. Then from the Bayes formula, a calculation shows that the transformation of the matrix elements takes the form $\sqrt{p_i}f_j \rightarrow \mathbb{E}[\sqrt{\pi_i(\xi)}\pi_j(\xi)] = \sqrt{p_i}f_j A_{ij}$. Here, the symmetric matrix $A_{ij}$ is given by

$$A_{ij} = \int \sqrt{f(\xi)}f(\xi + \omega_{ij}) \, d\xi,$$

where $\omega_{ij} = E_i - E_j$ and $f(x)$ is the density for $\epsilon$. Evidently, we have $A_{ii} = 1$ for all $i$ and $A_{ij} < 1$ for $i \neq j$ (assuming that $E_i \neq E_j$). Therefore, acquisition of information by the system will result in the damping of the off-diagonal elements of the density matrix. This is the so-called decoherence effect. In a typical (but not always the) case, the damping factor $A_{ij}$ of the off-diagonal element is more pronounced for wider energy gaps $\omega_{ij}$.

It should be evident that every biological process will exhibit a form of decoherence effect because an external observer has no access to the precise information acquired by the biological system, although the effect may not manifest in the form of a density matrix. The point is that there is a kind of trade-off of information flow: acquisition of information by the system will result in loss of information by the external observer. The amount of information gained by the system...
is the reduction of the Shannon–Wiener entropy associated with the transformation \( p_i \to \pi_i(\xi) \), and when averaged over \( \xi \) this is given by \( S_\xi - S_\xi \), where \( S_\xi = -\int f(x) \log f(x) \, dx \) is the entropy (measure of uncertainty) of noise and \( S_\xi = -\int p(y) \log p(y) \, dy \) is the entropy of the information \( \xi \).

This follows simply by averaging the entropy change

\[
\Delta S = -\sum_i \pi_i(\xi) \log \pi_i(\xi) + \sum_i p_i \log p_i.
\]

By contrast, upon the system’s acquisition of information, the observer loses track of the state of the system, and hence loses information, and this is measured in terms of the von Neumann entropy, given by \(-\text{tr}(\hat{\rho} \ln \hat{\rho})\). The value of the von Neumann entropy, however, does not agree with the change of the Shannon–Wiener entropy, because the density matrix \( \hat{\rho} \) does not contain all the distributional information of the density function \( p(\xi) \).

13. Conversely, decoherence implies acquisition of information

The fact that information acquisition leads to decoherence suggests that an even stronger result might hold, namely, that decoherence is necessarily accompanied by information acquisition. Specifically, we conjecture the following. Suppose that the density matrix \( \hat{\rho} \) of a system decoheres in the basis of a given physical observable. This means that when expressing the matrix elements of \( \hat{\rho} \) in the basis of that observable, the off-diagonal elements of \( \hat{\rho} \) become smaller. Then on average the system extracts a positive amount of information from its environment concerning the value of that observable.

While it appears difficult to establish this claim in general, we can verify its validity in two dimensions. Let the observable in question be the energy of the system. Then the initial state of the system can be expanded in the energy basis:

\[
|\Psi\rangle = \sqrt{p}|E_1\rangle + \sqrt{1-p}|E_2\rangle.
\]

The associated density matrix in the energy basis is therefore

\[
|\Psi\rangle\langle\Psi| = \begin{pmatrix}
\frac{p}{\sqrt{p(1-p)}} & \sqrt{p(1-p)} \\
\sqrt{p(1-p)} & 1-p
\end{pmatrix}.
\]

Now suppose that the state of the system transforms such that \( p \to \pi \) for some \( \pi \). Without loss of generality we can let \( \pi = p\alpha \) for a suitable \( \alpha \). Here, \( \alpha \), which typically will depend on \( p \), is a random variable whose value is in general unknown to the external observer. Hence after the transformation the density matrix of the system becomes

\[
|\Psi\rangle\langle\Psi| \Rightarrow \hat{\rho} = \begin{pmatrix}
\frac{pE[\alpha]}{\sqrt{p(1-p)}} & \sqrt{p(1-p)}\Lambda \\
\sqrt{p(1-p)}\Lambda & 1-pE[\alpha]
\end{pmatrix},
\]

where

\[
\Lambda = E\left[\sqrt{\frac{\alpha(1-p\alpha)}{1-p}}\right],
\]

and where \( E[-] \) denotes expectation over \( \alpha \). Decoherence therefore means that \( \Lambda < 1 \), and hence that the off-diagonal elements of the density matrix become smaller.

What about the energy uncertainty of the system? Our claim is that if \( \Lambda < 1 \) then the energy uncertainty will on average reduce, and hence the system acquires positive information. Writing
\( E_2 - E_1 = \omega \), the initial energy variance is \( p(1 - p)\omega^2 \), while after the transformation \( p \to p\alpha \) it is \( p\alpha(1 - p\alpha)\omega^2 \). Therefore, the average change of the standard deviation of energy is given by

\[
\Delta_{sd} = \mathbb{E} \left[ \left( \sqrt{p\alpha(1 - p\alpha)} - \sqrt{p(1 - p)} \right) \omega \right].
\]

If the system acquires information about its energy, then it must be that the standard deviation reduces so that \( \Delta_{sd} < 0 \). Dividing \( \Delta_{sd} \) by \( \sqrt{p(1 - p)} \omega \) we find that

\[
\frac{\Delta_{sd}}{\sqrt{p(1 - p)}\omega} = \Lambda - 1,
\]

and hence that \( \Delta_{sd} < 0 \) if and only if \( \Lambda < 1 \), which establishes the claim.

We remark incidentally that in general the diagonal elements of the density matrix can also be modified under an arbitrary transformation \( p \to p\alpha \) of the squared expansion coefficients of the wave function. However, if the transformation is associated with an acquisition of information, and if it is ‘rational’ in the sense that \( p\alpha \) represents the conditional probability resulting from information acquisition (as opposed to an arbitrary updating of probability that is independent of acquired information), then we have \( \mathbb{E}[\alpha] = 1 \) on account of the Bayes formula, and hence the diagonal elements of the density matrix will not be affected. Such a rational transformation is also efficient because it maximizes the averaged reduction of uncertainty [46]. The observation that decoherence typically does not involve changes of diagonal elements therefore suggests that decoherence effects indeed represent efficient information acquisition.

It is worth noting in this connection that in the literature, decoherence is conventionally associated with the system losing information into its environment [47]. Needless to say this interpretation is based on the analysis of the von Neumann entropy of the density matrix \( \hat{\rho} \) of the system, which increases when the system gains information; in contrast to the averaged Shannon–Wiener entropy of the system, which we have shown to decrease. The reversed interpretation proposed here seems more natural in the context of understanding adaptive dynamics, namely, for the system to evolve dynamically in response to the conditions of its environment, it is necessary that the system extracts information about the conditions of the environment.

14. Quantum evolution is efficient in that it corresponds to optimal signal detection

More generally, for a broad range of quantum systems immersed in a general open environment, the state of the system as perceived by an external observer is described by a density matrix, whose dynamical evolution is typically described by the Lindblad equation [48]. This equation is deterministic, because the effect of noise is averaged over all random realizations of the noisy information when transforming from a (random) wave function to a (non-random) density matrix. Given the deterministic Lindblad equation for the density matrix, finding a randomly evolving wave function \( |\Psi\rangle \) such that the associated density matrix \( \mathbb{E}[|\Psi\rangle\langle\Psi|] \) obeys this equation is known as the stochastic unravelling problem. In other words, can we find a stochastic evolution of the wave function of a system such that when the effect of stochasticity is averaged over, the dynamics obeys the Lindblad equation?

It has been demonstrated recently that solutions to the stochastic unravelling of the Lindblad equation for open quantum dynamics are those for the optimal signal processing [46]. That is to say, a noisy evolution of the wave function that gives rise to the Lindblad equation is one that corresponds to the optimal detection of the condition of the environment. Given that the Lindblad equation describes the dynamics of a very wide range of quantum systems [48], the fact that the equation is underpinned by optimal signal detection supports our hypothesis that quantum systems evolve so as to on average maximally reduce the uncertainty of the conditions of the environments as encoded in the wave function.
The optimality condition here is important, because it establishes the informational efficiency of quantum dynamics. Hence the feature of an efficient adaptation to environmental conditions is not unique to biological systems, and is embedded at the quantum-mechanical level. In fact, we would argue that this is why biological systems, built out of efficient quantum particles, are able to efficiently process information so as to minimize the energy expenditure associated with adaptation. The added ‘benefit’ of such an optimal evolution is that the change of the state of the system, on average, is the smallest possible while maintaining consistency with the information acquired [14]. It follows that the deviation away from deterministic unitary motion is also minimized.

15. From quantum to biological dynamics

The foregoing observations suggest that the dynamical equation governing the evolution of the wave function of an open quantum system is associated with the optimal signal detection under noisy exchange of information with the environmental particles—about the conditions of the environment. If so, then a more realistic description of a quantum system is obtained by the specification of the noisy information flow concerning the system–environment interaction, along with the application of optimal signal detection. This then provides a more complete characterization of a quantum system. Putting it differently, because of the prevalence of noise, what matters ultimately is not the energy but the information about the energy, or more generally information about the state of the environment. If this is the case, then the adaptive dynamics of a system, based on noisy information about the conditions of the environment, is not unique to biology, but is a universal feature applicable equally to quantum systems as well as to biological. That is, signal transduction is applicable universally across all scales. This, in turn, leads to our proposal that mathematical models used to describe the dynamics of open quantum systems can be applied, mutatis mutandis, to model the dynamics of biological systems.

Motivated by these hypotheses, stochastic Schrödinger equations have been applied recently to model heliotropic and gravitropic motions of green plants [46]. These models have the advantage of predicting the statistics of biological dynamics. Further, one can use these models to work out the amount of information required to be processed in order to achieve certain objectives (for example, for a flower to identify the location of the sun and turn towards it). While these models are effective in some ways, it is legitimate to ask whether any of the quantum effects might play a role in the biological context. The fact that signal detection underpins the dynamics of quantum systems as well as those of biological systems, in itself, does not imply that quantum effects manifest themselves in the biological context.

16. Manifestation of a quantum effect in biology

To better understand the role that quantum features might play in biology and ecology, we remark first that the stochastic Schrödinger equations are specified by two drivers, namely, the Hamiltonian \( \hat{H} \) and the Lindblad operator \( \hat{L} \). Now one of the fundamental features of quantum theory is that observable quantities need not be compatible. So for instance while in classical physics a particle will always have a definite position and a definite momentum, in quantum theory there exists no state (wave function) of a particle such that its position and momentum take definite values (i.e. with no uncertainty) simultaneously. In the case of a stochastic Schrödinger equation, we have the operators \( \hat{H} \) and \( \hat{L} \). They can either be compatible so that \( \hat{H}\hat{L} = \hat{L}\hat{H} \) (the matrix product is commutative), or incompatible so that \( \hat{H}\hat{L} \neq \hat{L}\hat{H} \) (matrices do not commute). In the latter case, no state can take definite values for both \( \hat{H} \) and \( \hat{L} \).

When a stochastic Schrödinger equation is applied in the biological context, the Hamiltonian \( \hat{H} \) models the change of environmental conditions itself, while the Lindblad operator \( \hat{L} \) models adaptation in response to environmental cues. It is more often the case that these two effects are not compatible; biological systems are capable of adaptation so long as the environmental conditions do not change too abruptly. Otherwise, a rapid change of conditions can be
catastrophic for survival. Hence there are two phases, one phase in which adaptation is feasible, and another phase in which adaptation is impossible. Such an effect can be modelled with a stochastic Schrödinger equation for which, and only for which, $\hat{H}$ and $\hat{L}$ are incompatible. That is, depending on the relative magnitudes of $\hat{H}$ and $\hat{L}$, the dynamics of the system exhibits different characteristics. Although detailed features of such phase transitions have not been fully uncovered, their existence is well documented [49,50].

Therefore, while from a purely signal-detection perspective there is little evidence that some of the counterintuitive quantum features (such as entanglement or phase coherence) play any role in biology and ecology, the lack of compatibility among observable quantities—another quantum feature—does appear to play an important role. This observation makes the stochastic Schrödinger equation a useful and effective mathematical tool for characterizing biological dynamics.

### 17. Quantifying information contained in environmental cues

Whether classical or quantum signalling models are employed to characterize biological dynamics, the use of these models has the advantage—apart from being able to predict the statistics of future events—of allowing for the quantification of information. This is of particular interest in the case of plants, because we do not normally associate the notion of ‘information processing’ to plants, and yet, plants do process environmental information at all times. Thus, models can be used to assist estimating the information contents of environmental cues. Take, for instance, the example considered earlier in which the signal is modelled by the random variable $X$, taking the value $x_i$ with the probability $p_i$, and noise by $\epsilon$, with the density $f(x)$. Then the information contained in the noisy observation $\xi = X + \epsilon$ about the value of $X$ is measured by the mutual information $I(\xi, X)$. This is the amount of information contained in environmental cues concerning the signal of interest for the plant. Writing $p(\xi) = \sum_i p_i f(\xi - x_i)$ for the density of $\xi$, the mutual information can be shown to be given by the entropy difference [51,52]

$$I(\xi, X) = \int f(x) \log f(x) \, dx - \int p(\xi) \log p(\xi) \, d\xi.$$

Remarkably, this agrees with the negative of the average change of entropy obtained earlier. Therefore, once a model for the signal and noise is chosen, one can predict the statistics of biological dynamics by using the a posteriori probabilities. Model parameters can then be calibrated by comparing the statistics thus obtained against empirical data. When a model is calibrated, it can be used to quantify the information content. In other words, even though there is neither an intentional transmitter of the signal nor a purposefully built communication channel, it is nevertheless possible to estimate the information content of environmental cues.

An interesting question that arises here is the calibration of the a priori probability of the signal $X$ experienced by the plants. In some cases, a symmetry argument may be considered to estimate the density of $X$, such as in the example of circumnutation of the bean plants discussed above. In other cases, the a priori probability can be estimated from data. For instance, if the signal $X$ concerns the location of the sun for a heliotropic plant, then the a priori distribution of $X$ can be estimated by studying the orientations of the flowers and leaves of the plant before dawn. In the case of a young sunflower, the distribution will then be sharply peaked at around eastern direction [53], but this will be different for other plants such as daisy flowers.

### 18. Discussion

The routine threats experienced by developing plants are numerous. Compared with animals, the sessile plant only requires the physical constituents of their environments: light, CO$_2$, H$_2$O and minerals [2]. A serious lack or imbalance of any of these can threaten viability as can a substantial number of different mechanical, thermal and biological challenges. Phenotypic plasticity is a common behavioural response; tune the phenotype to the experienced environmental conditions.
Alterations occur either via numbers of branch roots, shoot branches, leaves or buds, or by changing their physical parameters, such as leaf area, stem thickness, stiffness or proportions of different cell types. The ability to efficiently process and erase information is vital for plants surviving in wild and agricultural circumstances.

The information-theoretic approach to understanding biological dynamics is useful because it offers a way of modelling the dynamical behaviours of biological systems and enables predictions. We believe it is particularly advantageous in understanding better the behaviour of green plants, for it is otherwise difficult to assess or measure informational quantities associated with them. In particular, the mutual information involves the entropy of the noisy observation $\xi$, which is certainly difficult to estimate from data alone, if we had no model. But what do we learn from these information measures about plant biology? And what are the open challenges from the informational perspective?

In the view of the fact that plants form the basis of almost all food chains, enhanced understandings of their behaviours, efficiencies and capabilities are becoming increasingly more important [2]. Our information-based approach will naturally contribute towards this endeavour. In particular, as well as processing information, we expect that biological systems erase some of the processed information. This is to be expected with transduction systems using $[\text{Ca}^{2+}]$, since at the end of the first transient the system is primed to respond to alternative signals. But erasure of information inevitably requires energy consumption and heat production, in accordance with Landauer’s principle in computation [54]. In particular, the less efficient is the computational capacity, the more energy it requires. Based on the recent experiments with bean plants that can identify an object in its vicinity to climb up [55], it has been conjectured that green plants must be able to process information more efficiently than, say, the best computers available [46]. Beyond this one estimate, little has been investigated or explored in this direction. However, the information-based approach offers a new avenue of research that can be supplemented by theoretical models [56].

Determining the computational efficiency of green plants is an important component in understanding how they can adapt to changing environments. The observation made here that techniques of communication theory can be applied to model biological dynamics (whether classical or quantum models are used), even when there are no active agents transmitting the signal or purposefully built communication channels, opens up the possibility of making significant progress in investigating and determining the informational efficiencies, capabilities and limits of plants. A deeper understanding of these issues may even uncover ideas for technological advances. To make significant progress in this area, however, more data are required on plants. These include, in particular, an understanding of how information is processed, how it is stored and how it is erased, in plants. Equally valuable information concerns the number of information-storing units in plants (for processed information, not genetic), and more generally how much energy is consumed by plant cells. For instance, with a nanokelvin-resolution thermometer [57], it may be possible to measure heat production associated with erasure of information in plants, which in turn will elucidate the computational efficiencies of plants or any other biological system for that matter. We hope to explore these ideas elsewhere.

We conclude by remarking that there are two levels of ‘efficiencies’ that have been explored here: one concerns the efficiency of processing noisy environmental information, and the other concerns that of possible erasure of processed information. The erasure (reset) of information appears to be a concept that has rarely been explored in the context of plant science, and can be investigated further through the study of various switching mechanisms, for instance, those associated with phytochrome (a type of photoreceptor in plants), which can be activated or deactivated by adjusting the light source. As for the processing of information, we have assumed, throughout the paper, that this has to be efficient, and thus will be consistent with the Bayes formula. This leads to three advantages that are closely interlinked. First, the change in plants induced by the detection of a noisy environmental information is on average a minimum that is nevertheless consistent with the detection. This ensures that on average, the energy consumption associated, for instance, with the tuning of the phenotype, or other responses, is minimized.
Second, the inference based on the Bayes formula will on average minimize uncertainties associated with the signal. This will lead to a dynamical behaviour that on average minimizes ‘surprise’ elements, and thus is consistent with ideas put forward previously based on the free energy principle [15]. Third, the change induced by signal detection is induced only by the arrival of new information. To understand this notion better, we note that while it is common to represent the information $\xi$ in the ‘signal-plus-noise’ form as we have done here, it is possible to decompose $\xi$ alternatively in the ‘known-plus-unknown’ form. That is, $\xi$ contains information that is already known to the plant about the signal, as well as unknown new information. Following the terminology of Wiener, in communication theory the term corresponding to the arrival of new information is known as the innovations representation [58]. The change from the prior to the posterior is then induced only by the new information, and this clearly makes the dynamics efficient because no information is wasted. In the case of an open quantum system, the dynamics governed by the von Neumann–Lüders projection postulate is consistent with these efficiency requirements [14], and it appears highly implausible that the same level of efficiencies does not persist all the way to biological evolution.

**Data accessibility.** This article has no additional data.

**Authors’ contributions.** D.C.B.: conceptualization, formal analysis, investigation, writing—original draft; A.T.: conceptualization, investigation, writing—original draft.

Both authors gave final approval for publication and agreed to be held accountable for the work performed therein.

**Conflict of interest declaration.** We declare we have no competing interests.

**Funding.** D.C.B. acknowledges support from the EPSRC (EP/X019926) and the John Templeton Foundation (grant no. 62210). The opinions expressed in this publication are those of the authors and do not necessarily reflect the views of the John Templeton Foundation.

**Acknowledgements.** The authors thank Jim Al-Khalili, Bernhard Meister and Simon Saunders for stimulating discussions.

**References**

1. Dobzhansky T. 1956 What is an adaptive trait? *Am. Nat.* 90, 337–347. (doi:10.1086/281944)
2. Gilroy S, Trewavas T. 2022 Agency, teleonomy and signal transduction in plant systems. *Biol. J. Linnean Soc.* 20, 1–16. (doi:10.1093/biolinnean/blac021)
3. Darwin C. 1871 *The descent of man*. London, UK: Murray.
4. Anastasi A. 1986 Intelligence as a quality of behaviour. In *What is intelligence? Contemporary viewpoints on its nature and definition* (eds RJ Sternberg, DK Detterman), pp. 19–21. Norwood, NJ: Ablex Publishing Corporation.
5. Beer RD. 1990 *Intelligence as adaptive behaviour*. San Diego, CA: Academic Press.
6. Romanes GJ. 1886 *Animal intelligence*. London, UK: Kegan Paul, Trench, & Co.
7. Parker GA, Maynard-Smith J. 1990 Optimality theory in evolutionary biology. *Nature* 348, 27–33. (doi:10.1038/348027a0)
8. Charnov EL. 1976 Optimal foraging, the marginal value theorem. *Theor. Popul. Biol.* 9, 129–136. (doi:10.1016/0040-5809(76)90040-X)
9. Kelly CK. 1992 Resource choice in *Cuscuta europaea*. *Proc. Natl Acad. Sci. USA* 89, 12 194–12 197. (doi:10.1073/pnas.89.24.12194)
10. McNickle GG, Cahill Jr JE. 2009 Plant root growth and the marginal value theorem. *Proc. Natl Acad. Sci. USA* 106, 4747–4751. (doi:10.1073/pnas.0807971106)
11. Endres RG, Wingreen NS. 2008 Accuracy of direct gradient sensing by single cells. *Proc. Natl Acad. Sci. USA* 105, 15 749–15 754. (doi:10.1073/pnas.0804688105)
12. Wiener N. 1948 *Cybernetics, or control and communication in the animal and the machine*. Boston, MA: The Technology Press of the MIT.
13. Friston K. 2010 The free-energy principle: a unified brain theory? *Nat. Rev. Neurosci.* 11, 127–138. (doi:10.1038/nrn2787)
14. Brody DC. 2023 Quantum formalism for cognitive psychology. (https://arxiv.org/abs/2303.06055)
15. Calvo P, Friston K. 2017 Predicting green: really radical (plant) predictive processing. *J. R. Soc. Interface* 14, 20170096. (doi:10.1098/rsif.2017.0096)
16. Kudla J, Batistic O, Hashimoto K. 2010 Calcium signals: the lead currency of plant information processing. *Plant Cell* **22**, 541–563. (doi:10.1105/tpc.109.072686)
17. Delormel TY, Boudsocq M. 2019 Properties and functions of calcium dependent protein kinases and their relatives in *Arabidopsis thaliana*. *New Phytol.* **224**, 585–604. (doi:10.1111/nph.16088)
18. Diaz J. 2011 Information flow in plant signaling pathways. *Plant Signal. Behav.* **6**, 339–343. (doi:10.4161/psb.6.3.13709)
19. Croucher T, Wright J, Carvalho ARR, Barnett SM, Vaccaro JA. 2019 Information erasure. In *Thermodynamics in the quantum regime* (eds F Binder, LA Correa, C Gogolin, J Anders, G Adesso), pp. 713–730. Berlin, Germany: Springer.
20. Trewavas AJ. 2017 The foundations of plant intelligence. *Interface Focus* **7**, 20160098. (doi:10.1098/rsfs.2016.0098)
21. Gagliano M, Renton M, Depczynski M, Mancuso S. 2014 Experience teaches plants to learn faster and forget slower in environments where it matters. *Oecologia* **175**, 63–72. (doi:10.1007/s00442-013-2873-7)
22. Nielsen MA, Chuang IL. 2010 *Quantum computation and quantum information*. Cambridge, UK: Cambridge University Press.
23. Kullback S. 1959 *Information theory and statistics*. New York, NY: John Wiley & Sons.
24. Cover TM, Thomas JA. 2006 *Elements of information theory*. Hoboken, NJ: John Wiley & Sons.
25. Cheong R, Rhee A, Wang CJ, Nemenman I, Levchenko A. 2011 Information transduction capacity of noisy biochemical signaling networks. *Science* **334**, 354–358. (doi:10.1126/science.1204553)
26. Mescher MC, Pearse IS. 2016 Communicative interactions involving plants: information, evolution, and ecology. *Curr. Opin. Plant Biol.* **32**, 69–76. (doi:10.1016/j.pbi.2016.06.015)
27. Trewavas A. 2012 Information, noise and communication: thresholds as controlling elements in development. In *Biocommunication of plants* (eds G Witzany, F Baluška). Berlin, Germany: Springer.
28. Thomas PJ. 2011 Every bit counts. *Science* **334**, 321–322. (doi:10.1126/science.1213834)
29. Trewavas A. 2014 *Plant behaviour and intelligence*. Oxford, UK: Oxford University Press.
30. Runyon JB, Mescher MC, De Moraes CM. 2006 Volatile chemical cues guide host location and host selection by parasitic plants. *Science* **313**, 1964–1967. (doi:10.1126/science.1131371)
31. Isham CJ. 1995 *Lectures on quantum theory*. London, UK: Imperial College Press.
32. Adler SL. 2004 *Quantum theory as an emergent phenomenon*. Cambridge, UK: Cambridge University Press.
33. Weber G, Ghirardi T. 1986 Unified dynamics for microscopic and macroscopic systems. *Phys. Rev. D* **34**, 470–491. (doi:10.1103/PhysRevD.34.470)
34. Pearle P. 1989 Combining stochastic dynamical state-vector reduction with spontaneous localization. *Phys. Rev. A* **39**, 2277–2289. (doi:10.1103/PhysRevA.39.2277)
35. Điösí L. 1989 Models for universal reduction of macroscopic quantum fluctuations. *Phys. Rev. A* **40**, 1165–1174. (doi:10.1103/PhysRevA.40.1165)
36. Gisin N, Percival IC. 1993 The quantum state diffusion picture of physical processes. *J. Phys. A* **26**, 2245–2260. (doi:10.1088/0305-4470/26/9/019)
37. Percival IC. 1994 Primary state diffusion. *Proc. R. Soc. Lond. A* **447**, 189–209. (doi:10.1098/rspa.1994.0135)
38. Gisin N, Percival IC. 1992 The quantum state diffusion model applied to open systems. *J. Phys. A* **25**, 5677–5691. (doi:10.1088/0305-4470/25/21/023)
39. Brody DC, Hughston LP. 2003 Lévy models for collapse of the wave function. *J. Phys. A* **36**, 125303. (doi:10.1088/1751-8121/acbe7f)
40. Gisin N. 1989 Stochastic quantum dynamics and relativity. *Helv. Phys. Acta* **62**, 363–371.
41. Brody DC, Hughston LP. 2006 Quantum noise and stochastic reduction. *J. Phys. A* **39**, 833–876. (doi:10.1088/0305-4470/39/4/008)
42. Adler SL, Brody DC, Brun TA, Hughston LP. 2001 Martingale models for quantum state reduction. *J. Phys. A* **34**, 8795–8820. (doi:10.1088/0305-4470/34/42/006)
43. Adler SL. 2002 Environmental influence on the measurement process in stochastic reduction models. *J. Phys. A* **35**, 841–858. (doi:10.1088/0305-4470/35/4/301)
44. Hughston LP. 1996 Geometry of stochastic state vector reduction. *Proc. R. Soc. Lond. A* **452**, 953–979. (doi:10.1098/rspa.1996.0048)
45. Brody DC, Hughston LP. 2002 Efficient simulation of quantum state reduction. *J. Math. Phys.* **43**, 5254–5261. (doi:10.1063/1.1512975)
46. Brody DC. 2022 Open quantum dynamics for plant motions. Sci. Rep. 12, 3042. (doi:10.1038/s41598-022-07102-w)
47. Zurek WH. 2009 Quantum darwinism. Nat. Phys. 5, 181–188. (doi:10.1038/nphys1202)
48. Breuer H-P, Petruccione F. 2006 The theory of open quantum systems. Oxford, UK: Oxford University Press.
49. Bassi A, Ippoliti E. 2004 Numerical analysis of a spontaneous collapse model for a two-level system. Phys. Rev. A 69, 012015. (doi:10.1103/PhysRevA.69.012105)
50. Brody DC, Longstaff B. 2019 Evolution speed of open quantum dynamics. Phys. Rev. Res. 1, 033127. (doi:10.1103/PhysRevResearch.1.033127)
51. Gel’fand IM, Yaglom AM. 1957 Calculation of the amount of information about a random function contained in another such function. Uspehi Mat. Nauk 12, 3–52.
52. Brody DC, Davis MHA, Friedman RL, Hughston LP. 2009 Informed traders. Proc. R. Soc. A 465, 1103–1122. (doi:10.1098/rspa.2008.0465)
53. Vandenbrink JP, Brown EA, Harmer SL, Blackman BK. 2014 Turning heads: the biology of solar tracking in sunflower. Plant Sci. 224, 20–26. (doi:10.1016/j.plantsci.2014.04.006)
54. Reihani A, Meyhofer E, Reddy P. 2022 Nanokelvin-resolution thermometry with a photonic microscale sensor at room temperature. Nat. Photonics 16, 422–427. (doi:10.1038/s41566-022-01011-0)
55. Kailath T. 1968 An innovations approach to least-squares estimation. Part I: linear filtering in additive white noise. IEEE Trans. Automat. Control 13, 646–655. (doi:10.1109/TAC.1968.1099025)