Science & Society

Plants Show Us the Light

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In a recent article, Arp *et al*. (*Science* 2020, 368, 1490–1495) propose a new theory as to why plants are green: plants prioritize the management of light fluctuations over maximal efficiency. Beyond plant science, this conclusion may inspire our sustainability strategies, to shift our societal goals from performance to resilience.

Life on our planet largely depends on the ability of plants to harvest light and convert it into metabolites and energy sources. However, it may come as a surprise to many that photosynthesis is in fact very inefficient. In theory, only up to 2% of the energy of the incident solar radiation is captured and this number drops to 0.3–0.85% when measured in real ecosystems [1]. This is reflected in part by the color of plants: they are green because they absorb much less green light than red and blue light (Figure 1). What could be the evolutionary advantage of such a wasteful strategy? A recent study goes one step further to explore the biophysical mechanism behind such apparent inefficiency. Plants are exposed to dynamic light properties and fluctuating molecular structures. Dealing with such noise has a cost and this implies wasting a lot of energy [2].

Some of the plant strategies that deal with light intensity fluctuations were already known. For instance, a sudden burst of light can lead to photo-oxidative stress in the photosynthetic light-harvesting complexes. One of the functions of carotenoid pigments is precisely to convert this excess of light energy into heat (i.e., to dissipate the excess of energy input). What is new here is that Arp *et al.*, dealt with the systemic response of light-harvesting complexes to noisy light fluctuations and internal cell dynamics.

In short, the quantum conversion of photons into energy is a physical process that works best when the input is steady. In theory, to reduce the fluctuations in the rate of energy flow, one would need to have absorbing peaks in very close light wavelengths (e.g., red and red–orange). However, this is not observed in real living systems, simply because both light and protein properties fluctuate: a light-harvesting system cannot be tuned like one fixes a radio [3]. What the authors find instead is that spread-out absorption peaks (i.e., red and blue) can effectively reduce noise, allowing steady input of energy, while being robust to fluctuations. This theory is strongly supported by the fact that the well-known absorption spectra of photosynthetic systems peak in red and in blue, also explaining why plants appear green [2] (https://www.quantamagazine.org/why-are-plants-green-to-reduce-the-noise-in-photosynthesis-20200730/).

This is a remarkable example illustrating how living organisms have selected robustness over performance during evolution. Efficiency is indeed not the common denominator of life. At the molecular scale, living systems are very random, redundant, heterogeneous, inconsistent... in short, not very efficient. This is in line with an ongoing revolution in molecular biology, where the many roles of stochasticity are beginning to be understood through quantitative approaches [4,5]. The recent work by Arp *et al*. [2] illustrates the need to consider much longer time scales, within which local inefficiencies can balance each other to generate robustness. In other words, this analysis of photosynthesis illustrates the trade-offs between efficiency and resilience in biology.

Back to societal questions, the current coronavirus disease 2019 (COVID 19) crisis illustrates how such a trade-off may also be relevant to other sectors (https://www.chelseagreen.com/2020/limits-to-growth-covid-epidemic/). Seeing the Anthropocene as the era of man-made uncertainties, taking inspiration from such a viewpoint might be very timely. The environmental crisis is indeed largely caused by the blind compass of humans towards efficiency increments, a bit like the light-harvesting complex going into photo-oxidative stress. This is a trivial observation when considering the green revolution and the associated negative externalities on desertification, pollutions, and biodiversity collapse. The same applies to strategies supporting over-fishing, over-mining, or over-consumption. Gains in efficiency can be counterproductive and this has already been theorized [6]. It is even the basis of the rebound effect, or the so-called 'curse of efficiency': gains of efficiency usually make a technology more attractive, meaning that resource consumption is not reduced, but does increase globally [7,8]. Many reports, and most notably the Meadows reports on the limits to growth, have implicitly warned humanity against such excesses for the long-term viability of our civilization [9,10].

The lesson from plant light-harvesting complexes not only sheds light on our past, it could also question our future sustainable development strategies. Dealing with noisy environments is a well-known challenge in engineering (e.g., when designing energy grid architecture) [11]. In fact, such suboptimal strategy is observed in many contexts, from technological to cultural spheres [12]. How could this translate into future policies and research questions? For instance, should we first consider the fluctuating nature of supplies (e.g., rare earth availability) and environmental conditions (e.g., increasing wind variance in the climate crisis), instead of prioritizing the gains in efficiency in energy conversion when developing renewable energy solutions? With geo-engineering, are we not trying to optimize our climate (i.e.,

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Figure 1. Plants Reflect Green Light, Dissipating and Wasting a Lot of Solar Energy. Designing future sustainable bio-inspired strategies will depend on our ability to avoid the trap of over-optimization (i.e., on our ability to understand what resilience entails). Adapted from technology photo created by jannoon028 - www.freepik.com https://www.freepik.com/free-photo/plant-growing-bulb_969640.htm

to customize it for our needs in a reductionist framework), instead of embracing uncertainty?

During Earth's history, living organisms have demonstrated their ability to adapt to unthinkable conditions. Organisms do not build such resilience on increased efficiency, but instead on their intrinsic inefficiencies [13]. How can this work? As shown in the photosynthetic light-harvesting complexes, robustness is an emerging property of the interactions between apparent weaknesses. This can be illustrated in other biological contexts too. For instance, most of the molecular factors in our cells occur in very small numbers, which partly explains the unpredictability of living beings, even at that scale. However, there is great redundancy in these families of molecules and in biological processes, which partly compensates for randomness. Finally, two 'weaknesses', randomness and redundancy, balance each other out. It is a bit like a car, where acceleration and braking allows a stable speed regardless of the slope of the road. For living beings, the maintenance of such autonomy allows resilience in the face of environmental fluctuations. This also applies to biomechanics: most living systems are experiencing a balance between tension and compression. This balance provides them with a mechanical resistance to external noise, a bit like a suspension bridge (with its threads under tension and its deck under compression) when it is exposed to wind.

Such suboptimality may very well be a source of inspiration for our future sustainability. Three key principles could be put forward:

(i) Based on how inefficient biological systems are intrinsically (e.g., the 2% maximal yield of photosynthesis), we might vastly underestimate the 'slack' needed for true resilience in our societies.
(ii) Biological systems can afford many internal weaknesses, because those are also often antagonistic (e.g., randomness versus redundancy); conversely, this generates a form of autonomy and thus a built-in shield against environmental fluctuations (a component of resilience).

(iii) Efficiency is more easily understood when referring to the individual scale, whereas resilience usually always applies to the population and thus implies systems thinking.

Although suboptimality is likely to be a key element of our sustainable future, we could be blinded by the attractive and shiny prospect of short-term efficiency. In that respect, our green world is not only harvesting the light, it may very well show us the path to resilience.

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Spotlight

Silicon Defence in Plants: Does Herbivore Identity Matter?

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Silicon accumulation is a key defence against herbivorous pests, but may have wider detrimental impacts if plants become unpalatable for livestock. We argue that some herbivores are better adapted to silicon-rich diets than others; herbivore anatomy and physiology, and the nature of silicon deposition, are crucial to understanding these differences.

Plant scientists and agronomists are keen to exploit the potential of plant silicification for crop protection against pests and diseases [1], but they also need to be mindful of the potential downsides of silicon (Si) deposition, which is an irreversible process. The recent paper by Cougnon *et al*. (2020) [2] provides an important example: Si reduces the *in vitro* digestibility of organic matter (DOM) and this could be detrimental to grazing livestock. They demonstrate the heritability of Si concentrations and discuss the merits of selecting forage grasses with low Si concentrations, while acknowledging that this needs to be balanced against the benefits of silicification, giving the example of plant pathogen resistance.

Silicon concentrations were purposefully not manipulated in this study, so the relationship between Si and predicted DOM is based upon natural variation in Si concentrations among varieties and among samples from different time points. Because concentrations of cell wall polysaccharides and lignin are primary drivers of plant digestibility and can be expected to have covaried with Si concentrations, the specific role of Si in this study remains unclear. Moreover, we suggest that there are two important issues that need to be considered when evaluating the potential benefits and disadvantages of plant silicification. The first is that selecting for grasses with low Si is based on the assumption that grazing livestock are as consequentially and detrimentally affected by Si-rich forage diets as some other vertebrate herbivores (see examples in [3]), which is far from certain. Secondly, selecting plants solely on the basis of Si concentrations may be an over-simplification: the nature and localisation of Si deposition may be more important than total Si in determining how herbivores are affected.

Si can be deposited within and between cells, at the leaf surface and cuticle, as well as in discrete structures such as spines, macro-hairs, and trichomes [4,5]. These distinct forms of deposition are likely to affect herbivores differently, depending on their feeding behaviour, physiology, and digestion. The consequences are best understood for invertebrate herbivores and can include reduced nutrient absorption, wearing down of mouthparts, lacerations to digestive organs, and inhibition of movement and feeding [1]. Some of these effects are also relevant for vertebrate herbivores, such as dental wear [6] and reduced nutrient absorption [3].

The magnitude of the digestibility-reducing effects of Si reported by Cougnon *et al*. [2] are in agreement with previous *in vitro* studies, but how Si