

Ignite

Information theory and plant ecology

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To survive, all organisms must sense and respond to information from their environment. This is true of many organisms, including plants, which need to do all the things that other organisms do while operating under the limitations of being sessile and lacking a central nervous system. In this article, we explore how information theory can apply to plants and briefly review the types and sources of information and the mechanisms that plants use to perceive and respond to their environment. We identify and describe three primary modes by which a plant receives information: chemical, electromagnetic and mechanical. We describe how plants integrate information to detect the state of their neighbors, capture resources and regulate growth and metabolism. Overall, we find that plants interpret information from their surroundings as an emergent property of distributed information processed by a network of cells. We end with a prospectus of directions for future research including decoding signal from noise, storage of information, additional means of information transmission and two-way information signaling with biotic partners.

Keywords: communication, information, information entropy, information theory, plant ecology

Introduction

Behavioural ecology seeks to understand how organisms assess and respond to cues in their environment, and why organisms use the particular responses we observe. For example, animal behaviourists may ask questions about a behaviour (e.g. bird-song) in terms of their proximate causes (e.g. biomechanics of bird song) or ultimate causes (e.g. why birds sing at all) (sensu Tinbergen 1963). There is a whole field of animal ecology that explicitly uses information theory as a framework for understanding biological responses (Battail 2013). Similar to animals, plants assess and respond to cues in their environment. Most plant biologists call this plasticity, but occasionally authors have explicitly used theory and models from animal behavioural ecology to generate hypotheses about plant plasticity (Satter and Galston 1973, Silvertown and Gordon 1989, Hutchings and de Kroon 1994, McNickle and Brown 2014). Here, we view plant plasticity and plant behaviour as synonyms and

consider plant behavioural plasticity through the lens of proximate causes. Specifically, we argue that certain questions about proximate causes lend themselves naturally to the framework of information theory (Fig. 1).

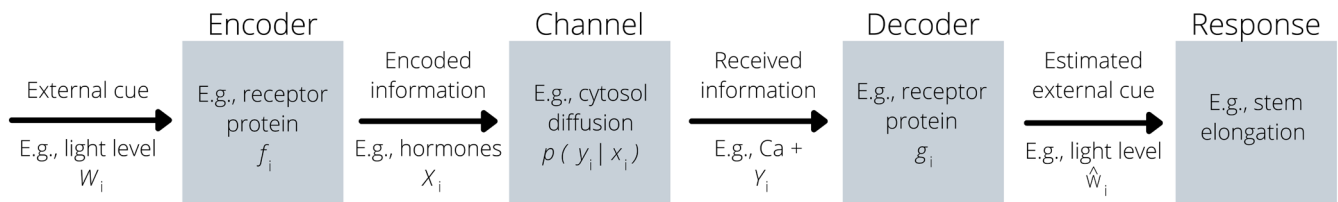
If plants exhibit adaptive plasticity in response to some external cues, then they must have mechanisms that allow them to both encode and decode this information within their cells and tissues. We define information as a signal or attribute expressing the probability of occurrence of one out of two or more alternative sequences of conditions or quantities: $W_1, W_2, \dots, W_n$ (Shannon 1948, Shannon and Weaver 1949). Examples of quantities of information under this definition are changes in light quality, water potential of the soil or the presence or absence of certain species around the plant. Information theory is a mathematical treatment that seeks to define quantification, storage and communication of information. Three concepts in information theory which we believe can be useful in understanding the proximate causes of behaviour are: 1) entropy; 2) channel capacity, and; 3) mutual information (Fig. 1). First, entropy attempts to quantify the amount of uncertainty or noise there is in a signal (Shannon 1948). Second, channel capacity defines both the maximum amount of information and the rate at which information can be relayed from one place to another. Third, mutual information defines the way that one type of signal may contain information about another type of signal. Thus, for plants to process information about the external environment, and then mount an adaptive plastic response, they must possess mechanisms that encode external cues (receivers), mechanisms to conduct the encoded information from one place to another (channels), and mechanisms to decode information to activate a response (Fig. 1). Entropy,

channel capacity and mutual information will affect a plant's ability to respond to stimuli with accuracy.

In the remainder of this short essay, we review the types of information that are accessible to plants as they assess and respond to their environment in the context of information theory defined above. Using a few examples, we describe some of the known mechanisms that allow plants to encode and decode information, and the subsequent responses plants have to such information. We also link these to ideas about entropy, channel capacity and mutual information when possible. This essay focuses on the basic modes of information that plants access with some examples: chemical, electromagnetic radiation and mechanical (Table 1, Fig. 1). We conclude by proposing some future directions that might enhance our understanding of proximate causes of plant behaviour by explicitly using an information theory framework.

Chemical information

Plant receivers of chemical information occur mostly in the cells of plant roots and leaves, though they might occur in any plant tissue (Lamers et al. 2020). Species vary widely in the types of chemicals they sense, and their subsequent responses. Basic types of chemical information include nutrient and water content in the soil and concentrations of gases in the air. Additionally, information about competitors, enemies and mutualists can also come in the form of chemical signals such as root exudates (Semchenko et al. 2014), herbivore saliva (Vega-Muñoz et al. 2020, Arimura et al. 2021, Sharma et al. 2021) or microbial effectors (Saijo et al. 2018). In most cases, the reception of information begins when external chemicals bind to receptor proteins (Osakabe et al.



$$\text{Entropy: } H(X_i) = - \sum_{i=1}^n p(x_i) \log p(x_i)$$

$$\text{Mutual information: } I(X_i|X_j) = p(x_i|x_j) \log \left[\frac{p(x_i|x_j)}{p(x_i)p(x_j)} \right]$$

$$\text{Channel capacity: } C = \sup I(X_i|X_j)$$

Figure 1. Schematic of how the true state of the environment (W_i) is estimated ($\hat{W}_i$) by plant cellular biochemistry. This requires some way of biochemically encoding information via a function, f_i , and some way of decoding that information via the function, g_i , to produce a response. The set of information that becomes encoded within a plant is defined by X_i and the set of the information travelling within a plant body is Y_i , where X_i and Y_i might be vectors, matrices or other complex ways of representing information. The conditional probability that a plant will recognize the set of information, Y_i , given that it received the set X_i is given by a probability distribution, $p(x_i)$. Entropy emerges from p , mutual information emerges from the joint probability distributions of different types of X_i , and channel capacity is the supremum of the mutual information. (Note: If the upper bound of $I(X_i|X_j)$ is known then $\sup I(X_i|X_j) = \max I(X_i|X_j)$, which is intuitive for channel capacity, but the supremum function is more general than the maximum function in those cases where the upper bound of $I(X_i|X_j)$ remains unknown (Shannon and Weaver 1949).)

Table 1. We present a non-exhaustive list of the types of information available to plants, their responses and mechanisms to the information, and relevant literature for further reading. We placed information into three broad categories – chemical (C), electromagnetic (EM) and mechanical (M) – which are based on the medium through which the information is delivered to the plant. As plants lack a central nervous system, the response of nearly all information is ultimately driven by chemical mechanisms, subsequently launching an integrated, whole-plant response.

Information	Responses	Mechanisms	References
Nutrients (C)	Altered uptake regulation and nutrient use efficiency Metabolic regulation Chemotropism Altered root architecture Allelopathy Root exudation	Nutrient concentration activates protein, enzyme and hormones	Fichtner et al. 2021 Htwe et al. 2021 Vives-Peris et al. 2020 O'Brien et al. 2016 Nacry et al. 2013 Kroon et al. 2012
Water/salinity (M)	Hydrotropism Altered root architecture Stomatal activity Allelopathy	Water potential gradient detected Proteins and hormones trigger hydrotropism	Dietrich 2018 Dinneny 2019 Buckley 2005
Temperature (EM)	Altered phenology Hypocotyl length Stomatal activity Altered metabolism Immune system regulation	Thermosensitive proteins and hormones	Lin and Zhu 2021 Jin and Zhu 2019 Gill et al. 2015
Light (EM)	Phototropism Morphogenesis Shade avoidance Metabolic regulation Allelopathy Altered phenology	Proteins activated by UV/blue light (290–500 nm)	Liscum et al. 2020 Vanhaelewyn et al. 2020 Ballaré and Pierik 2017 Fankhauser and Christie 2015 Galvão and Fankhauser 2015 Liscum et al. 2014 Dayan 2006 Izaguirre et al. 2006 Vives-Peris et al. 2020 Tsai and Schmidt 2021
pH (C)	Root exudation Changes in gene expression	Unknown but likely through proton pumps and <i>trans</i> -acting factors that regulate DNA expression	
Gravity (M)	Gravitropism	Sedimentation in starch-filled plastids (statoliths) changes with plant orientation	Nakamura et al. 2019 Vandenbrink and Kiss 2017 Morita et al. 2010 Fasano et al. 2002 Uesugi et al. 2019 Gundel et al. 2014 Pierik et al. 2013 McNickle et al. 2009
Competition (C, EM, M)	Excess growth Shade avoidance Allelopathy	Allelochemicals and hormones released by neighboring plants taken up by roots and leaves, activates proteins, enzymes and hormones Leaf proteins sensitive to red-shifted light	
CO ₂ concentration (M)	Stomatal activity Metabolic regulation	Differential between atmospheric and internal CO ₂ concentration.	Driesen et al. 2020 Yang et al. 2020 Assmann and Jegla 2016 Xu et al. 2016
Mutualism (C, M)	Fungal and bacterial mutualisms Immune system regulation	Signaling factors exchanged between host plant and microbial partner	Lanfranco et al. 2018 Padje et al. 2016 Jones et al. 2007
Pests, parasites and pathogens (C, M)	Allelopathy Immune system regulation	Mechanical and molecular signals from wound site, differentiable from benign wounds	Arimura 2021 Sharma et al. 2021 Vega-Muñoz et al. 2020 Qi et al. 2018 Karban 2008
General			Bilas et al. 2021 Pang et al. 2021 Driesen et al. 2020 Muthert et al. 2019 Ninkovic et al. 2019 Mizutani and Kanaoka 2018 Karban 2015 Cahill and McNickle 2011 McNickle et al. 2009 Monshausen and Gilroy 2009 Aphalo and Ballare 1995

2013). The receptor proteins must then encode this information into a biochemical signals that can then be decoded to elicit a behavioural response in plants. In general, receptor proteins encode information into chemical messengers such as calcium and calcium-binding proteins that can travel through cells, tissues or entire plant bodies (Tang et al. 2020). The channels that conduct the encoded information can be cytosol diffusion, diffusion in intercellular spaces or movement through xylem and phloem depending on the distance the signal travels. Therefore, channel capacity is likely limited by factors such as temperature and transpiration rates which drive diffusion and movement of molecules in the vascular tissue. Eventually, encoded chemical messengers then bind to other proteins to be decoded at the site of some cellular- or tissue-level response (Van Norman et al. 2011). Such responses may be decoded locally at the reception site as in the case of nutrient foraging by roots (Zhang and Forde 2000, Forde and Walch-Liu 2009), or the encoded chemical messengers may travel to other parts of the plant to allow integrated, whole-plant responses to information as in the case of chemical defense against herbivores (Viswanathan et al. 2007a, Karban 2011). In this way, complex plant responses occur as emergent properties of the encoding and decoding of information from multiple sources, across channels and, distributed throughout the cells of the plant.

Electromagnetic radiation information

Plants are sensitive to a wide spectrum of electromagnetic (EM) radiation spanning ultraviolet to infrared wavelengths that they use to acquire information about seasons, time of day, temperature and the presence of neighboring competitors. The primary receivers of electromagnetic radiation are in leaves, though again, they may occur in any plant tissue (e.g. negative root phototropism (van Gelderen et al. 2018)). Responses to visible and ultraviolet light include phototropism, shade avoidance and metabolic regulation (Table 1). The intensity and length of exposure and the relative proportions of different frequencies of light are important in triggering different responses, including responses to other abiotic and biotic stressors (Roeber et al. 2020). Both animals and plants respond to photoperiod (Parker et al. 1952), and one of the most well-studied phenomena in plants is the photoperiodic regulation of flowering (Shrestha et al. 2014, Song et al. 2015). Plants also use light to provide information about competitors. Light that is transmitted through a leaf canopy contains a greater proportion of near-infrared light (Ballaré et al. 1987, Casal 2013). Plants in the understory receive less intense, 'red-shifted' light which is differentiable from the shade of, e.g. a rock face (Ballaré and Pierik 2017). Plants respond to red-shifted light by allocating resources to stem growth, presumably to prevent further competition for light (Givnish 1982, King 1990, Falster and Westoby 2003). Many recent reviews describe the specific reception-signal transduction-responses in plants, including Casal (2013), Demarsy et al. (2018) and Pierik and Ballaré (2021). In the case of electromagnetic radiation, information encoding begins with photoreceptor

proteins which contain photopigment that reacts to light to initiate a change in the conformation of the receptor protein.

For example, a well-known behavioural response to shifts in the ratio of red-to-far-red light is stem elongation. In this case, phytochrome proteins are the photoreceptors, and information about the relative amounts of red (650–670 nm) and far-red light (705–740 nm) are encoded through changes in the conformation of the phytochrome molecule itself (Bae and Choi 2008, Pham et al. 2018). Photoreceptors in the phytochrome family have two conformations: 1) the inactive Pr conformation which, when struck by red light, encodes information about red light levels, and; 2) the active Pfr form which encodes information about far-red light levels when struck by far-red light. In this example, the information channel is diffusion through the cytoplasm and nucleus. The inactive Pr form travels to the cytosol, while the active Pfr form travels to the nucleus. The information about the quality of light surrounding the cell that was encoded in the active phytochrome molecule is then decoded inside the nucleus where it interacts with multiple factors, and controls multiple plant responses directly through gene expression (Van Buskirk et al. 2012, Klose et al. 2015). This is a form of mutual information, as it encodes information about the quality of photosynthetically active radiation, as well as information about the competitive environment.

At infrared wavelengths, radiation is interpreted as heat, but can also cause direct damage to tissues which is another quantity of information. Temperature is an important source of information for plants (especially in early developmental stages) that affects phenology, seedling height and stomatal density and aperture (Table 1). Temperature may also cause plant death. Similar to photoreceptors, thermosensitive proteins are responsible for encoding infrared radiation (Jin and Zhu 2019, Lin and Zhu 2021). When stimulated, thermosensitive proteins activate a signal-transduction pathway of hormones and proteins, prompting a response in the plant. For example, using the cumulative time of cooling temperatures throughout the season, in addition to several other cues, plants appropriately time leaf senescence (Gill et al. 2015). However, it is not really understood how information about temperature is stored.

Mechanical information

Plants also assess and respond to information about their environment via the gravity vector and mechanical interactions with the physical environment. Information about gravity is thought to be encoded by differential pressure on membranes and the plant cytoskeleton, followed by enhanced or repressed cell division and elongation on different sides of an organ (typically roots or shoots) that causes the stem to reorient (Blancaflor 2013). Interestingly, the mechanism by which plants encode and decode information about gravity is not completely understood, but in roots it is thought to involve starch molecules called statoliths that settle in the cell and interact with the cytoskeleton allowing roots to grow downwards (Blancaflor 2013). Similar phenomena occur in trees

that produce secondary growth as reaction wood (also called compression or tension wood) in response to beginning to tip in one direction more than another (Groover 2016).

Thigmotropism is a general term for plant responses to touch, which include cell differentiation, changes to growth rates and the production of specialized secondary metabolites, among others (Jaffe et al. 2002). Similar to gravity, climbing plants respond to information obtained from touch with, for example, differences in cell elongation that allow climbing plants to wrap around objects for support (Fasano et al. 2002). Roots also navigate the heterogeneous soil matrix, in part, using touch-related information about the penetrability of different regions of soil (Falik et al. 2005, Yamamoto et al. 2008). For example, roots can begin to grow away from hard objects in soil in ways that help them continue to explore the soil volume.

Finally, although relatively rare, some plants (e.g. *Dionaea muscipula* and *Mimosa pudica*) can respond to information about touch with rapid nastic movement (Brauner 1954). Nastic movement is achieved by a combination of ion action potentials (homologous to neuron action potentials) which encode information about touch and are decoded into rapid changes in turgor pressure and elasticity of cellular structures. Growth (cell division and elongation) may be necessary to reset the plant to its original form. *D. muscipula* uses trigger hairs that require two touches by its insect prey before nastic movement closes and captures the insect to be digested as a source of nutrients (Forterre et al. 2005). Although rarely described as such, this double-touch trigger is perhaps one of the best studied plant adaptations that guards against information entropy. By requiring two touches to the trigger hair, *D. muscipula* can filter false information from random touches (e.g. falling debris, wind, rain) from information with a higher probability of being true about the presence of insect prey.

Future directions

Through this short ignite essay, we briefly summarized some of the proximate causes of plant responses to external cues through a lens of information theory (Fig. 1). We acknowledge that there is a rich, decades-old body of knowledge in plant molecular biology that cannot be adequately explored in this essay. We also acknowledge that there is enormous diversity in plant adaptations, and while at least one example exists for each response described above (e.g. nastic movements of *D. muscipula*), there are many more examples where there are plant species that do not have a specific response (~300 000 non-carnivorous plants) or the response has not been discovered yet and, thus, nothing described above should be considered universal. We surveyed the types of information most important to certain plants, and here, we suggest some potential areas for future research that we believe could lead to novel insights into plant ecology:

- 1) What unknown sources of information can plants assess? One example is the hypothesis that plants may be able to detect and produce electrochemical information (i.e. action potentials) especially within the plant and at the root tips (Davies 2006, de Toledo et al. 2019). Such work would fit in the realm of the chemical modality of information described above; however, more research is needed in this area.
- 2) Mechanisms associated with encoding and decoding information. In general, more is known about the plastic responses plants possess than the mechanisms involved in producing responses. For example, gravitropism is relatively easy to observe by turning a potted plant on its side, but the exact mechanism remains elusive. The same is true for soil pH (Tsai and Schmidt 2021), and root responses to neighbors (Semchenko et al. 2014). These are active areas of research and we look forward to continued discovery in this area.
- 3) What adaptations do plants possess to deal with information entropy? Nature is full of noisy signals, and plants must have mechanisms to filter this noise and respond in adaptive ways. The double touch trigger on the *D. muscipula* is one clear example, but we found little focused discussion on how entropy may limit adaptive responses in plants (Volkov 2017).
- 4) How and when does channel capacity limit plant responses to their environment? For example, the cytosol is a busy place with many ions, hormones, proteins, mRNAs and other molecules diffusing to myriad places within and among cells. Furthermore, plants have relatively few hormones and any single hormone can be associated with multiple plastic responses (Kohli et al. 2013, Altmann et al. 2020). Can the co-occurrence of many external cues lead to a reduced ability for plants to respond to their environment?
- 5) Whether and how plants store information. Animals can hold a record of information received in their central nervous system, i.e. memory. Plants, without a central nervous system, do not have the ability to retain information this way. That said, their growth responses to information may be a form of storage. Plants may modulate their responses to be constituent or induced which can affect later responses to information (Thellier and Lüttge 2013). In extreme environments, information may trigger epigenetic responses which are passed onto progeny (Chang et al. 2020).
- 6) Lastly, what is the nature of active communication and eavesdropping by plants to other organisms? Understanding information involved in biotic interactions is critical to an understanding of plant ecology. Interactions with neighboring plants, herbivores, pollinators and other mutualists represent dynamic processes which can be described by eco-evolutionary games, involving the exchange of information among players and their strategic responses (McNickle and Dyzinski 2013, Brown 2016). This may indicate active communication or simply eavesdropping among plants. Indeed, new plant responses to biotic information have recently been discovered. For example, plant root responses to neighbors were first described in by Gersani et al. (2001), but whether they are responses to neighbors or artefacts of poor experimental design remain contested and debated (Chen et al. 2015, 2020, McNickle 2020, Cabal 2022).

Conclusion

Information theory is a mathematical representation of how information can be quantified, stored and communicated through channels. In the context of plant biology, external environmental cues must be encoded into some biochemical structure, which must travel to the site of response, subsequently decoded to generate a plastic response (Fig. 1). Key concepts such as information entropy, channel capacity, mutual information and their mathematical definitions may shed light onto important and unresolved questions in plant plasticity and its ecological consequences.

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Author contributions

Laura H. Jessup: Conceptualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Abdel H. Halloway:** Conceptualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Michael V. Micklebart:** Conceptualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Gordon G. McNickle:** Conceptualization (equal); Writing – original draft (equal); Writing – review and editing (equal).

Data availability statement

This paper contains no original data.

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