

REVIEW



Plants make smart decisions in complex environments

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ABSTRACT

This review proposes that plants make smart decision and encourages scientists to formulate and test hypotheses about plant's decisions as an option to investigate complex phenomena that are hardly explained through the predominant mechanistic approach. Three physiological processes (seed germination and seedling emergence, abortion of reproductive structures, and regulation of photosynthesis) are discussed to illustrate the plant's ability to make decisions from three different perspectives. It is proposed that plant scientists could access a rich pool of information by formulating and testing hypothesis on plant's decisions, even when it is not possible elucidating the full mechanism underpinning the decision. Decisions with a strategic component are discussed for seed germination and seedling emergence, in which the plant depends on limited information for making early decisions that will influence its survival and potential growth. Decisions consistent with an analysis of benefit/cost are illustrated with observations from abortion of reproductive structures. Decisions that search the optimization of complex processes are exemplified with the regulation of photosynthesis. For each type of decision, some draft experiments are suggested as exercise on how this framework could be applied. It is proposed that scientists could make experiments with plant's decisions adapting methods that were developed for other disciplines.

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Introduction

Starting from the recognition that plants are able to sense the environment and its own internal condition, this article proposes that plants are also able to process complex information for making smart decisions. Experimentation with plants would benefit from this approach because it supports the elaboration of scientific hypotheses that are not commonly proposed.

It is well established in the scientific literature that the growth and development of plants are influenced by the cues sensed from the environment, although the concept that the plants integrate large amounts of information for underpinning its decisions is scarcely explored.¹⁻⁵ At first, this concept seems awkward because plants do not possess a brain, neurons, or a specific organ for making decisions;¹ however, plants developed non-neural mechanisms that were shaped along evolution and are very effective for processing the information and deciding on what matters for its survival and reproduction.

Three relevant processes in plant physiology are discussed from the perspective of decision-making, some examples are given to illustrate how this approach can be broader and more flexible for investigating complex phenomena in comparison to the predominant mechanistic method, and a few draft experiments are suggested as examples on how to apply this framework. Plant's decisions are discussed with different perspectives like with a strategic component, based on an analysis of benefit/cost, and as the integration of complex variables for optimization of a physiological process. This is an attempt to expand our concept of plant behavior beyond physiology in order to apply the scientific thinking to comprehend how and why plants do what they do.⁶

Plant's ability for making decision is a subject for science

The choice of words to express plant's cognitive abilities is under scientific debate. Due to the lack of words for adequately expressing the phenomena occurring in plants, plant scientists borrowed terms that were restricted to animals or humans.^{1,5,7} However, scientific writing requires precision in the definitions and meaning of the words to prevent misinterpretation of concepts and findings. For instance, the term "neurobiology"⁸ is questioned because plants do not have neurons.⁹ The term intelligence is also questioned but acceptable as the word intelligence was introduced in fields not related to humans, such as artificial intelligence¹⁰ and machine intelligence. The most contentious debate is about plants having consciousness,^{7,9,11-13} which could be more precisely expressed with the word awareness⁵ that implies the perception of environment and plant's intrinsic factors. As precise definitions are always difficult to find consensus, it was proposed that scientists should experiment rather than define.¹⁴

The debate also goes around to what extent plants possess cognitive behavior.^{1,3,6-9,11-15} On the one hand, it is accepted that plants respond to environmental stimuli, memorizes some information for later response, learn, and act in a manner that requires a cognitive capacity.¹⁶ On the other hand, it is questioned to what extent plant's responses to environment are just the result of biochemical reactions from which the plant cannot deviate, if the cognition is homologous to human or animal intelligence and consciousness, and if plants possess something equivalent to neurons and synapses.

Assuming that plants have cognitive abilities, some tools and frameworks developed for human psychology can be borrowed by plant scientists as a comparative psychology,¹ like the model of Judgment and Decision Making and the Risk Sensitivity Theory which were both applied for plants.²⁻⁴ This article explores the specific plant's cognitive ability of making decisions and elaborates on how this assumption can be useful for Plant and Cropping Sciences.

What is a plant's decision?

Plant sciences are experiencing rapid progress in areas such as metabolomics, proteomics, genes expression, and plant growth regulators, and this knowledge is expected to be part of the solution to major challenges in world agricultural production such as increasing productivity, reducing environmental impact, and resisting abiotic stresses. However, there is a gap between the information produced and the adoption of that knowledge on the solution of agricultural challenges. One of the reasons for the gap is that the complexity of living organisms does not fit in the predominant mechanistic approach, in which the object of study needs to be reduced to pieces that can be controlled.^{6,8}

Despite the initial proposal in 1926¹⁷ that plants have a neural system, there is no evidence that plants possess a brain or anything resembling a centralized organ for memorizing and making decisions as found in animals.^{1,3} Instead of an animal-like centralized decision organ, plants developed decentralized non-neural mechanisms, which consists of a very complex network of genes, RNA, hormones, proteins, many types of signaling substances, and ecological interactions. All those mechanisms act with cross regulations, feedbacks, and overlapping or redundant functions.

A plant's decision is an action that a plant takes influenced by a large number of variables that could be hardly measured or defined. However, the careful analysis of the plant's action and of its consequences reveals that it is not just a passive physiological response, but it is rather a reasonable output of an elaborated analysis, and among the options that the plant could choose, hypothetically the plant chooses the option that results in the best output for its growth and reproduction considering its internal condition and the cues that were sensed. A decision differs from the traditional physiological response to experimental treatments because it is expected that the plant always responds in the same manner when exposed to an equal stimulus. In contrast, the plant's decision can be divergent under apparently equal treatments because there are variables that cannot be controlled but that are able to influence the output. When the physiological response is measured in traditional experiments, the individual plant's decisions are not considered, but the average of individual decisions is assumed as the mean response.

The data of a field experiment with castor plants (*Ricinus communis*)¹⁸ illustrate the meaning of plant's decision. A sample of 48 sequential castor plants in a field, which were not exposed to any experimental treatment, were assessed for

height and leaf area from emergence to harvest. Assuming that everything was equal among those 48 plants (seed lot, soil properties, planting time, depth, temperature, water availability, etc.), it was expected that all the plants should be equal. The height and leaf area of all plants were measured at regular intervals along the season. As early as 10 days after emergence, the plant's height varied from 3 to 18 cm, and their leaf area varied from 10 to 180 cm². The differences were exacerbated by the establishment of dominance among neighboring plants, and at the harvest time, the production of individual plants varied from 2,0 to 75,7 g of seed.

A physiological response would predict equal plants from emergence to harvest. But the sequential decisions that each individual plant made accumulated along the season and resulted in the large variability observed among plants.¹⁸ Each small decision had consequences for that plant, and the following decisions were made considering the condition that the individual eventually happens to be. For example, two seeds sowed side by side germinated at different times because of individual decisions, and one of them begun earlier to grow leaves. A few weeks later, one plant decided to initiate flowers, while the other plant decided to remain in the vegetative phase growing more leaves. Along the season, many divergent decisions were made between neighboring plants in regard to allocation of biomass among organs and definition of yield components.

There is relevant progress in the elucidation of physiological processes occurring in plants; however, the current knowledge is not able to model and predict all the responses of plants to the environment and to its internal condition because the variables and interactions at field condition are too complex. The study of plant's decisions is an option to collect useful information from experiments dealing with this kind of complex process. Compared with the mechanistic approach, it provides for an alternative standpoint of valid scientific observations. Exploring the ability of plants to make decisions opens new avenues for hypothesis, experiments, and results that are not accessible through the prevailing methods.

Seed germination and seedling emergence – strategic decisions based on limited information

This section discusses how plant's decisions made along the seed germination and seedling emergence have a strategic component. Strategy in this context is defined as the decision made by a plant, picking one option among many possible choices, being exposed to variables that are not under its control, and having limited information available. This is the scenario in which a germinating seed and an emerging seedling make its initial decisions.

Although early decisions are critical for its survival and potential growth, the seed relies on just a few cues. It receives some information from the mother-plant,¹⁹ senses the environment in the quiescent phase before hydration,^{20,21} and, during germination, it senses environmental cues like the water potential, temperature, light, oxygen, nutrient content in the soil solution, and several substances dissolved in the soil

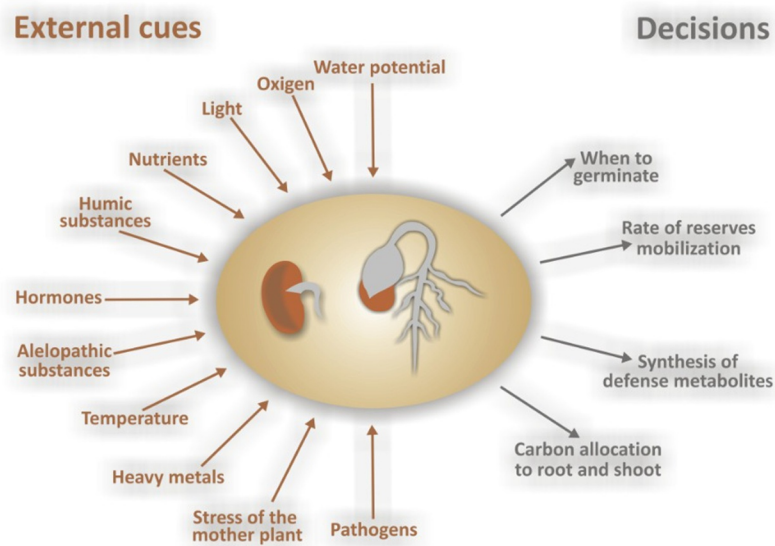


Figure 1. A germinating seed and emerging seedling sense many environmental cues, processes that information, and makes strategic decisions that will eventually impact its survival and growth.

solution like plant growth regulators, humic substances, toxic aluminum, and heavy metals.^{22–26} Those many pieces of information shall be integrated to make the strategic decisions (Figure 1).

The seed's decisions are influenced by factors that occur prior to germination, like the amount of abscisic acid (ABA) produced by the seed while it is still linked to the mother plant.^{19,27} *Petunia x hybrida* plants exposed to different stresses influenced the germination time of its seeds.²¹ Vernalization and seeds that germinate after a fire are also examples of seeds sensing information before the beginning of germination.²²

Seeds make individual decisions

In germination tests performed under laboratory conditions, a large sample of seeds is exposed to controlled and uniform conditions (water quantity and quality, moisture, temperature, light, etc.). Nevertheless, each seed germinates at a different time along many days. Many factors are known to influence the rate and time for germination,^{20,22,23,26–30} but most studies address this effect from the perspective of a seed population. An alternative approach is that each seed decides by itself when to germinate.³¹ This is not a collective decision because seeds do not receive any kind of external coordination to decide when to germinate or release dormancy. There are convincing reasons in Ecology to justify why seeds do not decide to germinate at same time, particularly for avoiding emerging all the seedlings in an occasional unfavorable environment.^{27,32,33}

While the traditional experimentation measures the effect of one or few factors on germination, actually the seed is exposed to multiple factors, and it seems more reasonable to assume

that the decisions are always based on several cues even when just a few experimental treatments are being applied^{22,24,27,29} (Figure 1). For example, the seed senses light incidence, amplitude of daily temperature, light/dark alternation, temperature, and osmotic potential for evaluating how deep it is in the soil or if it is at the soil surface.^{22,27} The variability on germination time and initial growth offers some room for experimentation on hidden factors that influence the seed's decisions.

The speed and amount of reserves mobilization

The speed and amount of reserves mobilization is a strategic decision that starts before external signs of germination are visible.³¹ Seeds need to spend carefully the limited amount of carbohydrates, proteins, and nutrients stored for building stem, leaves, and roots. On the one hand, if the seed promptly mobilizes its entire reserves, it will express a high vigor, emerging quickly and expanding its roots to explore a bigger volume of soil;³⁰ however, if environmental conditions are not optimal, it has a high risk that the reserves exhaust before the seedling is fully established. On the other hand, a slow rate of reserves mobilization results in delayed emergence. With additional time, the seedling has more flexibility for assessing the environment and adjusting its growth to occasional hurdles (*e.g.*: hard soil, shaded environment, drought spell, and competitors).

The three main classes of seed storage compounds are starch, protein, and lipid,^{31,34,35} and each of those classes can be mobilized in a different rate as seed's decision. Fast germination is generally associated with increased mobilization of carbohydrates and proteins.³¹ Carbohydrates and lipids compete as

source of energy and building material for the developing seedling, but different species diverge in what component is preferentially mobilized,^{31,34,35} and it is not clear if the plant's decision influence that choice or what are the trade-offs of the preference between the initial mobilization of starch or lipids.

Variability in the rate of reserves mobilization and in the fraction of total reserves that is allocated to the seedling biomass was observed among genotypes of common bean (*Phaseolus vulgaris*).³⁰ The reserves mobilization is usually slower in seeds germinating under stressful conditions, as observed in wheat (*Triticum aestivum*) under drought or salinity stress,³⁶ on common bean exposed to Cadmium toxic level,²⁶ on cashew (*Anacardium occidentale*) under NaCl stress,³⁵ and on wild poinsettia (*Euphorbia heterophylla*) in the dark.³⁴ Different classes of proteins (e.g., globulins, albumins, and prolamins) can also be mobilized at different times.³⁴ The decision regarding mobilization of reserves in response to environmental stresses is an unexplored field for experimentation. For instance, to what extent the reduced reserves mobilization in stressful environments occurs because the seed intentionally decides to save part of the reserves as a strategy to endure the stress or the mobilization of reserves is physiologically impaired by the unfavorable condition?

Trade-offs of biomass allocation

Allocation of biomass between root and shoot is another strategic decision with relevant trade-offs.³⁷ Seedlings adjust biomass allocation considering multiple cues that they sense as they grow. If the early cues are of abundant supply of water and nutrients, the seedling will likely grow less roots and allocate reserves to stem and leaves instead. If it senses a dry or chemically poor soil, reserves will be spent to grow roots. If the seed senses being very deep in the soil, the hypocotyl will require more carbon to reach the soil surface, so less biomass is allocated to the other compartments.³⁸ For example, *Paspalum wettsteinii* seedlings decided on favor of roots when the soil texture was coarser and on favor of shoot when the soil was finer.³⁹ Soybean (*Glycine max*) seedlings grew more roots when exposed to drought but decided to grow more shoot when exposed to toxic aluminum or under saline conditions.²⁴ Nanoplastics increased the biomass allocation to wheat seedling's root.⁴⁰

For another layer of complexity, the seedling may assess each nutrient separately.^{37,41} Seedlings of 97 species in a forest decided to grow more root when phosphorus was scarce, but the opposite when Nitrogen was the scarce nutrient; the light intensity magnified the influence of phosphorus favoring root growth.³⁷ *Betula pendula* seedlings favored root growth when the substrate was poor in N, P, or S, and favored shoot growth under low supply of K, Mg, or Mn; while the deficiency of Ca, Fe, and Zn did not influence the decision on biomass allocation.⁴¹

Building defensive substances is another relevant allocation decision. The seed allocates reserves to build osmotically active metabolites like proline, sugars, and polyols when it senses high salinity or drought.^{42,43} Seeds decided to increase production of malondialdehyde (MDA), superoxide dismutase (SOD), guaiacol peroxidase (POD), and ascorbate peroxidase (APX) when exposed to heavy metals.²⁸ The incidence of pathogens requires decisions by the seedling that divert energy from

growth to defense and impair its growth.⁴⁴ It should also be considered that the seed metabolism requires energy and part of the reserves is spent for respiration.³⁶ For that reason, the seedling dry weight just before the beginning of photosynthesis is smaller than the initial seed dry weight.

Seedling vigor depends on a sequence of seed decisions

Seedling vigor is an enigmatic trait that is hardly explained from the seed's measurable characteristics.³⁸ The reasons for the high variability in seed vigor are complex and remain little understood. The investigation of seed vigor as the result of a sequence of decisions made by each individual seed along germination and emergence could shed some light on the variability in seedling vigor, particularly under stressful conditions. The ideal seed vigor is defined as a high rate and uniformity of germination and emergence in a broad range of environments.³⁸ In other words, the maximal vigor requires that all the seeds decide to germinate early and at the same time regardless of the environmental conditions. Therefore, as previously discussed, a component of vigor is influenced by the individual decisions made by each germinating seed and growing seedling. Some vigor indexes also consider a calculation that includes germination rate and seedling length.^{30,45} In this case, high vigor also depends on seed's decision for fast reserves mobilization and allocation to elongation of hypocotyl and root axis.

Rice seeds had increased vigor when primed with specific salts like CaCl₂ and KCl, and the increased vigor in rice resulted from both faster germination and faster seedling growth.⁴⁵ At field conditions, seedling vigor should be observed with care. Cotton seedlings expressed reduced vigor because they had low rate of shoot growth while they decided to favor root growth for some days; the measurable vigor was lower when only shoot was being considered, but at harvest, they had similar productivity because their root capacity was stronger and compensated the low vigor observed in the early stage.⁴⁴ The initial decision that appeared unfavorable was proven beneficial at a later stage, which demonstrates the ability of cotton seedlings for strategic decisions.

Seed priming effect from the perspective of decisions

The priming effect consists in exposing the seed to controlled germinating conditions in order to trigger the pre-germinative metabolism but interrupting the process by drying the seed before it enters in full-germination. The priming conditions are optimal or under a mild stress. When planted, primed seeds have increased germination rate, seedling vigor, and improved performance under stress.^{45,46} As alternative interpretation, a primed seed makes initial decisions preparing to germinate in the environment with controlled conditions (moisture, osmotic potential, temperature, light, and nutrients); however, when the process is interrupted and the seed is later planted in a different environment, its metabolism is still influenced by the decisions that had been made in the priming environment.

Rice seeds were primed with several chemical and hormonal agents and germinated faster under chilling temperature.^{43,45} In other words, the rice seeds germinated under chilling temperature following decisions made under the priming conditions. The priming treatments were still influencing the plant's decision at the seedling stage, but to a lesser extent.⁴³ Priming effect resembles the proposed memory ability of plants.^{1,5,16}

Deciding to release from dormancy

Seed dormancy can be studied from the perspective of decision-making in complement to the traditional approach of the control exerted by morphology, hormones, genes, and environment.^{19,20,25,32,47} The hypothesis based on decision is that dormancy occurs because the seed decides postponing its germination, despite apparently favorable environmental conditions, until it senses specific environmental cues. Studies using the mechanistic approach for such a complex process are frequently inconclusive, and seed dormancy is still regarded as one of the least understood phenomena in seed biology.^{19,20,25,27,47}

Sometimes, a slight change in one of the factors triggers the seed's decision to release from dormancy.²⁵ Natural selection shaped the dormancy decision in each plant species to permit germination only when growing conditions are suitable and capable to distinguish the correct season from, for example, a short warm spell in middle of winter.³³ In order to detect correctly the cues, the influence of environment on dormancy is sometimes tricky. For example, *Fraxinus excelsior* requires a prolonged warm period followed by cold periods of stratification; however, the cold period needs to alternate with warm periods, and if the warm daily period is longer than the cold one, the dormancy is not released.²⁷ *Suaeda salsa* is a halophyte that produces two types of seeds, black, and brown, in the same plant (dimorphism). Each type of seed decides the time for germination at different time considering the soil salinity, light intensity, its own size, and the nitrogen availability.³² The mechanistic approach has a reduced precision for predicting dormancy release because it disregards factors that play only secondary roles, and the models fail to integrate large number of variables that are actually considered in the seed's decision.

The mechanisms underpinning seed and seedling's decisions are heavily based on hormones.^{19,23,25} The use of hormones and plant growth regulators in agriculture can also be regarded as a way to influence the plant's decisions by changing its perception of the environment and of its internal condition.

Experimenting with plant' strategic decisions

In addition to seed germination, experiments with strategic decisions can be run with many processes of Plant Physiology. For instance, pea plants (*Pisum sativum*) were exposed to situations of resources variability and availability to measure how they respond to risk, and they made the most

rational decision.^{2,4} The plants preferred variability when mean nutrient levels were low and the opposite when nutrients were high.

A suggested experiment on plant's strategic decisions can be derived from the example of 48 castor plants discussed in the previous section.¹⁸ Each individual in a group of young plants has its own strategy on how to grow and produce seeds (in a cultivated field or in a forest). The experiment consists in measuring how each environmental factor influences the decisions made by individual plants. After a rain or irrigation episode (or any factor that influences plant growth), one plant may decide to expand the leaf area, while another plant may keep its leaf area unchanged but grow taller. Which factors were underpinning these divergent decisions? Which are the long-term consequences of each decision (e.g., for the yield formation or biomass accumulation)? What strategy was eventually the winner? Is it possible to model and predict the plant's decision?

Abortion of reproductive structures – decisions based on the analysis of benefit/cost

This section discusses how plants make decisions that are analog to the concept of benefit/cost, a common analysis employed in finances and many other disciplines. The concept is explored here from the perspective of the plant's decision rather than financial analysis. This analytical ability seems awkward when attributed to plants because it requires a rational model, ability for data processing, and support from mathematics. However, the natural selection defined the key processes to be regulated, optimized the specific weights for the risk factors according to the output in a wide range of environmental conditions, and implemented the mechanism using the physiological tools that were available, like gene regulation, regulation of protein activity, and hormones.

In the search for increased productivity in agriculture, abortion of reproductive structures is commonly blamed as a reason for poor yield.^{48–52} Despite the incontestable detrimental impact of abortion on productivity, it should be considered that the rate of abortion of flowers, fruits, pods, or seeds is a rational plant's decision. There is extensive scientific literature on the physiology of abortion of reproductive structures, particularly on the role played by genes regulation, hormones, carbohydrates, source-sink ratio, and environmental conditions.^{51–54} Seed abortion was chosen to illustrate the benefit/cost analysis influencing plant's decisions, and the same reasoning may be employed for the abscission and abortion of all reproductive structures (flowers, pods, young fruits, and seed).

Phases of seed development

Seed development occurs in two non-overlapping phases. It will be explained later that non-overlapping these two phases is crucial for the benefit/cost decision. Phase 1 begins just after

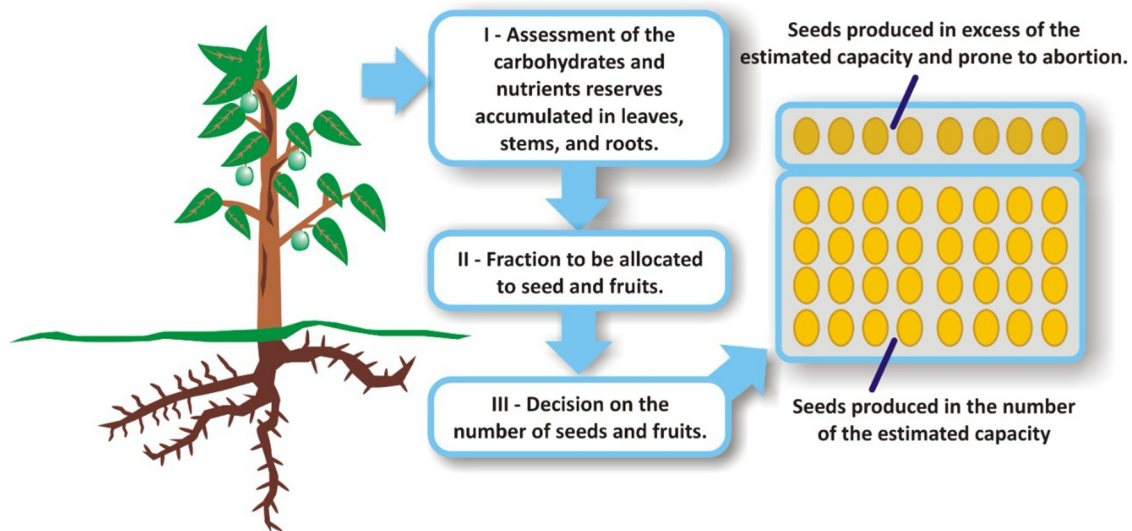


Figure 2. Schematic representation of the steps for defining the number of seeds: I – assessment of the total accumulated reserves in the plant, II – definition of the fraction to be allocated to reproductive structures, III – decision on the number of seeds or fruits to be produced, and the production of seeds in excess of the estimated capacity.

pollination and consists of cell division and expansion of the seed to about its final size.^{55–58} The important detail is that in Phase 1 the seed cells accumulate negligible amounts of carbohydrates and nutrients. In castor seed, at the end of Phase 1, although the seed has about the final size, it has just 20% of the dry weight that will be reached at maturity, and it is mostly composed of water.^{57,58} Potassium was the only nutrient found with relevant content in aborted castor seed, and the K content of an aborted seed compares to a regular and mature seed.^{59,60} Dry matter accumulation (protein, starch, oil, and nutrients) occurs only in Phase 2, which is when the seed's dry weight increases.^{56,61} Once the seed initiates Phase 2, it can no longer be aborted.^{53,57,61–64}

The number of seeds to be produced is also a decision made by the plant, and it can vary in a wide range.^{51,54,65,66} The plant assesses how much reserve (assimilated carbon and nutrients) it has stored, decides on the amount reserves that will be allocated to seed (or for reproduction in the broad sense), and then it defines how many seeds it can produce.^{48,53,67,68}

The concept of benefit/cost is employed along Phase 1. The plant has many benefits at a low cost by initiating seeds in excess of its actual capacity (Figure 2), and that is the decision often made in most plant species.^{64,66,68} The low cost occurs because along Phase 1, the plant does not allocate to the seed its valuable resources such as nutrients (only potassium)⁵⁹ and the allocation of carbohydrates is relatively small. In the other side, the benefits of initiating seeds in excess are that (i) the plant postpones by some critical weeks the final decision on how many seeds will be filled; (ii) the plant promotes a competition among developing reproductive structures in a way that seeds that are underperforming (malformed, damaged by insects or diseases, unfavorably positioned in the plant) can be discarded, and (iii) the plant can take advantage of exceptionally favorable environmental conditions that occasionally occur along the

duration of Phase 1, in a way that more seeds than initially estimated can be sustained. The reproductive structures that are confirmed to be in excess of the plant's capacity (or for any other reason) are aborted along Phase 1.^{48,51–53,64,66} When environmental conditions are not restrictive, plants that continually bear an excessive number of reproductive structures have the option to, at any moment, decide on the number of seeds that will be filled.⁶⁶ While in Phase 1 the plant has a low cost for deciding to initiate seeds in excess, before entering in Phase 2 it needs to be cautious regarding the number of seeds that will be filled because this step is costly and irreversible.

Estimation of initial seed number (before abortion) can also be based on the plant growth rate along the critical phase.⁶⁷ At that phase, the plant has just a projection of the final biomass assuming the maintenance of the current growth rate. Only at a later time, the plant is able to assess the effective accumulated biomass, and then it can decide on the number of seeds that can be filled.

Seed and fruit abortion is a plant's decision

A study on seed abortion of six varieties of castor⁶⁴ demonstrated that, on average, 12% of the seeds were aborted, varying from 7.4 to 18.1% among different genotypes. In response to a manipulation of source and sink, the number of aborted seeds increased when the source was reduced (the leaves were removed), but it did not decrease in comparison to the control treatment when the sink was reduced (competing racemes were removed). This result confirms that even when environmental conditions are favorable (abundant source) the plant keeps producing seeds in excess of its capacity. Castor plants exposed to drought had more aborted seeds (8.5%) than well-watered plants (3.1%), confirming that the plant decides increasing the abortion rate aiming to reduce the number of seeds to be filled

when environmental conditions are unfavorable. The biomass allocated to the 12% of aborted castor seeds (in number) represent no more than 2.5% of the total biomass (in weight) allocated to seed production. This is a quantification of how little assimilated carbon is actually wasted through seed abortion. The hypothesis is that wasting 2.5% of biomass pays off the benefits of that plant's strategy.

The influence of environmental conditions on abortion rate of reproductive structures was observed in response to drought, shade, plant density, and leaf pruning in pepper (*Capsicum annuum* L.),^{51,53} birdsfoot trefoil (*Lotus corniculatus*),⁶⁶ corn (*Zea mays*),⁴⁸ and chickpea (*Cicer arietinum* L.).⁵² The plants of birdsfoot trefoil had the same rate of abortion when resources were either depleted or abundant,⁶⁶ but pepper plants adjusted the abortion rate to the source-sink balance.⁵¹ The plants of chickpea increased the abortion rate after being exposed to drought, and the young fruits or those positioned in secondary branches were more likely to be aborted.⁵² The observation that full-sized pods (supposedly in Phase 2 of seed development) of chickpea are never aborted⁵² can be alternatively interpreted as: it is not a smart decision to abort a pod after having spent carbohydrates and nutrients to partially fill it. In another study, drought-stressed corn plants partially reverted the abortion rate of ovaries when sucrose was artificially fed to the stem.⁴⁸ This observation can be alternatively interpreted as: the corn plant sensed two diverging cues: some signals inform that the plant is under drought stress, while the sugar content (applied as an experimental treatment) informs that carbohydrates are available; so, the plant made an intermediate decision by maintaining the development of a number of seed balanced between the perceived sugar availability and the perception of drought.

Gaps in the knowledge regarding reproductive partitioning

The complexity of the decisions regarding abortion of reproductive structures is one of the weak points of crop growth models when predicting productivity because simulations based only on source-sink ratio are not accurate.^{51,68} For instance, the decision regarding abortion is made considering not only photosynthates availability, but it also considers the reserves of nutrients.⁵³ Experimenting on abortion as a plant's decision would make models more open to the multiple factors influencing this physiological process, including plant-to-plant variability and patchiness of environmental conditions.

It is questionable to what extent abortion can be blamed for the reduced fruit set and seed yield of cultivated plants, as usually assumed. In fact, abortion is just an adjustment of the plant's sink to its real source capacity.^{51,53} If heat or drought stress increases fruit abortion rate, the reason for the reduced yield is the stress, and not the plant's decision for the abortion.

Experimenting with plant's decisions on benefit/cost

In addition to abortion of reproductive structures, resuming growth in spring in temperate environments is another example of decision with benefit/cost implications. The plant decides resuming growth after the winter when it senses a rise in air temperature (among other cues). The plant that sprouts earlier

has an advantage in relation to the competitors that remain dormant. However, there is a high risk that the re-growth is too early, if a false-spring is followed by freezing temperatures.^{3,69} This question was analyzed from the perspective of risk and probability,⁶⁹ and it could also be analyzed considering the costs of losing the biomass spent in a failed early growth compared with the benefits of starting ahead. Are the plants deciding their sprouting time assuming a level of risk appropriate to an environment under changing climate? Which other variables does the plant considers for making the decision to resume growth?

Another suggestion of experiment involves decisions regarding leaf morphology. There are many decisions that need to be made regarding leaf thickness, leaf area, nitrogen content per leaf area, and nitrogen allocation.⁷⁰⁻⁷² Light interception depends on the leaf area, and the plant may decide to grow larger leaves if harvesting more light is needed (like in a low irradiance environment). However, growing many leaves has a cost. The photosynthesis rate depends on the Nitrogen content per leaf area and leaf thickness⁷⁰⁻⁷² in a way that spending the same amount of carbohydrates and Nitrogen the plant can choose either building large leaves with low photosynthetic rate or building small leaves with high photosynthetic rate. There are different protein pools in which Nitrogen can be allocated, like the light harvesting proteins (associated with chlorophyll), electron transport, Rubisco, and structural proteins.^{70,71} The adequate balance between those pools depends on environmental factors, and it is hypothesized that plants decide among them based on the benefit and cost of each option. This introductory discussion on leaf morphology is an oversimplification because many other factors are actually involved in those decisions.

A proposed experiment would be measuring the cost and benefits involved in the decisions regarding leaf configuration (leaf area, leaf thickness, and nitrogen allocation) among plants exposed to treatments of light, water availability, and nutrients. If the environment changes, to what extent can plants change configurations in the same leaf and among leaves in the same plant? Which leaf traits are flexible for plant's decisions and what cannot be adjusted?

Regulation of photosynthesis – decisions for optimization of complex processes

Another aspect of plant's decisions is the ability to optimize very complex processes. Regulation of photosynthesis is discussed in this section to illustrate that aspect of decision-making. Photosynthesis was chosen because it is regarded as the most intricate physiological processes in plants.

The photosynthetic mechanism is up- and downregulated by a long list of variables: stomatal conductance, leaf and air temperature, rate of photorespiration, activity of Rubisco, carboxylation efficiency, inhibition of ATPase, pH of the thylakoid lumen, redox state of the plastoquinone, water potential in the leaf and in the soil, light intensity and quality, phototropin, sink strength, hydrogen peroxide, inorganic Phosphate (P_i), nitrogen to carbon balance, sucrose level, starch accumulation in the vacuole, infection of pathogens, and attack of insects, cytokinin,

abscisic acid, nutritional status of the whole plant, xylem sap pH, xylem hydraulic conductance, farnesyltransferase activity, vapor pressure deficit, sub-stomatal (C_i) and atmospheric CO_2 concentration, reactive oxygen species (ROS), and circadian cycle.^{73–85} All the factors influencing photosynthesis are interconnected with cross-talks and feedbacks. The control of stomatal conductance itself is not completely elucidated, as there is a wide variability in the effect, such as in the response to elevated CO_2 ⁷⁴ or in the relationship between temperature and water use efficiency.⁸⁰ The variability on data related to photosynthesis is so high that researchers predominantly need to make measurements in a specific time of the day (e.g., around noon), in leaves located in one specific position (completely exposed to sun radiation, usually recently developed in the top of the plant), and at full sunlight (avoiding cloud days).^{77,85,86} The measurement of photosynthesis and gas exchange made in specific leaves, in a small leaf area, and in a short time is very useful for deciphering the physiological mechanisms, but they are poorly related to the real CO_2 assimilation integrated in the whole canopy and along the plant's growth.⁸⁶

Photosynthesis and leaf temperature

It is well known that each species has a temperature range for optimal photosynthesis, like 20–25°C for wheat, 25–30°C for rice (*Oryza sativa*) and barley (*Hordeum vulgare*),

and 25–29°C for cotton (*Gossypium hirsutum*).^{80,87–89} Observing the leaf and canopy temperature with a thermal camera under different environmental conditions, it is noticeable that to some extent the plant influences its own temperature in a logical manner. Thus, the hypothesis proposed here is that the intricate regulation of photosynthesis is a mechanism by which leaves make customized decisions considering internal and external conditions. Such mechanism provides that the decisions are fine-tuned along the day.

Assuming that temperature is a key factor influencing photosynthesis rate,^{77,80,81,83,84} the plasticity of adjustments in photosynthesis is illustrated with thermal pictures. The author disclaims that the pictures presented in this section are not a scientific experiment, but just observations that are coherent with the proposed plant's ability to make decisions for optimization of photosynthesis. Careful experimentation with this subject will be required for a scientific conclusion.

The pictures were taken using a Flir One Pro® camera in a rainfed cotton field in Alagoinha, Brazil (6.965 S, 35.551 W), between April and June/2020. The plants received no experimental treatment. The hypothesis is that each photosynthesizing cell actively adjusts stomatal conductance to influence its own temperature, making decisions that optimize the balance between carbon assimilation and water use. Leaf temperature results from the energy balance between the entrance of heat through sun radiation incidence and loss of heat through evaporation and convection.^{83,84,86,88,89} There are other minor



Figure 3. Visible and thermal pictures of cotton plants. Illustration of the ability of leaves to make decisions that are customized for each point of the photosynthesizing area aiming to adjust temperature and balancing between carbon assimilation and water transpiration. (A) Young cotton plant with limited variation in temperature across the canopy contrasting with the warm soil. (B) Cotton leaf with areas under both shaded and lit with intense irradiance and temperatures varying from 29.6 to 35.9°C in the leaf blade. (C) Cotton plants with high contrast in temperatures between leaves in the top and in the middle of the canopy despite both being lit by direct sun radiation. (D) Contrasting temperatures between the reproductive structures (34.5°C) that transpire poorly and the transpiring leaf (31.1°C) that actively adjusts its temperature.

components in the heat balance that are not being considered. The leaf adjusts the stomatal conductance to keep the temperature in the optimal range whenever it is possible.⁸⁴

Decisions for optimization of photosynthesis

A young cotton plant with plenty supply of water and in the phase of fast growth manages to adjust the temperature of all leaves to the optimal range of 27 to 30°C (Figure 3a). Despite the difference in irradiance from the top to the bottom, each leaf adjusted the stomatal conductance to keep the temperatures in the optimal range. It is supposed that the shaded leaf in the bottom has a lower photosynthesis rate than the leaf on the top, but both are adjusted to the optimal temperature range and assimilating carbon in the highest rate possible for their specific conditions. The soil receiving the same irradiance of the top leaf is warmer (40.5°C), and the difference between the soil and the leaf is attributed to leaf transpiration. The petioles are warmer than leaf blades because they lack stomata and cannot decide on their temperature.

Assuming that, to some extent, plants decide on their own temperature opposes to the general assumption that plants are poikilotherm, which are organisms unable to control their own temperature. In fact, plants can influence the leaf temperature to a limited extent. Leaf temperature of forest trees was found to deviate from the surrounding air temperature in a wide range of latitudes, from subtropical to boreal environments.⁹⁰ The leaf-to-air temperature deviation occurred when photosynthesis was active. Cooling the leaf depends on water for transpiration and warming up the leaf depends on sun radiation. When both components are available, the leaf is able to actively adjust its temperature up and down.

The hypothesis of active control of temperature was previously observed in cotton plants.⁸⁹ In that study, even when air temperature reached 40°C, the cotton leaves managed to remain in the optimal range, provided that water was available in the soil. The consistent difference between air and leaf temperatures was also observed in several forest tree species, in which the gradient was either positive or negative always bringing leaves to the optimal range.⁸⁴ Models of photosynthesis estimation may become biased if the active influence of plant's decision on temperature is disregarded.⁸³

The temperature in a single leaf blade can vary in a wide range (Figure 3b). The hypothesis is that each photosynthesizing cell makes its own customized decision operating the complex mechanism that integrates environmental and plant's internal conditions. The leaf (Figure 3b) is lit with intense sun radiation, and the temperature reached 35.9°C in the region around the main vein, while in the edges of the leaf blade, despite being lit by the same intense radiation, the temperature was adjusted to the optimal range. In both the shaded region (white circle in Figure 3b) and in the target sign, the temperature was adjusted to 29.6°C. The temperatures are similar on the leaf tip under intense radiation and on the shaded area, despite the contrasting irradiance between those two points. Keeping the temperatures in the optimal range requires active and precise tuning of the stomatal conductance, as proposed for the desert plant *Citrullus colocynthis*.⁹¹ The decision to adjust contrasting temperatures in different points of the leaf

blade supposedly optimizes the photosynthesis considering the environment variables and internal condition of each point of the leaf (Figure 3b).

Photosynthesis regulation offers many questions and hypothesis regarding plant's decisions that could be subjected to scientific experimentation. A study on isotopic composition of cellulose in trees⁹⁰ found that despite variations in mean air temperature across a wide range of latitudes, photosynthesis predominantly occurred when leaf temperature was in a narrow range of temperatures, which was estimated as $21.4 \pm 2.2^\circ\text{C}$. The importance of this result is that the leaf temperature is not in this narrow range at all the time, but specifically when the photosynthesis is active. This observation corroborates the hypothesis of active regulation of temperature for optimization of photosynthesis.

Another aspect of the mechanism of decisions for optimization of photosynthesis is that different leaves in the same plant and at the same time can make diverging decisions. A cotton plant under drought, heat, and light stress (these conditions were not measured but assumed based on observation) has some leaves at 27.5°C and others at 33.1°C (Figure 3c). Shaded leaves adjusted to the optimal range for photosynthesis, while the leaves directly lit by sun radiation were allowed to reach temperatures above 30°C. When water supply is limited in the soil, it is not possible to transpire at a rate enough to reduce the temperature of leaves under intense radiation. Nevertheless, the plant can perform a low-rate photosynthesis in shaded leaves with optimized water use efficiency. Under controlled conditions, synchronism in the adjustment of stomatal conductance and assimilation rate was observed in cotton leaves of similar age and conditions⁸⁵ implying that there are some cues that to some extent influence all the leaves at same time. The plant's decision integrates the cues that affect all the leaves with variables that are specific to each point in the leaf.

The photosynthetic apparatus resists temperatures as high as 44°C,⁸⁶ so that plants can decide to allow leaves to reach high temperatures during some hours along the day and transpire only when the photosynthesis may occur with higher water use efficiency. Non-photosynthesizing structures are not able to adjust its temperature. The leaf blade is at 31.1°C while bracts and petioles are at 34.5°C (Figure 3d). Although cotton bracts have a few stomata, they usually have low conductance⁹² and do not transpire in a rate enough to cool it.

It is a common place in the scientific literature on photosynthesis that the attempts to explain or model all parameters of carbon assimilation fail to reach precise estimations.^{73,74,76,80,81,83,87} Maybe it happens because experiments are predominantly made with a reductionist approach that limits a few factors to be analyzed, while the plant actually decides based on large number of cues with interactions arranged in a structure that can hardly be fixed, controlled, or even estimated. The proposal of this section is that many scientific hypotheses can be tested around the approach that the regulation of photosynthesis is an active process of decision-making that integrates the multiple mechanisms discussed in the literature. The suggestion is not for replacing or competing with the predominant method of experimentation,

but just considering the possibility for other perspectives in the definition of hypothesis and interpretation of scientific observations.

Experimenting with decisions for optimization of complex processes

There are limited reports in the literature that can be used to check the hypothesis of decisions for optimization of photosynthesis. Suggestions of experiments for that objective consists in manipulations of environmental conditions at leaf or plant level followed by observation in changes of temperature and other related variables. As observed in [Figure 3b](#), leaf disks can be sampled at different points of a leaf blade exposed to the same sun radiation but displaying contrasting temperatures. These disks can be analyzed for composition or characteristics that influence the decision on temperature (like thickness, moisture content, starch content, hormones, genes, and enzymes activity etc.). A half of the leaf can be shaded (to varying intensity) while the other remains at full radiation to measure the changes in temperature. The change in temperature can be recorded for estimation on the time that leaves require to adjust stomatal conductance to a sudden change in irradiance. A cooling object or wind can be applied to a small area below a sunlit leaf blade to estimate if the leaf is able to customize stomatal conductance for that point and keep it in the optimal range.

In addition to photosynthesis, experiments are also suggested for investigations on hormones, which are another complex research field. Hormones are involved in every aspect of plant growth and development,⁹³ and most of the plant's decisions discussed in this paper are mediated by hormone signaling. The role played by each hormone is being progressively elucidated, but their overall action is extremely complex because the biosynthesis, transport, degradation, and effect of each hormone are interrelated by synergistic or antagonistic cross-talk with the others hormones,^{93,94} besides the interaction with enzymes, genes, and many other substances. Unraveling hormone roles is also challenging because the same hormone may influence many different physiological processes at the same time. Besides the substances that are presently recognized as plant hormones, it is likely that many other hormones are yet to be discovered.⁹³

For example, hormones play an important role in the phenomenon in which the fruits developing in the same branch have a kind of hierarchy.⁵⁴ The so-called “king fruit” has reduced probability of abscission in comparison with the dominated fruits, which are more likely to suffer abscission. However, just the balance between auxins and ethylene is not enough to explain how abscission is controlled.⁵⁴ This kind of phenomenon can be investigated testing hypotheses based on the plants' ability to make optimizing decisions and integrating other factors from the environment and the plant's internal conditions that actually are involved in the decision for fruit abscission. Interactions of hormones with anatomical characteristics can be investigated, like in influence of the angle of basal cutting influencing rooting pattern of *Jatropha curcas* plant.⁹⁵ In addition to the specific role played by each

hormone, investigations should also elucidate why the plant made each decision. Beside the mechanisms that underpin the decisions, there is useful scientific information in the reasons and consequences of each plant's decision.

Methods for experimenting with plant's decisions

In the absence of methods for experimenting with plant's decisions, there are many frameworks and quantitative methods employed for the study of the decision-making process in areas like Psychology, Medicine, Business Administration, Engineering, Design, Education, Logistics, Public Transport, and Computing.^{3,96–105} These tools are not commonly adopted in Plant Science because it is not usual considering that plants make decisions. Just like other branches of science adopted quantitative methods to cope with the high complexity of decisions, many aspects of Plant Science could also enrich their possibilities exploring the ability of plants to make smart decisions and taking advantage of its integration power and the mature tools that can be borrowed from other disciplines.

The Judgment and Decision-Making is a model developed for human's decisions.^{3,103} It proposes that a decision follows the phases of (i) information, (ii) judgment (discrimination, categorization, assessment, and recognition), (iii) decision (preference, choice), and finally (iv) action. Although developed for humans, this framework can be employed for plants³ with the due precaution to interpret it as analogy because plants cannot express things like recognition and preference in the way that people do.

The Analytic Hierarchy Process (AHP) is a multicriteria decision-making tool employed in many areas, like the choice of a project to be funded, the location for a store, or the road to be repaired.^{104,105} In the traditional use of AHP, all the variables that can potentially influence the decision are identified and sorted according to an arbitrary hierarchy or to the perceived structure of relation between the variables and the decision. Each variable is assigned with a quantitative weight for ponderation of its influence in the final decision. The value of each variable (judgment) is measured or determined by stakeholders or experts in the issue. The method is flexible to accept that in exceptional situations, one variable may overrule the others. AHP can also be combined with other methods such as Linear Programming, Quality Function Deployment, and Fuzzy Logic.¹⁰⁵ For studies with plants, AHP should be applied backward because the decisions are actually made by the plant. The observer may register the plant's decisions and tests hypothesis on what are the variables driving the decision, what is the hierarchy or structure of the variables, and what are the weights for ponderation.

The Pugh Matrix or “decision-matrix” is a technique used to support decisions that involve qualitative traits.¹⁰² The matrix is arranged with the list of possible decisions in the columns and the set of criteria in the lines. One of the options is assigned as the reference, and the other options are compared to the reference with judgments of better, equal, or worse (or +, =, -). The frequency of better or worse is just counted, without further ponderation or calculation. This technique can be applied for plant's decisions also in the backward direction, having the plant's decision as input, and the set of criteria as proposed

hypotheses to be tested. This method is an option for experimenting with plant's qualitative traits like color, shapes, texture, dark/light, and many other aspects that are not quantitative.

These are just three methods among many available for supporting the process of decision-making. They are just briefly commented, and their use in Plant Science requires further work. The intention here is just to call attention to the possibility of borrowing techniques that were originally developed for other disciplines.

Conclusions

This review article proposes that plants make decisions and that scientists would be exposed to new perspectives if experiments were based on hypothesis about plant's decisions. It also discussed that plant's decision may contain elements like strategy, benefit/cost analysis, and optimization of intricate variables. This approach is more open for the complexity of environment compared with the traditional method of reducing the studies to a few variables that can be controlled.

Scientists predominantly dedicate research efforts to explain details of the mechanisms involved in the plant's response, like the genes, proteins, hormones, nutrients, and the physiological interactions. Scientific investigation on the plant's decision itself could be promoted without prejudice to the prevalent method. In observations to which scientists are unable to offer a detailed explanation of the physiological mechanism, they should be encouraged to consider the decision made by the plant as the experimental subject and move forward to explore another pool of information that otherwise would not be accessed.

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References

- Castiello U. (Re)claiming plants in comparative psychology. *J Comp Psychol.* 2021;135:127–141. <http://dx.doi.org/10.1037/com0000239>.
- Dener E, Kacelnik A, Shemes H. Pea plants show risk sensitivity. *Curr Biol.* 2016;26:1763–1767. <https://doi.org/10.1016/j.cub.2016.05.008>.
- Karban R, Orrock JL. A judgment and decision-making model for plant behavior. *Ecology.* 2018;99:1909–1919. <https://doi.org/10.1002/ecy.2418>.
- Schmid B. Decision-making: are plants more rational than animals? *Curr Biol.* 2016;26:R675–R678. doi:10.1016/j.cub.2016.05.073.
- Trewavas A. Awareness and integrated information theory identify plant meristems as sites of conscious activity. *Protoplasma.* 2021;258:673–679. <https://doi.org/10.1007/s00709-021-01633-1>.
- Van Volkenburgh E, Mirzaei K, Ybarra Y. Understanding plant behavior: a student perspective. *Trends Plant Sci.* 2021;26:423–424. doi:10.1016/j.tplants.2021.02.012.
- Taiz L, Alkon D, Draguhn A, Murphy A, Blatt M, Thiel G, Robinson D.G. Reply to Trewavas et al. and Calvo and Trewavas. *Trends Plant Sci.* 2020;25:218–220. doi:10.1016/j.tplants.2019.12.020.
- Baluška F, Mancuso S. Plant neurobiology as a paradigm shift not only in the plant sciences. *Pant Signal Behav.* 2007;2:205–207. <https://doi.org/10.4161/psb.2.4.4550>.
- Taiz L, Alkon D, Draguhn A, Murphy A, Blatt M, Hawes C, Thiel G, Robinson DG. Plants neither possess nor require consciousness. *Trends Plant Sci.* 2019;24:677–687. doi:10.1016/j.tplants.2019.05.008.
- Schmidhuber J. Deep Learning in neural networks: an overview. *Neural Networks.* 2015;61:85–117. doi:10.1016/j.neunet.2014.09.003.
- Mallatt J, Blatt MR, Draguhn A, Robinson DG, Taiz L. Debunking a myth: plant consciousness. *Protoplasma.* 2020;258:459–476. doi:10.1007/s00709-020-01579-w.
- Robinson DG, Draguhn A, Taiz L. Plant “intelligence” changes nothing. *EMBO Rep.* 2020;21:e50395. <https://doi.org/10.15252/embr.202050395>.
- Calvo P, Trewavas A. Physiology and the neurobiology of plant behavior: a farewell to arms. *Trends Plant Sci.* 2020;3:214–216. doi:10.1016/j.tplants.2019.12.016.
- Maher C. Experiment rather than define. *Trends Plant Sci.* 2020;25:213–214. doi:10.1016/j.tplants.2019.12.014.
- Calvo P, Baluška F, Trewavas A. Integrated information as a possible basis for plant consciousness. *Biochem Biophys Res Commun.* 2021;564:158–165. <https://doi.org/10.1016/j.bbrc.2020.10.022>.
- Galviz YCF, Ribeiro RV, Souza GM. Yes, plants do have memory. *Theor Exp Plant Physiol.* 2020;32:195–202. doi:10.1007/s40626-020-00181-y.
- Bose JC. The nervous mechanism of plants. London, UK: Longmans Green and Co; 1926.
- Severino LS, Auld DL, Vale LS, Marques LF. Plant density does not influence every castor plant equally. *Ind Crops Prod.* 2017;107:588–594. <https://doi.org/10.1016/j.indcrop.2017.05.061>.
- Kucera B, Cohn MA, Leubner-Metzger G. Plant hormone interactions during seed dormancy release and germination. *Seed Sci Res.* 2005;15:281–307. <https://doi.org/10.1079/SSR2005218>.
- Koornneef M, Bentsink L, Hilhorst H. Seed dormancy and germination. *Curr Opin Plant Biol.* 2002;5:33–36. doi:10.1016/S1369-5266(01)00219-9.
- Nguyen CD, Chen J, Clark D, Perez H, Huo HA. Effects of maternal environment on seed germination and seedling vigor of *Petunia × hybrida* under different abiotic stresses. *Plants.* 2021;10:1–13. doi:10.3390/plants10030581.
- Chauhan BS, Johnson DE. Influence of environmental factors on seed germination and seedling emergence of ecleipta (*Eclipta prostrata*) in a tropical environment. *Weed Sci.* 2008;56:383–388. doi:10.1614/WS-07-154.1.
- Xiao S, Liu L, Wang H, Li D, Bai Z, Zhang Y, Sun H, Zhang K, Li C, Li C. Exogenous melatonin accelerates seed germination in cotton (*Gossypium hirsutum* L.). *PlosOne.* 2019;14:e0216575. doi:10.1371/journal.pone.0216575.
- Steiner F, Zuffo AM, Teodoro PE, Aguilera JG, Teodoro LPR. Multivariate adaptability and stability of soya bean genotypes for abiotic stresses. *J Agron Crop Sci.* 2021;207:354–361. <https://doi.org/10.1111/jac.12446>.
- Finkelstein R, Reeves W, Ariizumi T, Steber C. Molecular aspects of seed dormancy. *Annu Rev Plant Biol.* 2008;59:387–415. <https://doi.org/10.1146/annurev.arplant.59.032607.092740>.
- Sfafi-Bousbih A, Chaoui A, Ferjani EE. Cadmium impairs mineral and carbohydrate mobilization during the germination of bean seeds. *Ecotox Environ Safe.* 2010;73:1123–1129. <https://doi.org/10.1016/j.ecoenv.2010.01.005>.
- Finch-Savage WE, Leubner-Metzger G. Seed dormancy and the control of germination. *New Phytol.* 2006;171:501–523. doi:10.1111/j.1469-8137.2006.01787.x.

28. Sethy S, Ghosh S. Effect of heavy metals on germination of seeds. *J Nat Sci Biol Med.* 2013;4:272–275. <https://doi.org/10.4103/0976-9668.116964>.
29. Neto VG, Ribeiro PR, Del-Bem LE, Bernal DT, Lima STC, Ligterink W, Fernandez LG, Castro RD. Characterization of the superoxide dismutase gene family in seeds of two *Ricinus communis* L. genotypes submitted to germination under water restriction conditions. *Environ Exp Bot.* 2018;155:453–463. <https://doi.org/10.1016/j.envexpbot.2018.08.001>.
30. Padilha MS, Coelho CMM, Andrade GC. Seed reserve mobilization evaluation for selection of high-vigor common bean cultivars. *Rev Caatinga.* 2020;33:927–935. <https://doi.org/10.1590/1983-21252020v33n407rc>.
31. Zhao M, Zhang H, Yan H, Qiu L, Baskin CC. Mobilization and role of starch, protein, and fat reserves during seed germination of six wild grassland species. *Front Plant Sci.* 2018;9:234. <https://doi.org/10.3389/fpls.2018.00234>.
32. Li W, Liu X, Khan MA, Yamaguchi S. The effect of plant growth regulators, nitric oxide, nitrate, nitrite and light on the germination of dimorphic seeds of *Suaeda salsa* under saline conditions. *J Plant Res.* 2005;118:207–214. doi:10.1007/s10265-005-0212-8.
33. Fernández-Pascual E, Carta A, Mondoni A, Cavieres LA, Rosbakh S, Venn S, Satyanti A, Guja L, Briceño VF, Vandeloek F, et al. The seed germination spectrum of alpine plants: a global meta-analysis. *New Phytol.* 2021;229:3573–3586. doi:10.1111/nph.17086.
34. Suda CNK, Giorgini JF. Seed reserve composition and mobilization during germination and initial seedling development of *Euphorbia heterophylla*. *Rev Bras Fisiol Veg.* 2000;12:226–244. doi:10.1590/s0103-3131200000300006.
35. Voigt EL, Almeida TD, Chagas RM, Ponte LFA, Viégas RA, Silveira JAG. Source-sink regulation of cotyledonary reserve mobilization during cashew (*Anacardium occidentale*) seedling establishment under NaCl salinity. *J Plant Physiol.* 2009;166:80–89. doi:10.1016/j.jplph.2008.02.008.
36. Soltani A, Gholipour M, Zeinali E. Seed reserve utilization and seedling growth of wheat as affected by drought and salinity. *Environ Exp Bot.* 2006;55:195–200. <https://doi.org/10.1016/j.envexpbot.2004.10.012>.
37. Umaña MN, Cao M, Lin L, Swenson NG, Zhang C. Trade-offs in above- and below-ground biomass allocation influencing seedling growth in a tropical forest. *J Ecol.* 2021;109:1184–1193. <https://doi.org/10.1111/1365-2745.13543>.
38. Finch-Savage WE, Bassel GW. Seed vigour and crop establishment: extending performance beyond adaptation. *J Exp Bot.* 2016;67:567–591. doi:10.1093/jxb/erv490.
39. Wang Y, Huang X, Cai LP, Zheng HX, Hou XL, Zhou CF, Zhang H, Huang PP, Hua C. Effects of soil particle composition on seed germination and seedling growth of *Paspalum wettsteinii* under different temperatures. *Cao Ye Xue Bao.* 2018;27:45–55. doi:10.11686/cyxb2018012.
40. Lian J, Wu J, Xiong H, Zeb A, Yang T, Su X, Su L, Liu W. Impact of polystyrene nanoplastics (PSNPs) on seed germination and seedling growth of wheat (*Triticum aestivum* L.). *J Hazard Mater.* 2020;385:121620. doi:10.1016/j.jhazmat.2019.121620.
41. Ericsson T. Growth and shoot: root ratio of seedlings in relation to nutrient availability. *Plant Soil.* 1995;168:205–214. doi:10.1007/BF00029330.
42. Al-Farsi SM, Nawaz A, Ahmad A, ur-Rehman SK, Nadaf AM, Al-Sadi KHM, Farooq SM. Effects, tolerance mechanisms and management of salt stress in lucerne (*Medicago sativa*). *Crop Pasture Sci.* 2020;71:411–428. doi:10.1071/CP20033.
43. Hussain S, Khan F, Hussain HA, Nie L. Physiological and biochemical mechanisms of seed priming-induced chilling tolerance in rice cultivars. *Trends Plant Sci.* 2016;7:116. doi:10.3389/fpls.2016.00116.
44. Bourland F. Functional characterization of seed and seedling vigor in cotton. *J Cotton Sci.* 2019;23:168–176.
45. Anwar MP, Jahan R, Rahman MR, Islam AKMM, Uddin FMJ. Seed priming for increased seed germination and enhanced seedling vigor of winter rice. *IOP. C Ser Earth Env.* 2021;756:012047. <https://doi.org/10.1088/1755-1315/756/1/012047>.
46. Paparella S, Araújo SS, Rossi G, Wijayasinghe M, Carbonera D, Balestrazzi A. Seed priming: state of the art and new perspectives. *Plant Cell Rep.* 2015;34:1281–1293. doi:10.1007/s00299-015-1784-y.
47. Longo C, Holness S, De Angelis V, Lepri A, Occhigrossi S, Ruta V, Vittorioso P. From the Outside to the Inside: new insights on the main factors that guide seed dormancy and germination. *Genes.* 2021;12:52. doi:10.3390/genes12010052.
48. Boyer JS, Westgate ME. Grain yields with limited water. *J Exp Bot.* 2004;55:2385–2394. <https://doi.org/10.1093/jxb/erh219>.
49. Arshad MS, Farooq M, Asch F, Krishna JSV, Prasad PVV, Siddique KHM. Thermal stress impacts reproductive development and grain yield in rice. *Plant Physiol Biochem.* 2017;115:57–72. <https://doi.org/10.1016/j.plaphy.2017.03.011>.
50. Ruan Y-L, Patrick JW, Bouzayen M, Osorio S, Fernie AR. Molecular regulation of seed and fruit set. *Trends Plant Sci.* 2012;17:656–665. doi:10.1016/j.tplants.2012.06.005.
51. Marcelis LFM, Heuvelink E, Hofman-Eijer LRB, Bakker JD, Xue LB. Flower and fruit abortion in sweet pepper in relation to source and sink strength. *J. Exp. Bot.* 2004;55:2261–2268. <https://doi.org/10.1093/jxb/erh245>.
52. Fang X, Turner NC, Yan G, Li F, Siddique KMH. Flower numbers, pod production, pollen viability, and pistil function are reduced and flower and pod abortion increased in chickpea (*Cicer arietinum* L.) under terminal drought. *J Exp Bot.* 2010;61:335–345. doi:10.1093/jxb/erp307.
53. Wubs AM, Heuvelink E, Marcelis LFM, Hemerik L. Survival analysis of flower and fruit abortion in sweet pepper. *Acta Hort.* 2007;764:617–624. doi:10.17660/ActaHortic.2007.761.86.
54. Bangerth F. Abscission and thinning of young fruit and their regulation by plant hormones and bioregulators. *Plant Growth Regul.* 2000;31:43–59. doi:10.1023/a:1006398513703.
55. Egli DB. The role of seed in the determination of yield of grain crops. *Aust J Agric Res.* 2006;57:1237–1247. <https://doi.org/10.1071/AR06133>.
56. Munier-Jolain NG, Ney B. Seed growth rate in grain legumes II. Seed growth rate depends on cotyledon cell number. *J Exp Bot.* 1998;49:1971–1976. <https://doi.org/10.1093/jxb/49.329.1971>.
57. Severino LS, Auld DL. Study on the effect of air temperature on seed development and determination of the base temperature for seed growth in castor (*Ricinus communis* L.). *Aust J Crop Sci.* 2014;8:290–295.
58. Vallejos M, Rondanini D, Wassner DF. Water relationships of castor bean (*Ricinus communis* L.) seeds related to final seed dry weight and physiological maturity. *Eur J Agron.* 2011;35:93–101. doi:10.1016/j.eja.2011.04.003.
59. Lucena AMA, Severino LS, Beltrão NEM, Bortoluzi CRD. Physical and chemical characterization of seeds of castor oil plant cv. BRS Nordestina by coat cColor. *Revista Brasileira de Oleaginosas e Fibrosas.* 2010;14:83–90.
60. Severino LS, Auld DL. A framework for the study of the growth and development of castor plant. *Ind. Crops Prod.* 2013;46:25–38. <https://doi.org/10.1016/j.indcrop.2013.01.006>.
61. Egli DB. Seed biology and the yield of grains. New York, NY, USA: Cab International; 1998.
62. Duthion C, Pigeaire A. Seed lengths corresponding to the final stage in seed abortion of three grain legumes. *Crop Sci.* 1991;31:1579–1583. doi:10.2135/cropsci1991.0011183X003100060040x.
63. Ney B, Duthion C, Turc O. Phenological response of pea to water stress during reproductive development. *Crop Sci.* 1994;34:141–146. doi:10.2135/cropsci1994.0011183X003400010025x.
64. Severino LS, Auld DL. Seed abortion and the individual weight of castor seed (*Ricinus communis* L.). *Ind Crops Prod.* 2013;49:890–896. doi:10.1016/j.indcrop.2013.06.031.

65. Severino LS, Auld DL. Seed yield and yield components of castor influenced by irrigation. *Ind Crops Prod.* 2013;49:52–60. doi:10.1016/j.indcrop.2013.04.012.
66. Stephenson AG. The regulation of maternal investment in an indeterminate flowering plant (*Lotus corniculatus*). *Ecology.* 1984;65:113–121. doi:10.2307/1939464.
67. Vega CRC, Andrade FH, Sadras VO. Reproductive partitioning and seed set efficiency in soybean, sunflower and maize. *Field Crops Res.* 2001;72:163–175. doi:10.1016/S0378-4290(01)00172-1.
68. Vega CRC, Andrade FH, Sadras VO, Uhart SA, Valentinuz OR. Seed number as a function of growth. A comparative study in soybean, sunflower, and maize. *Crop Sci.* 2001;41:748–754. <https://doi.org/10.2135/cropsci2001.413748x>.
69. Augspurger CK. Reconstructing patterns of temperature, phenology, and frost damage over 124 years: spring damage risk is increasing. *Ecology.* 2013;94:41–50. doi:10.1890/12-0200.1.
70. Evans JR, Poorter H. Photosynthetic acclimation of plants to growth irradiance: the relative importance of specific leaf area and nitrogen partitioning in maximizing carbon gain. *Plant Cell Environ.* 2001;24:755–767. doi:10.1046/j.1365-3040.2001.00724.x.
71. Evans JR. Photosynthesis and nitrogen relationships in leaves of C3 plants. *Oecologia.* 1989;78:9–19. <https://doi.org/10.1007/BF00377192>.
72. Vile D, Garnier E, Shipley B, Laurent G, Navas M-L, Roumet C, Lavorel S, Diaz S, Hodgson JG, Lloret F, et al. Specific leaf area and dry matter content estimate thickness in laminar leaves. *Ann Bot.* 2005;96:1129–1136. <https://doi.org/10.1093/aob/mci264>.
73. Medrano H, Escalona JM, Bota J, Gulías J, Flexas J. Regulation of photosynthesis of C3 plants in response to progressive drought: stomatal conductance as a reference parameter. *Ann Bot.* 2002;89:895–905. doi:10.1093/aob/mcf079.
74. Leakey A, Ainsworth EA, Bernacchi CJ, Rogers A, Long SP, Ort DR. Elevated CO₂ effects on plant carbon, nitrogen, and water relations: six important lessons from FACE. *J Exp Bot.* 2009;10:2859–2876. doi:10.1093/jxb/erp096.
75. Paul M, Foyer C. Sink regulation of photosynthesis. *J Exp Bot.* 2001;52:1383–1400. <https://doi.org/10.1093/jexbot/52.360.1383>.
76. Li Z, Wakao S, Fischer BB, Niyogi KK. Sensing and responding to excess light. *Annu Rev Plant Biol.* 2009;60:239–260. <https://doi.org/10.1146/annurev.arplant.58.032806.103844>.
77. Hernández GG, Winter K, Slot M. Similar temperature dependence of photosynthetic parameters in sun and shade leaves of three tropical tree species. *Tree Physiol.* 2021;5:637–651. doi:10.1093/TREEPHYS/TPAA015.
78. Medeiros DB, Barros JAS, Fernie AR, Araújo WL. Eating away at ROS to regulate stomatal opening. *Trends Plant Sci.* 2020;3:220–223. doi:10.1016/j.tplants.2019.12.023.
79. Shimazaki K-I, Doi M, Assmann SM, Kinoshita T. Light regulation of stomatal movement. *Annu Rev Plant Biol.* 2007;58:219–247. <https://doi.org/10.1146/annurev.arplant.57.032905.105434>.
80. Huang G, Yang Y, Zhu L, Peng S, Li Y. Temperature responses of photosynthesis and stomatal conductance in rice and wheat plants. *Agric For Meteorol.* 2021;300:108322. <https://doi.org/10.1016/j.agrformet.2021.108322>.
81. Chaves MM, Pereira JS, Maroco J, Rodrigues ML, Ricardo CPP, Osorio ML, Carvalho I, Faria T, Pinheiro C. How plants cope with water stress in the field. photosynthesis and growth. *Ann Bot.* 2002;89:907–916. <https://doi.org/10.1093/aob/mcf105>.
82. Dodd AN, Salathia N, Hall A, Kévei E, Tóth R, Ferenc N, Hibberd JM, Millar AJ, Webb AAR. Plant circadian clocks increase photosynthesis, growth, survival, and competitive advantage. *Sci.* 2005;5734:630–633. doi:10.1126/science.1115581.
83. Still CJ, Sibley A, Page G, Meinzer FC, Sevanto S. When a cuvette is not a canopy: a caution about measuring leaf temperature during gas exchange measurements. *Agric Forest Meteorol.* 2019;279:107737. doi:10.1016/j.agrformet.2019.107737.
84. Dong N, Prentice IC, Harrison SP, Song QH, Zhang YP. Biophysical homeostasis of leaf temperature: a neglected process for vegetation and land-surface modelling. *Global Ecol Biogeogr.* 2017;26:998–1007. doi:10.1111/geb.12614.
85. Marengo RA, Siebke K, Farquhar GD, Ball MC. Hydraulically based stomatal oscillations and stomatal patchiness in *Gossypium hirsutum*. *Funct Plant Biol.* 2006;33:1103–1113. doi:10.1071/FP06115.
86. Snider JL, Chastain DR, Collins GD, Grey TL, Sorensen RB. Do genotypic differences in thermotolerance plasticity correspond with water-induced differences in yield and photosynthetic stability for field-grown upland cotton? *Environ Exp Bot.* 2015;118:49–55. doi:10.1016/j.envexpbot.2015.06.005.
87. Farquhar GD, von Caemmerer S, Berry JA. A biochemical model of photosynthetic CO₂ assimilation in leaves of C3 species. *Planta.* 1980;149:78–90. doi:10.1007/BF00386231.
88. Mahan JR, Upchurch DR. Maintenance of constant leaf temperature by plants - I. Hypothesis - Limited homeothermy. *Environ Exp Bot.* 1988;4:351–357. doi:10.1016/0098-8472(88)90059-7.
89. Upchurch DR, Mahan JR. Maintenance of constant leaf temperature by plants - II. Experimental observations in cotton. *Environ Exp Bot.* 1988;4:359–366. doi:10.1016/0098-8472(88)90060-3.
90. Helliker BR, Richter SL. Subtropical to boreal convergence of tree-leaf temperatures. *Nature.* 2008;454:511–514. <https://doi.org/10.1038/nature07031>.
91. Althawadi AM, Grace J. Water use by the desert curcubit *Citrullus colocynthis* (L.) Schrad. *Oecologia.* 1986;70:475–480. doi:10.1007/BF00379514.
92. Hu YY, Oguchi R, Yamori W, Von Caemmerer S, Chow WS, Zhang W-F. Cotton bracts are adapted to a microenvironment of concentrated CO₂ produced by rapid fruit respiration. *Ann Bot.* 2013;112:31–40. doi:10.1093/aob/mct091.
93. Peleg Z, Blumwald E. Hormone balance and abiotic stress tolerance in crop plants. *Curr Opin Plant Biol.* 2011;14:290–295. <https://doi.org/10.1016/j.pbi.2011.02.001>.
94. Korver RA, Koevoets IT, Testerink C. Out of shape during stress: a key role for auxin. *Trends Plant Sci.* 2018;23:783–793. doi:10.1016/j.tplants.2018.05.011.
95. Severino LS, Lima RLS, Lucena AMA, Freire MAO, Sampaio LR, Veras RP, Medeiros KAAL, Sofiatti V, Arriell NHC. Propagation by stem cuttings and root system structure of *Jatropha curcas*. *Biomass Bioenergy.* 2011;35:3160–3166. <https://doi.org/10.1016/j.biombioe.2011.04.031>.
96. Boghani HC, Ambur R, Blumenfeld M, Saade L, Goodall RM, Ward CP, Plášek O, Gofton N, Morata M, Roberts C, et al. Sensitivity enriched multi-criterion decision making process for novel railway switches and crossings – a case study. *Eur Transp Res Rev.* 2021;13:6. <https://doi.org/10.1186/s12544-020-00467-x>.
97. Kosmol L, Maiwald M, Pieper C, Plötz J, Schmidt T. An indicator-based method supporting assessment and decision-making of potential by-product exchanges in industrial symbiosis. *J Clean Prod.* 2021;289:125593. <https://doi.org/10.1016/j.jclepro.2020.125593>.
98. Lawani MA, Turgeon Y, Côté L, Légaré F, Wittman HO, Morin M, Kroger E, Voyer P, Rodriguez C, Giguere A. User-centered and theory-based design of a professional training program on shared decision-making with older adults living with neurocognitive disorders: a mixed-methods study. *BMC Med Inform Decis Mak.* 2021;21:59. doi:10.1186/s12911-021-01396-y.
99. Long X, Li H, Du Y, Mao E, Tai J. A knowledge-based automated design system for mechanical products based on a general knowledge framework. *Expert Syst Appl.* 2021;178:114960. <https://doi.org/10.1016/j.eswa.2021.114960>.
100. Shi Q, Zhang K, Weng J, Dong Y, Ma S, Zhang M. Evaluation model of bus routes optimization scheme based on multi-source bus data. *Transp Res Interdiscip Perspect.* 2021;10:100342. <https://doi.org/10.1016/j.trip.2021.100342>.

101. Smith EA, Cooper NJ, Sutton AJ, Abrams KR, Hubbard SJ. A review of the quantitative effectiveness evidence synthesis methods used in public health intervention guidelines. *BMC Public Health*. 2021;21:278. <https://doi.org/10.1186/s12889-021-10162-8>.
102. Frey DD, Herder PM, Wijnia Y, Subrahmanian E, Katsikopoulos K, Clausen DP. The Pugh Controlled Convergence method: model-based evaluation and implications for design theory. *Res Eng Des*. 2009;20:41–58. doi:10.1007/s00163-008-0056-z.
103. Blumstein DT, Bouskila A. Assessment and decision making in animals: a mechanistic model underlying behavioral flexibility can prevent ambiguity. *Oikos*. 1996;77:569–576. doi:10.2307/3545948.
104. Saaty TL. How to make a decision: the analytic hierarchy process. *Eur J Oper Res*. 1990;48:9–26. doi:10.1016/0377-2217(90)90057-I.
105. Vaidya OS, Kumar S. Analytic hierarchy process: an overview of applications. *European J Oper Res*. 2006;169:1–29. doi:10.1016/j.ejor.2004.04.028.